Title
Performance trade-offs define a fundamental dental dichotomy in mammals.

Journal
Science (New York, N.Y.), 393(6808)

ISSN
0036-8075

Authors
Chatar, Narimane
Vankelst, Melvin
Pérez-Ramos, Alejandro
et al.

Publication Date
2026-07-01

DOI
10.1126/science.aee3453

PALEONTOLOGY

Performance trade-offs define a fundamental dental dichotomy in mammals

Narimane Chatar[1,2]*, Melvin Vankelst[3], Alejandro Pérez-Ramos[2], Tahlia I. Pollock[4,5], Davide Tamagnini[6], Margot Michaud[3,7,8], Levi Yoder Raskin[9], Z. Jack Tseng[1]

Teeth define mammalian evolution, and one of many adaptive dental breakthroughs in crown mammals is the tribosphenic molar: a tooth with a dual shearing-crushing function, often considered a key adaptation in crown mammals. However, we do not know how potential trade-offs between these antagonistic functions may influence the macroevolutionary outcomes of mammalian lineages. Here, we show that predatory mammals evolved dichotomized performance in their tribosphenic carnassial teeth, with slicing constrained to a narrow set of optimal phenotypes and crushing exhibiting redundant solutions. Less than 1% of predators evolved optimized shearing and crushing. The fundamental trade-off in functions of the tribosphenic architecture promoted divergent macroevolutionary specializations rather than functional duality. These results highlight how key innovations can drive early evolutionary success while simultaneously constraining subsequent diversification.

Teeth are the primary interface between most vertebrates and their food, making them central to understanding ecological adaptations and interactions (*1*, *2*). Their exceptional preservation in the fossil record and close relationship with both diet and biomechanical demands of food processing have long made them essential sources in the study of mammalian evolution (*3*, *4*). Teeth also record developmental stress and provide insight into evolutionary dynamics across extinct communities (*5*, *6*). A key element in understanding the ecological versatility of mammals lies in heterodont dentition (the development of distinct tooth types within the toothrow of an individual), which contrasts with the homodonty of most other vertebrate animals, particularly predators such as crocodiles or theropod dinosaurs (*7*, *8*). Although heterodonty originated earlier in nonmammalian synapsids (*9*), the emergence of the tribosphenic molar within crown mammals marked the beginning of a modern radiation of diversity in tooth structure that is unmatched by other living vertebrates (*10*). In this architecture, the trigonid (for slicing) and talonid (for crushing) regions of the lower molars work in concert with the upper protocone, offering dual-function occlusion (*11*, *12*) (Fig. 1). The evolution of this architecture enabled both shearing and grinding in one stroke and established a blueprint for modern mammalian dental and ecological diversity (*10*) (Fig. 1), which likely expanded dietary and ecological versatility and have therefore often been considered a key adaptation (feature that imparted an evolutionary advantage) underlying the evolutionary success and diversification of mammals. However, the evolutionary implications and consequences of potential trade-offs between the two antagonistic functions are unclear. Morphological traits that favor slicing (tall, sharp cusps and aligned crests) maximize shear efficiency at the expense of high surface area and complexity for crushing. By contrast, traits reinforcing crushing abilities (broad, low talonid basins, thick and blunt cusps) tend to reduce slicing efficiency and are more prominent in herbivory. These opposing functions underlie both therian origins and also the subsequent explosive radiation of crown mammals after the end-Cretaceous mass extinction (*13*, *14*).

Among placental mammals, multiple lineages independently evolved highly specialized teeth, called "carnassials," demonstrating recurring solutions to a predominantly meat-based diet (*15*, *16*). Although many of these lineages are now extinct, living Carnivora remain highly diverse in both ecology and geographic distribution. With about 300 species occupying a range of dietary niches from large hypercanivorous predators to small herbivores (*17*, *18*), carnivorans share the presence of a single carnassial pair, with many taxa still featuring the tribosphenic condition with a developed talonid for crushing and trigonid for slicing (*11*, *19*). The lower carnassials of carnivorans show the widest range of talonid morphologies among extant mammals (*16*, *20*, *21*). Furthermore, their high ecological breadth suggests evolutionary flexibility that may relate to the potential functional optimization of their dentition. Hypercarnivorous taxa tend to exhibit reduced talonids or blade-like and enhanced slicing crests whereas omnivores retain broader, more robust talonids for processing varied foods, and herbivores tend to exhibit the most developed talonids (*22*). This general pattern emerged after the end-Cretaceous extinction and continues to the present day.

Multiple placental mammal groups evolved carnassial teeth independently over the last 66 million years. Notably, Hyaenodonta and Oxyaenodonta, two extinct lineages historically referred to as "creodonts," evolved multiple pairs of carnassials that highlight alternative evolutionary solutions to those seen in Carnivora (*11*, *16*). These repeated evolutionary events across distant predator lineages underscore a deep evolutionary trend toward convergent morphologies that are specialized for carnivory. However, despite initial success, these other lineages eventually disappeared, raising the broader question of whether the tribosphenic molar, although opening evolutionary opportunities, also channels evolution along a limited set of functional pathways. To evaluate this evolutionary scenario, we developed an approach that integrates high-density three-dimensional (3D) geometric morphometric data with mechanical performance testing in a functional landscape framework across extinct and extant species.

Evolutionary canalization in the lower carnassial of carnivorous mammals

We quantified lower carnassial dental shape in 250 Feliformia (cats and their relatives), Caniformia (dogs and their relatives), "creodonts" (Hyaenodonta and Oxyaenodonta, extinct carnivorous mammals), and early-diverging carnivoramorphans by digitizing each tooth with 2000 3D point coordinates (pseudolandmarks) using a semiautomated protocol (supplementary text and fig. S1). We developed a morphospace (Fig. 2) that mainly captures the extent of talonid development with lower values corresponding to a reduced or absent talonid and higher values indicating a more developed talonid (PC1), representing a spectrum from obligate carnivores to omnivorous-herbivorous species (Fig. 2A). PC2 reflects crown aspect ratio, ranging from tall, compact teeth of insectivores to elongate, low-cusp morphologies of hard-food specialists (Fig. 2A). Density contour peaks in the morphospace highlight two main recurring carnassial morphologies that define major

