The lost jackals from the Brazilian caves: insights on the taxonomy and paleoecology of Pleistocene bush dog *Speothos pacivorus* (Carnivora, Canidae)

Juan V. Ruiz, Gabriel S. Ferreira, Fabio A. Machado, Christina Kyriakouli, Pedro L. Godoy, Carsten Gundlach, Mariela C. Castro & Felipe C. Montefeltro

View supplementary material ☐

Published online: 28 Jan 2025.

Submit your article to this journal ☐

Article views: 188

View related articles ☐

View Crossmark data ☐

Check for updates

ARTICLE

THE LOST JACKALS FROM THE BRAZILIAN CAVES: INSIGHTS ON THE TAXONOMY AND PALEOECOLOGY OF PLEISTOCENE BUSH DOG *SPEOTHOS PACIVORUS* (CARNIVORA, CANIDAE)

JUAN V. RUIZ, [*,1,2,3] GABRIEL S. FERREIRA, [3,4] FABIO A. MACHADO, [5] CHRISTINA KYRIAKOULI, [3,4]
PEDRO L. GODOY, [6,7] CARSTEN GUNDLACH, [8,9] MARIELA C. CASTRO, [10] and FELIPE C. MONTEFELTRO [1]

[1]Laboratório de Paleontologia e Evolução de Ilha Solteira, UNESP, Ilha Solteira, São Paulo, Brazil;
[2]Programa de Pós-Graduação em Biodiversidade, UNESP, São José do Rio Preto, São Paulo, Brazil;
[3]Eberhard Karls University of Tübingen, Tübingen, Baden-Württemberg, Germany;
[4]Senckenberg Centre for Human Evolution and Palaeoenvironment at the University of Tübingen, Tübingen, Baden-Württemberg, Germany;
[5]Department of Integrative Biology, Oklahoma State University, U.S.A.;
[6]Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, São Paulo, Brazil;
[7]Department of Anatomical Sciences, Stony Brook University, Stony Brook, U.S.A.;
[8]Department of Physics, Technical University of Denmark, Kgs. Lyngby, Denmark;
[9]3D Imaging Centre, Technical University of Denmark, Kgs. Lyngby, Denmark;
[10]Laboratório de Biologia Integrativa e Conservação, Universidade Federal de Catalão, Catalão, Goiás, Brazil

ABSTRACT—*Speothos pacivorus* from the Pleistocene of Brazilian Intertropical Region (BIR) is distinguished from the extant bush dog *S. venaticus* by its larger size and key characters of the skeleton and teeth. Nonetheless, its taxonomic status is volatile, with some authors still considering both species as synonymous. Here, we aimed to summarize morphofunctional differences between *S. pacivorus* and *S. venaticus* through a comparative description of their skull and dentition, geometric morphometric analysis (GMM), and finite element analysis (FEA). Our GMM revealed *S. pacivorus* significantly separated from the sampled specimens of *S. venaticus*, and a regression analysis showed that the morphological differences of its cranium are not size-related, reinforcing its status as a separate species. Both exhibited very akin von Mises' stress average and distribution on FEA's results, suggesting similar prey-capturing strategies. Our results bolster the hypothesis that the coexistence of these hypercarnivorous canids in the BIR could be explained by a diverse megaherbivore community, allowing resource partitioning between different canid species. Following the demise of these megaherbivores in the Pleistocene–Holocene boundary, other large hypercarnivorous canids also became extinct, leaving the small *S. venaticus*, able to subsist on smaller prey, as the sole surviving species of this specialized lineage.