[1]Functional Anatomy and Vertebrate Evolution Lab, Department of Integrative Biology University of California, Berkeley, Berkeley, CA, USA. [2]Departamento de Ecología y Geología, Universidad de Málaga, Málaga, Spain. [3]Evolution and Diversity Dynamics Lab, UR Geology, Université de Liège, Liège, Belgium. [4]Palaeobiology Research Group, University of Bristol, Bristol, UK. [5]School of Biological Sciences, Monash University, Monash, Australia. [6]Department of Biology and Biotechnologies "Charles Darwin," Sapienza University of Rome, Rome, Italy. [7]Institut Polytechnique UniLaSalle, Université d'Artois, Mont-Saint-Aignan, France. [8]Departement Formation et Recherché Sciences et Technologie, Université de Guyane, Cayenne, Guyane. [9]Huelsenbeck Lab, Department of Integrative Biology University of California, Berkeley, Berkeley, CA, USA. *Corresponding author. Email: narimane.chatar@berkeley.edu

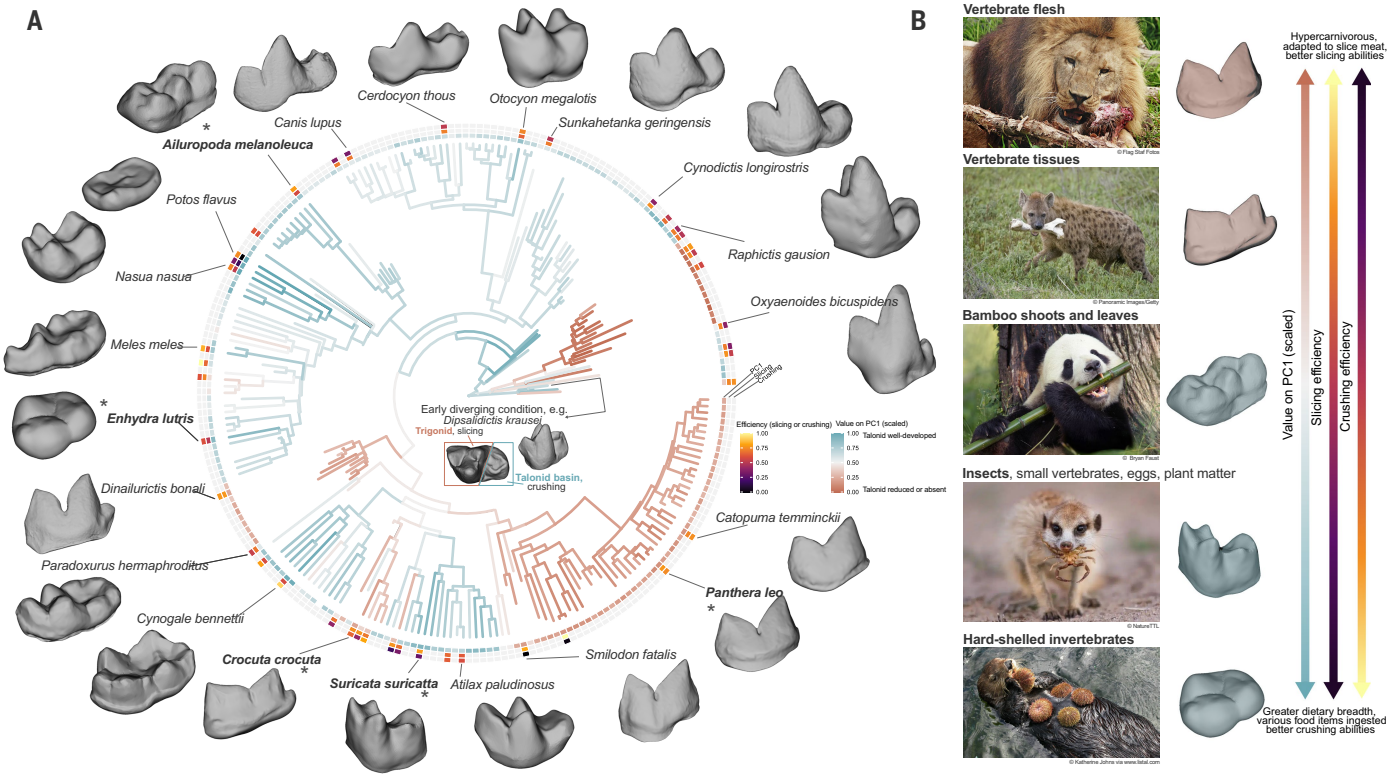

Fig. 1. Tooth efficiency for slicing and/or crushing is driven by the development of the two original regions of the tribosphenic architecture: the talonid basin and trigonid. (**A**) Evolution of PC1 values (capturing the development of the talonid basin), crushing and slicing efficiency in our dataset, showing that teeth with a developed talonid tend to be better at crushing than at slicing. (**B**) Subset of extant taxa and their diet, linking the dental efficiency metrics to observed diet.

morphofunctional pathways for predatory mammals (Fig. 2C): a highly specialized, hypercarnassialized bicuspid form with a reduced talonid [negative PC1, average PC2; e.g., hypercarnivorous cats (*23*) and hyenas (*24*)], and a more developed talonid morphotype corresponding to broader dietary breadth [positive PC1, negative PC2; e.g., omnivorous dogs and bears (*25*)]. These results align with previous developmental studies showing that whereas trigonid structures on teeth are relatively stable, minor shifts in genetic signaling can produce substantial changes in talonid morphology, including cusp height and number (*21*). Other studies further underscore strong constraints at the molecular and genetic level, suggesting that subtle molecular shifts (heterotopy) and iterative growth rules generate the vast diversity of cusp arrangements seen in mammalian teeth (*26*, *27*).

We quantitatively assessed carnassial slicing and crushing performance by 3D printing a subset of teeth and testing them in two experimental setups: one using multimaterial medical-grade gelatins mimicking living tissues to measure slicing performance, and another using 3D-printed bone models to measure crushing performance (supplementary text and figs. S1 to S4). We then used an interpolated performance landscape integrating actual teeth and theoretical shapes spanning the variation present in the morphospace (Fig. 3), and a Pareto front analysis to identify optimized morphofunctional configurations (Fig. 4B). Optimal Pareto solutions range from specializations favoring slicing over crushing, to balanced performance in both functions, to adaptations prioritizing crushing at the expense of slicing. We found that functional optimization in the carnassials often comes at the cost of versatility: Efficient slicers are rarely efficient crushers and vice versa. Further, the two recurring morphotypes are optimized for different biting performances. In addition to soft materials (e.g., animal muscle and viscera but also fleshy fruits), slicing may also involve mechanically resistant tissues such as tendons, which can represent some of the toughest materials processed by carnivores. Slicing efficiency peaked in hypercarnivorous forms with low PC1 and mid PC2 values (Fig. 3A). These taxa required low force to create deep puncture marks in the gelatin models. By contrast, forms with more developed talonids (higher PC1) required two to three times more force and often failed to penetrate all gelatin layers. Caniforms (bears, dogs, raccoons, and relatives) exhibited the lowest slicing capabilities overall. The bicuspid carnassial of hypercarnivorous taxa was shown to be very close in shape to an "ideal" theoretical slicing object, suggesting these teeth have the best shape for their function and that those shapes are not substantially limited by developmental constraints (*28*). Carnassialized molars appeared independently, across an extreme body size spectrum (*16*, *28*, *29*), indicating that slicing constraints are not as size-dependent as other constraints on the dentition (*28*).

Although not all taxa analyzed feed on large bones (particularly herbivorous taxa or smaller species), we employed the bone models within a comparative framework to evaluate relative crushing abilities against a material with fully characterized material properties approximating the structural properties of natural hard tissues encountered by at least some taxa in our dataset. Studies have suggested that other biological hard tissues (e.g., bamboo) can present similar mechanical challenges from a dietary point of view, resulting in convergence in durophagous species despite different diets (*30*). The crushing experiments produced a more rugged landscape than that of slicing (Fig. 3, E and F), suggesting multiple mechanically equivalent phenotypic configurations (Fig. 3B). Most efficient crushers had well-developed talonids, relied less on carnivory, and occupied high PC1, low PC2 regions. Our results capture what appears to be a mammalia-wide phenomenon, showing that the talonid is the principal structure enabling effective crushing (*31*). The talonid was also shown to exhibit greater morphological variability (*31*) and appears more responsive to

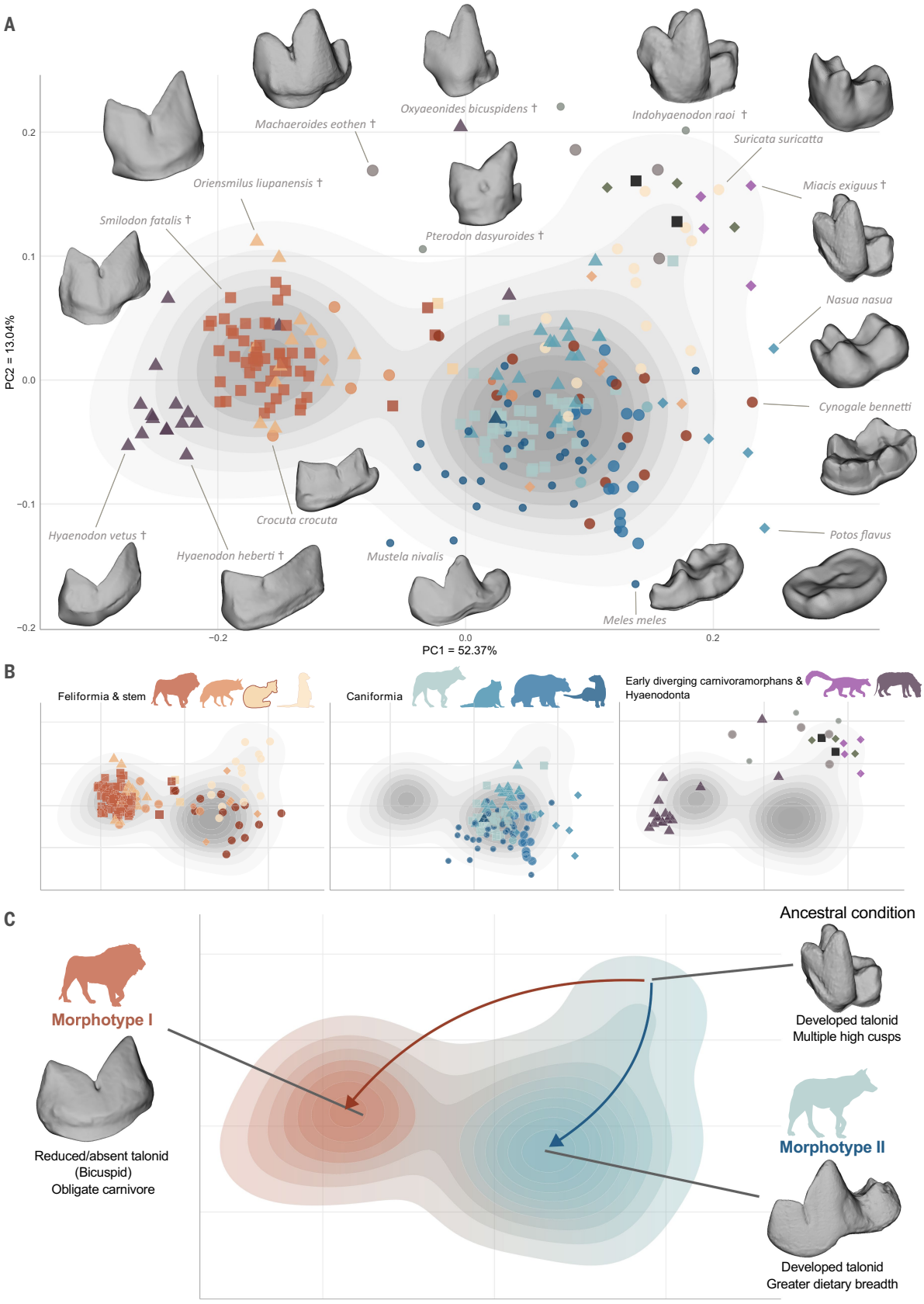

Fig. 2. Shape variation in the lower carnassial. (**A**) Global morphospace obtained from a PCA of 250 specimens with density contours. (**B**) Morphospace per clade (Feliformia & stem, Caniformia, early-diverging carnivoramorphans and Hyaenodonta). (**C**) Simplified plot highlighting the two recurring morphologies in the lower carnassial of carnivorous mammals: a morphotype with reduced or absent talonid corresponding to hypercarnivorous taxa (secodont; fig. S12), and a morphotype with a more developed talonid, corresponding to taxa with a greater dietary breadth.