SUPPLEMENTARY FILES—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

INTRODUCTION

The Lagoa Santa Karst region in Minas Gerais, Brazil, is of great importance for Brazilian Paleontology. It was the place in which the Danish naturalist Peter Lund (1801–1880) conducted his famous works on the natural history of the Brazilian central plateau (Holten & Sterll, 2011). By the mid-19th century, Lund collected numerous fossils and described 22 extinct and eight living species of mammals from the caves of the region, from rodents to saber-toothed cats and even human remains (Auler, 2020; Cartelle, 2020), a pioneering work that gave him the title of father of Brazilian Paleontology (Holten & Sterll, 2000). Among the specimens, Lund identified the remains of five species of Cerdocyonina, the South American canids, including the only known fossils of the genus *Speothos* (Ruiz et al., 2024)

Cerdocyonina encompasses an interesting diversity of living and extinct species (Chavez et al., 2022; Zrzavý et al., 2018). This clade has two major lineages: a foxlike clade, with small, generalist species, and another clade composed by only two very distinctive living species, the bush dog (*Speothos venaticus*) and the maned wolf (*Chrysocyon brachyurus*, Chavez et al., 2022; Zrzavý et al., 2018). The *Speothos–Chrysocyon* lineage also contains many extinct taxa, including the genus *Dusicyon*, jackal-like forms closely related to the maned wolf, and the medium to large-sized hypercarnivores *Protocyon*, *Theriodictis*, and associated forms (Prevosti, 2010; Zrzavý et al., 2018). The bush dog is the only living species of this hypercarnivorous lineage (Fig.

*Corresponding author.

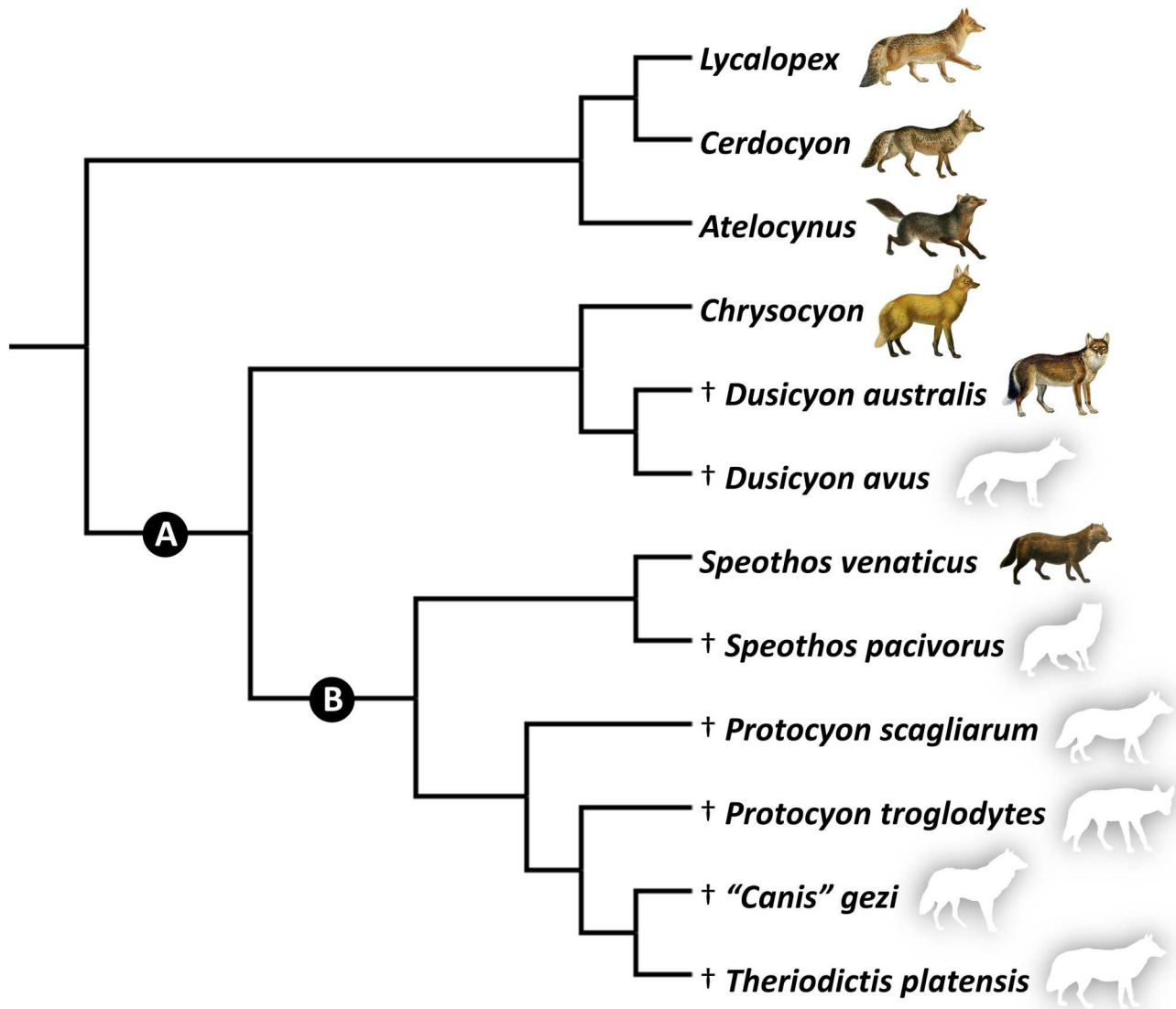Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