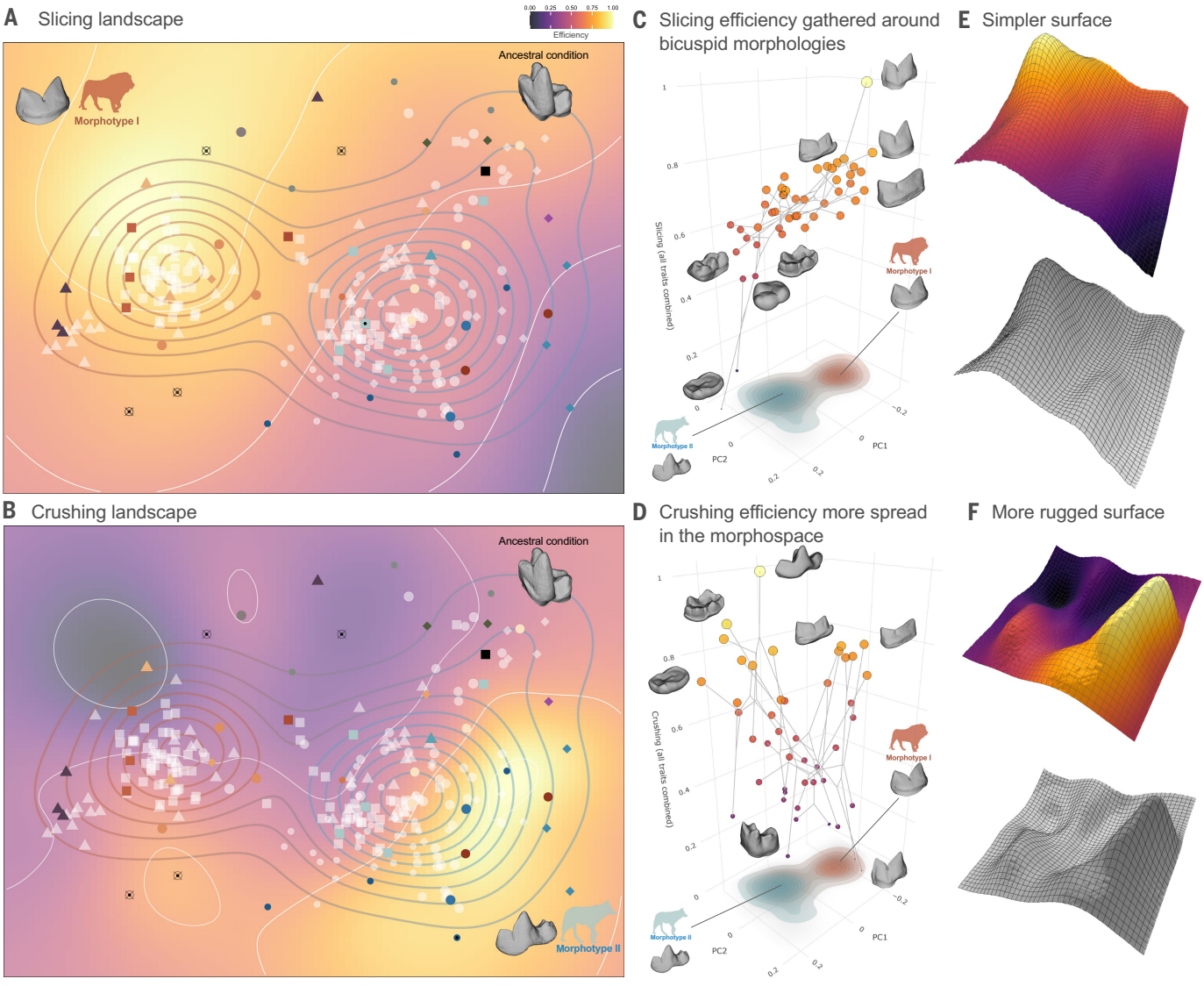

Fig. 3. Performance landscapes for each function and 3D phenogram showing their distribution in the phylogeny. (**A**) Landscape for slicing and (**B**) crushing data. Detailed legend in fig. S7; black circles with crosses represent theoretical shapes. (**C**) Distribution of slicing efficiency in the phylogeny and (**D**) distribution of crushing efficiency in the phylogeny. 3D surfaces show the peaks and valleys in the (**E**) slicing and (**F**) crushing landscape.

selective pressures linked to food hardness (ability to resist localized deformation, e.g., from indentation or scratching) rather than toughness (ability to absorb energy and plastically deform without fracturing) (*28*), which altogether could explain the numerous solutions for efficient crushing that we observed. By contrast, hypercarnivorous species are tightly constrained: Their bicuspid teeth occupy a narrow region of the morphospace and exhibit catastrophic failure even under modest loads. Small structural refinements in dental shape can considerably affect performance: Optimal slicing aligns with bicuspid morphology but crushing efficiency varies and can be decoupled through subtle anatomical modifications (fig. S12C). We find that not all bicuspid forms performed poorly in crushing.

Among those bicuspid teeth withstanding the crushing simulations, some bore a carnassial notch, a keyhole-shaped notch between the two main cusps (paracone and protocone, fig. S12A). This feature has been hypothesized to help dissipate stress during compressive and shear loading (*32*), similar to notches in circular saws. Contactless, in-plane strain measurements obtained using digital image correlation analyses confirm that this notch helped dissipate strain across the blade. By contrast, taxa lacking the notch showed pooled stress near the protocone-paracone interface, a frequent failure zone where crack propagation initiated (supplementary text). The morphofunctional solution for slicing relies on precise occlusal alignment and high cusp penetration efficiency, determined by both cusp length and orientation (fig. S12, A to C). This configuration focuses bite pressure onto a small, highly localized area of the occlusal plane (fig. S12C), efficiently slicing soft tissues.

Our combined landscape of slicing and crushing metrics revealed a rugged adaptive landscape with two major ridges (Fig. 4A), indicating the presence of tooth phenotypes that exhibit the best trade-off between slicing versus crushing performance. Only two living taxa, the spotted hyena (*Crocuta crocuta*, with a combined slicing index of 0.75 and a combined crushing index of 0.65) and the Asian palm civet (*Paradoxurus hermaphroditus*, with a combined slicing index of 0.58 and a combined crushing index of 0.78), are aligned with the Pareto front of optimality, representing <1% of our dataset (Fig. 4B). Neither approaches a theoretical value of 1 for both functions simultaneously, which appears mechanically impossible, especially given the structural

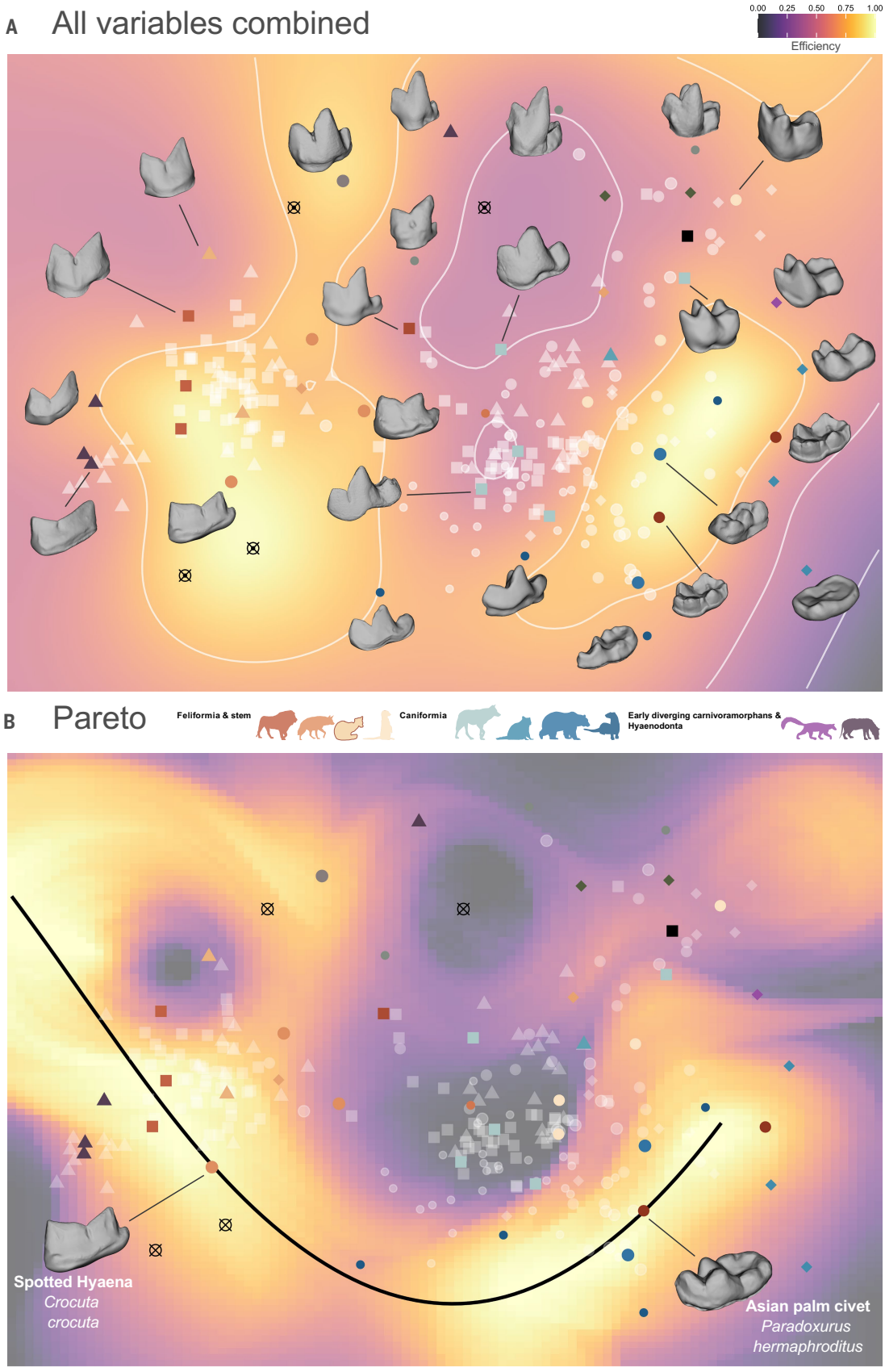

Fig. 4. Performance surfaces obtained for the slicing/crushing trade-off. Landscape obtained when (**A**) combining all five variables (two for slicing and three for crushing) in a single landscape and (**B**) the Pareto landscape obtained when combining all variables from a given aspect into a single one and estimating the trade-off between those two combined slicing and crushing variables.

constraints of the tribosphenic molar. It is possible that few species actually require simultaneous optimization of both functions, *C. crocuta* being a notable exception: A bone-cracking species that also consumes flesh (*33*). This is consistent with the idea that strong material property constraints (softer versus harder food items) limit the scope for true dual optimization. As critiqued by Gould and Lewontin (*33*), functional analyses tend to focus on parts within a complex system, at times interpreting those parts as a direct product of adaptive fine-tuning. Rather, phenotypes emerge from the interplay of adaptive trade-offs with selective pressure, fabrication noise resulting from material constraints, and/or modes of growth (sensu Seilacher's concept of morphodynamics) (*34*). The prevalence of taxa occupying suboptimal regions of the performance landscape may reflect constraints of structural and historical contingencies of evolution beyond what was measured in this study. These patterns also resonate with recent frameworks emphasizing the interplay between evolutionary trajectories and ecoevolutionary drivers shaping phenotypic diversification across adaptive landscapes (*35*). Apparent dental suboptimization additionally may be offset by alternative functional strategies, including complex jaw movements (*36*), behavioral adaptations such as food manipulation [e.g., tool use in *Enhydra lutris* (*37*)] or hunting tactics, and ecological factors such as reduced competition. Unoccupied valleys in morphospace corresponded to theoretical shapes with poor performance in both functions, suggesting strong functional constraints (Figs. 1 to 3). These results provide direct experimental validation of prevailing hypotheses positing "adaptive valleys" in the dental morphospace (*22*). However, note that our study focused on the lower carnassial, and that including the action of the upper dentition (P4 and M1, notably) or even different biting points in taxa with multiple carnassialized molars (e.g., genus *Hyaenodon*) might result in a slightly different landscape.