FIGURE 1. Simplified phylogenetic relationships within Cerdocyonina after Zrzavý et al. (2018). **A**, *Speothos–Chrysocyon* lineage; **B**, the clade of hypercarnivorous cerdocyonines. Illustrations from Mivart (1890), with silhouettes of extinct Pleistocene taxa (not to scale).

1, clade B), being also the only living Cerdocyonina which presents this specialized diet and other unique traits, such as pack-hunting behavior and polyestrous reproduction (Beisiegel & Zuercher, 2005; Perini et al., 2010; Porton et al., 1987; Van Valkenburgh, 2007).

The taxonomy of *Speothos* is historically confusing. The genus was first erected by Lund (1839, 1840), after the discovery of the remains in the Lapa da Cerca Grande cave (Lagoa Santa Karst region, Brazil), which encompass the materials referred here as *S. pacivorus*. After that, Lund also described fossil and extant specimens of the bush dog, first as a mustelid, *Cynogale venatica* (Lund, 1842) and then as a canid, *Icticyon venaticus* (Lund, 1842/43). Winge (1895) noticed the similarities between *Speothos* and *Icticyon venaticus*, but erroneously argued that *Icticyon* has priority as the genus name and considered *I. pacivorus* the ancestor of *I. venaticus* (Berta, 1984). The priority of *Speothos* was only recognized by the middle of the next century, by Kraglievich (1930). Although Berta (1984) concluded that there are enough morphological traits to differentiate *S. pacivorus* from

S. venaticus, some studies considered the observed differences as intraspecific variation (Prevosti & Forasiepi, 2018), with *S. venaticus* as a potential synonym of *S. pacivorus*. Finally, there are few phylogenetic analyses that include *S. pacivorus*. The 'conventional view' (i.e., *Speothos* as a clade containing two species, *S. pacivorus* and *S. venaticus*) is recovered by Okřinová (2013) and Zrzavý et al. (2018), in their analysis based on morphological, developmental, ecological, behavioral, and cytogenetic characters. In contrast, Perini et al. (2010), in a combined analysis with molecular and morphological data, did not recover *Speothos* as a monophyletic genus, with *S. venaticus* as the sister group of the clade *S. pacivorus* + (*Protocyon* + *Theriodictis*).

Even with the rich assembly of extinct Cerdocyonina, most of the works with this clade are oriented to new geographic records (Oliveira et al., 2005, Prevosti & Rincón, 2007; Prevosti et al., 2009, 2011; Ruiz-Ramoni et al., 2022), phylogenetic relationships (Perini et al., 2010; Prevosti, 2010), or ecological analyses, usually based on the diet, but *Speothos* is mostly absent in such works

(Dantas et al., 2022; Jacob et al., 2024; Prevosti et al., 2005; Prevosti & Schubert, 2013). Here, we employ quantitative analyses to study the biology of the Pleistocene *Speothos*, focusing on *S. pacivorus*, aiming to (a) elucidate the taxonomy of the genus based on a geometric morphometrics analysis performed with key characters of the cranium, and (b) investigate its hunting strategies using finite element analysis. With these two combined techniques, we were able to conduct the most comprehensive examination on the evolution and functional morphology of the genus in 40 years.