Slicing efficiency is more phylogenetically restrained than crushing efficiency

Slicing and crushing evolution exhibit substantially different phylogenetic patterns. The earliest-diverging taxa (high PC1/high PC2, corresponding to the most tribosphenic-shaped region of the dental morphospace), although not peak performers, clustered near the main adaptive ridges (Fig. 4). Those results suggest that the evolution of carnassial shape follows performance-driven trajectories along two primary functional axes: one toward enhanced slicing, the other toward improved crushing (fig. S16). Slicing adaptations appear both structurally and evolutionarily constrained. Taxa achieving high slicing efficiency share specialized bicuspid morphology (Figs. 1 to 3) and exhibit strong phylogenetic signals. By contrast, crushing appears more flexible, emerging across a broader range of tooth shapes, with low phylogenetic clustering, and reflects the greater plasticity of the talonid compared with the trigonid (*31*). The dichotomy between slicing and crushing is supported by results showing slicing traits with a consistent strong phylogenetic signal [$K > 0.5$, $\lambda > 0.5$, per (*38*), Table 1], whereas crushing traits show much weaker phylogenetic structure overall (supplementary text and Table 1). These results suggest that slicing ability is more evolutionarily conserved, consistent with an ancestral slicing function requiring precise occlusal alignment and limited morphological variance with very localized bursts in the trees (figs. S13 and S14). By contrast, crushing performance shows higher evolutionary rate variation, evolving repeatedly in lineages with tougher or more variable diets (figs. S15 to S17). These observations further highlight how the previously described dual-function architecture of the tribosphenic molar continues to structure patterns of functional diversification across lineages. In other words, the tribosphenic blueprint provided the boundary conditions of a structural framework within which differential functional specialization repeatedly emerged. This dichotomy persists despite wide-ranging morphological divergence from the ancestral condition (Figs. 1 and 2).

Functional versatility and evolutionary success

Understanding why some lineages persist longer than others remains a central question in evolutionary biology. One area of focus has been the comparison of groups exhibiting convergent functional traits, as some traits have been identified as potential correlates of extinction risk (*39*, *40*). Despite convergent evolution of slicing-specialized dentitions across several placental clades (e.g., hyaenodonts and oxyaenodonts), only carnivorans survive today, and mechanistic explanations underlying their evolutionary success are still debated (*15*, *19*, *22*, *29*, *41*). The less specialized dentition observed in living predator clades has been hypothesized to constitute an evolutionary advantage (*16*, *22*, *29*). Consistent with this thesis, it has been suggested that the success of carnivorans could be linked to the retention of more generalist features in some lineages, such as genets (Viverridae), mongooses (Herpestidae), or dogs and their relatives (Caniformia) (*11*). By contrast, previous work has suggested that in some extinct clades that emphasized shearing at the cost of crushing tooth morphology, hypercarnivory may have acted as a macroevolutionary ratchet; once the crushing talonid is lost, reversibility can become constrained, potentially contributing to reduced long-term evolutionary persistence in those lineages (*41*). Generalist taxa are expected to maintain moderate performance in multiple functional aspects rather than maximizing in one or the other, potentially resulting in optimized trade-offs in a Pareto framework. However, our findings do not unambiguously support this hypothesis. Notably, the two species situated on the Pareto front do not represent classic dietary generalists. The Asian palm civet *(P. hermaphroditus)*, a relatively specialized frugivore (Fig. 4), exhibits some of the highest crushing performance values while maintaining moderate slicing abilities. Detailed quantitative data on its diet in the wild remain scarce due to its elusive behavior, but available evidence suggests a strong reliance on fleshy fruit (*42*). In this case, the developed talonid might also be efficient at extracting nutrients from fruit through crushing. Similarly, hyena teeth, despite their highly specialized hypercarnivorous carnassials, perform exceptionally well in both slicing soft tissue and crushing hard tissue. Together, these findings suggest that achieving a high-performance compromise between slicing and crushing is not simply a matter of retaining primitive traits. Instead, optimal morphofunctional solutions appear to have been realized selectively in a very low number of taxa. A true mechanical optimum (excelling in both functions at once) is

Table 1. Result of the phylogenetic signal tests.

Aspect	Trait	Blomberg's K	*P*-value	Pagel's λ	*P*-value	Interpretation
Slicing	Maximum force	0.871	0.009	0.818	0.0006	High phylogenetic signal
	Maximum length	0.662	0.009	0.820	0.003	High phylogenetic signal
Combined slicing		0.850	0.012	0.921	0.003	High phylogenetic signal
Crushing	Adj Peak load	0.408	0.194	0.156	0.843	Low phylogenetic signal
	Adj distance to peak load	0.375	0.363	0.023	0.922	Low phylogenetic signal
	Adj slope	0.517	0.041	0.616	0.134	Moderate phylogenetic signal
Combined crushing		0.410	0.205	7.5×10^{-5}	1	No phylogenetic signal

structurally difficult to achieve, at least when considering the lower carnassial tooth. This limitation likely reflects both dietary pressures (few species require maximal efficiency in both functions) but also deeper architectural constraints. The tribosphenic molar division into distinct slicing and crushing regions (Fig. 1) may inherently restrict the potential for integrated optimization, channeling mammalian dental evolution along divergent pathways rather than enabling convergence on a single multifunctional peak.

The morphofunctional evolution of the tribosphenic-derived carnassial tooth thus follows two fundamental, mutually exclusive paths: slicing (more constrained) versus crushing (more labile). Whereas some lineages exploit crushing flexibility to expand dietary breadth, others may optimize slicing at the cost of evolutionary reversibility. Both theoretical and experimental studies indicate that mammalian teeth evolved within a narrow set of physical and developmental possibilities (*28*, *43*) with geometric and material constraints shaping the ways in which form accommodates function. Idealized models identify only a few mechanically optimal tooth architectures, such as the tribosphenic and carnassial morphotypes (*28*), whereas other aspects such as microstructural analyses show how features such as enamel prism decussation and self-healing tufts enhance durability within these constraints (*44*). Evolutionary modeling shows that the emergence of multicusped and modular molars represents a strategy to distribute stress and mitigate competing fracture modes (*45*). This is a pattern also mirrored in morphometric studies linking mechanical compromises to dietary diversification across mammals (*46*). In this context, the tribosphenic blueprint represents both an enabling innovation and a structural constraint: an evolutionary design space that allows for two sets of dental performances but one that is difficult to transcend. The duality of this mammal-specific tooth may be reconciled by observations showing that trade-offs are not an obstacle to change but a driver of innovation (*47*). The original tribosphenic architecture, with its two structurally distinct and functionally specialized regions, likely introduced inherent structural constraints (sensu *34*) that contributed to the observed trade-offs. These results highlight how key innovations can drive evolutionary success while simultaneously constraining subsequent diversification.

REFERENCES AND NOTES

1. S. B. Crofts, S. M. Smith, P. S. L. Anderson, *Integr. Comp. Biol.* **60**, 594–607 (2020).
2. T. I. Pollock, D. P. Hocking, A. R. Evans, *Zool. J. Linn. Soc.* **196**, 1138–1155 (2022).
3. C. W. Schmidt, R. Quataert, F. Zalzala, R. D'Anastasio, in *Taphonomy of Human Remains: Forensic Analysis of the Dead and the Depositional Environment*, E. M. J. Schotsmans, N. Márquez-Grant, S. L. Forbes, Eds. (Wiley, ed. 1, 2017), pp. 92–100.
4. B. Van Valkenburgh, R. K. Wayne, *Ecology* **75**, 1567–1581 (1994).
5. A. V. Badyaev, *Behav. Ecol.* **9**, 339–344 (1998).
6. A. Riga, M. G. Belcastro, J. Moggi-Cecchi, *Am. J. Phys. Anthropol.* **153**, 397–407 (2014).
7. B. Berkovitz, P. Shellis, *The Teeth of Non-Mammalian Vertebrates* (Elsevier, 2018).
8. B. Van Valkenburgh, *Integr. Comp. Biol.* **47**, 147–163 (2007).
9. A. K. Huttenlocker, S. A. Singh, A. C. Henrici, S. S. Sumida, *R. Soc. Open Sci.* **8**, 211237 (2021).
10. B. M. Davis, *J. Mamm. Evol.* **18**, 227–244 (2011).
11. A. J. Lang, T. Engler, T. Martin, *J. Morphol.* **283**, 91–108 (2022).
12. A. W. Crompton, *Zool. J. Linn. Soc.* **50**, 65–87 (1974).
13. Z.-X. Luo, R. L. Cifelli, Z. Kielan-Jaworowska, *Nature* **409**, 53–57 (2001).
14. P. S. Ungar, *Mammal Teeth: Origin, Evolution, and Diversity* (John Hopkins Univ. Press, 2010).
15. C. De Muizon, B. Lange-Badré, *Lethaia* **30**, 353–366 (1997).
16. B. Van Valkenburgh, *Annu. Rev. Earth Planet. Sci.* **27**, 463–493 (1999).
17. A. Goswami, A. Friscia, *Carnivoran Evolution: New Views on Phylogeny, Form and Function* (Camridge Univ. Press, 2010).
18. K. R. Selig, *Mammal Res.* **68**, 637–646 (2023).
19. A. J. Lang, T. Martin, *Mammal Res.* **69**, 533–548 (2024).
20. F. Solé, S. Ladevèze, *Evol. Dev.* **19**, 56–68 (2017).
21. E. Harjunmaa *et al.*, *Nature* **512**, 44–48 (2014).
22. B. Van Valkenburgh, in *Carnivore Behavior, Ecology, and Evolution*, J. L. Gittleman, Ed. (Springer, 1989), pp. 410–436.
23. M. W. Hayward, G. I. H. Kerley, *J. Zool.* **267**, 309–322 (2005).
24. J. R. Henschel, J. D. Skinner, *Afr. J. Ecol.* **28**, 69–82 (1990).
25. A. Hartstone-Rose, E. Dickinson, A. R. Deutsch, N. Worden, G. A. Hirschkorn, *Anat. Rec. (Hoboken)* **305**, 477–497 (2022).
26. J. Jernvall, S. V. E. Keränen, I. Thesleff, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 14444–14448 (2000).
27. J. Jernvall, I. Thesleff, *Mech. Dev.* **92**, 19–29 (2000).
28. A. R. Evans, G. D. Sanson, *Biol. J. Linn. Soc. Lond.* **78**, 173–191 (2003).
29. P. M. Butler, *Proc. Zool. Soc. Lond.* **116**, 198–220 (1946).
30. B. Figueirido, Z. J. Tseng, A. Martín-Serra, *Evolution* **67**, 1975–1993 (2013).
31. J. P. Hunter, N. Schottenstein, J. Jernvall, *Ann. Zool. Fenn.* **61**, 1975–1993 (2024).
32. A. Hartstone-Rose, *J. Zool.* **285**, 119–127 (2011).
33. S. J. Gould, R. C. Lewontin, . *Proc. R. Soc. B* **205**, 581–598 (1979).
34. A. Seilacher, *Syst. Zool.* **22**, 451 (1973).
35. D. Tamagnini, D. Canestrelli, C. Meloro, P. Raia, L. Maiorano, *Evol. Biol.* **48**, 379–393 (2021).
36. P. D. Smits, A. R. Evans, *BMC Evol. Biol.* **12**, 146 (2012).
37. C. J. Law *et al.*, *Science* **384**, 798–802 (2024).
38. J. M. Kamilar, N. Cooper, *Philos. Trans. R. Soc. B* **368**, rstb.2012.0341 (2013).
39. A. J. Gallagher, N. Hammerschlag, S. J. Cooke, D. P. Costa, D. J. Irschick, *Trends Ecol. Evol.* **30**, 61–65 (2015).
40. J. S. Kotiaho, V. Kaitala, A. Komonen, J. Päivinen, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 1963–1967 (2005).
41. J. A. Holliday, in *Carnivoran Evolution: New Views on Phylogeny, Form, and Function*, A. Goswami, A. Friscia, Eds. (Cambridge Univ. Press, 2010), pp. 189–224.
42. S. Su, J. Sale, *Small Carniv. Conserv.* **36**, 30–34 (2007).
43. C. M. Janis, M. Fortelius, *Biol. Biol. Rev.* **63**, 197–230 (1988).
44. B. R. Lawn, J. J.-W. Lee, P. J. Constantino, P. W. Lucas, *J. Mech. Behav. Biomed. Mater.* **2**, 33–42 (2009).
45. P. J. Constantino, M. B. Bush, A. Barani, B. R. Lawn, *J. R. Soc. Interface* **13**, 20160374 (2016).
46. S. A. Martin, B. H. Alhajeri, S. J. Steppan, *Biol. J. Linn. Soc. Lond.* **119**, 766–784 (2016).
47. D. L. Swiderski, M. L. Zelditch, *Evolution* **76**, 946–965 (2022).

ACKNOWLEDGMENTS

We thank the curators, collection managers, and staff, whose help and support was fundamental to collect all the scans we needed to perform this study. Particularly, we would like to thank: V. Fischer (ULiège, Liège, Belgium), O. Pauwels, A. Folie and T. Smith (RBINS, Brussels, Belgium), E. Gilissen (RMCA, Tervuren, Belgium), G. Véron and G. Billet (MNHN, Paris, France), D. Kalthoff and T. Mörs (NRM, Stockholm, Sweden), B. Kear (PMU, Uppsala, Sweden), E. Amson (SMNS, Stuttgart, Germany), S. Fraile and J. Morales (MNCN, Madrid, Spain), R. Pappa and P. Brewer (NHMUK, London, UK), P. Holroyd (UCMP, Berkeley, CA, USA), C. J. Conroy (MVZ, Berkeley, CA, USA), S.A. McLeod and X. Wang (NHMLA, Los Angeles, CA, USA), D. Berthet and F. Vigouroux (Musée des confluences, Lyon, France), B. Roussel (Musée de Valence, Valence, France), L. Costeur (NMBS, Basel, Switzerland), D. Brinkman and V. R. Rhue (YPM, New Haven, CT, USA), J. Meng, J. Galkin and R. O'Leary (AMNH, New York, NY, USA), and finally N. Pyenson, A. Millhouse, and M. Miller (NMNH, Washington, DC, USA).For providing us additional scans, we would like to thank all the institutions and individuals who made scans available on various platform, more precisely the University of Wyoming, the Field Museum of Natural History, the University of Florida, Idaho Museum of Natural History, Museu de Ciències Naturals de Barcelona, University of California, Los Angeles, Blaire Van Valkenburgh, Denis Geraads, as well as all the staff behind MorphoSource, Sketchfab, and Digimorph. We are also grateful to all the colleagues who shared the PhyloPic silhouettes we used for our figures: T. M. Keesey, L. Ancillotto, A. Farke. **Funding:** This work was supported by the following: Belgian American Educational Foundation (BAEF) Fellowship (to N.C.); European Union's Marie Skłodowska-Curie Actions (MSCA) Postdoctoral Fellowships 2024 (HORIZON-MSCA-2024-PF-01) grant agreement 101207039 https://doi.org/10.3030/101207039 (to N.C.); National Science Foundation grant NSF DBI-2128146 (to N.C. and Z.J.T.); Fonds de la Recherche Scientifique F.R.S.–FNRS grant FRIA FC 63999 (to M.V.); Labex BCDiv 10-LABX- 0003 and Fondation Fyssen (to M.M.); Doctoral school ED 227 "Sciences de la nature et de l'homme: évolution et écologie" (to M.M.); Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, "Dalla ricerca all'impresa," Investimento 1.4, Project CN00000033 (to D.T.); John Templeton Foundation Grant (JTF 62574) (awarded to E. J. Rayfield and P.C.J. Donoghue to hire T.I.P. while writing this article) (the opinions expressed in this article are those of the author and do not necessarily reflect the views of the John Templeton Foundation) (to T.I.P.); Leverhulme Early Career Research Fellowship Grant (ECF-2025-468) awarded by the Leverhulme Trust (to T.I.P.). **Author contributions:** Conceptualization: N.C., M.V., and Z.J.T.; Methodology: N.C., M.V., A.P.R., T.I.P., Z.J.T.; Investigation: N.C., M.V., A.P.R., Z.J.T.; Formal analysis: N.C. L.Y.R.; Software: N.C. L.Y.R.; Visualization: N.C.; Funding acquisition: N.C. Z.J.T.; Project administration: N.C. Z.J.T.; Supervision: N.C. Z.J.T.; Writing – original draft: N.C., M.V., Z.J.T.; Writing – review & editing: N.C., M.V., A.P.R., T.I.P., DT, M.M., L.Y.R., Z.J.T. **Competing interests:** Authors declare that they have no competing interests. **Data, code, and materials availability:** All data are available in the main text or the supplementary materials. All fossil specimens described in this study are cataloged and deposited in various institutions, more details can be found in the 'Material provenance' section in the supplementary material: a complete list of the specimens used along with their metadata (including specimen numbers and institution) can be found in Data S1.

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.aee3453
Materials and Methods; Supplementary Text; Figs. S1 to S17; Tables S1 to S4; References (*48*–*95*); Movies S1 to S8; Data S1 to S4

Submitted 2 December 2025; accepted 19 May 2026

10.1126/science.aee3453

Performance trade-offs define a fundamental dental dichotomy in mammals

Narimane Chatar, Melvin Vankelst, Alejandro Pérez-Ramos, Tahlia I. Pollock, Davide Tamagnini, Margot Michaud, Levi Yoder Raskin, and Z. Jack Tseng

Science **393** (6808), . DOI: 10.1126/science.aee3453

Editor's summary
Teeth in mammals vary in form and function both within individuals and across species depending on what they eat. One tooth that has been notable in its importance in mammalian—particularly carnivoran—evolution is the tribosphenic molar, which facilitates both crushing and slicing. Chatar *et al*. looked at the tooth across 250 species and found that true dual function was present in fewer than 1% of species. Most species instead evolved a trade-off prioritizing one or the other function, leading to specialization rather than duality. —Sacha Vignieri