MATERIAL AND METHODS

The Materials of *Speothos pacivorus*

The known specimens of *Speothos pacivorus* are deposited in the Peter Lund/Quaternary Collection of the Natural History Museum of Denmark, Copenhagen (NHMD), including a nearly complete cranium (the holotype, NHMD:211341, Fig. 2), as well as four other cranial and mandibular fragments (Fig. 3), at least 54 isolated teeth, and fragments of postcranial skeleton, including appendicular bones and one vertebra (Ruiz et al., 2024). Berta (1984) assumed that the holotype and the postcranial remains belong to the same individual based on the similar stage of development; considering the incomplete epiphyseal closure of ulna and tibia, she also concluded it was a subadult of about 7–8 months of age, though no more details were discussed. The holotype's cranium also presents unfused bones (see below), and although all the preserved teeth are permanent, it does not present extensive wear, which fits with the "adult 1" (A1) category proposed by Segura and Prevosti (2012), an ontogenetic classification we consider for our analyses as it is based on ontogenetic stages easily identified by teeth characters and also due to its extensive sampling. Linear measurements discussed in the comparative description (e.g., cranial length, palate width, etc.) were taken from pictures using the software ImageJ (Abràmoff et al., 2004). The osteological and dental nomenclatures follow Evans and de Lahunta (2012) and Berta (1984), respectively.

CT-Scanning

For this study, the specimen NHMD:211341 (complete cranium) was µCT-scanned at the 3D Imaging Centre, Technical University of Denmark, using a XT H225 ST system from Nikon. The scan was conducted using an aluminum filter (thickness of 0.002 mm), with a voltage of 120 kV and current of 417 µA, resulting in 3142 projections (voxel size of 0.1 mm). For comparison, we also scanned a skull of *S. venaticus* (hereafter bush dog), SMNS-Z-MAM-019136, which represents a large wild adult from Suriname, at the 3D Imaging Lab of the University of Tübingen, Germany, using a XT H 320 system from Nikon, scanned with an aluminum filter (thickness of 0.25 mm), with a voltage of 180 kV and current of 83 µA, resulting in 4476 projections (voxel size of 0.053 mm). The segmentation of the slices into a single material was performed with Amira 2021.1 (Thermo Fisher Scientific) and Biomedisa (Lösel et al., 2020), with small cracks and holes in NHMD:211341 being reconstructed posteriorly with Blender version 3.4 (DeVries et al., 2022; see also Ruiz et al., 2024).

Geometric Morphometrics

We photographed 77 individuals on the ventral view with a scale for geometric morphometric analyses. The sample consisted of the type specimen of *Speothos pacivorus* and 59 individuals of bush dog (Table S1), including only adult specimens from A1 to A3 categories proposed by Segura and Prevosti (2012)

considering dental eruption and wear. Of the 56 specimens with confirmed categorization, 24 were labeled as A1, 16 as A2, and 16 as A3 (see Table S2). For comparison, we also added other species of the *Speothos–Chrysocyon* lineage, including the extant *Chrysocyon brachyurus* (n = 6) and the extinct *Dusicyon avus* (n = 2), *D. australis* (n = 4), *Protocyon scagliorum* (n = 1), *P. troglodytes* (n = 2), '*Canis*' *gezi* (n = 1), and *Theriodictis platensis* (n = 1). See the supplementary information for a complete list of specimens (Table S1) and institutional abbreviations.

We registered the x and y coordinates of 35 landmarks on both sides of the cranium in ventral view (Table S3, Fig. S1) and registered the scale with the software TPSDig (Rohlf, 2015). Because the resulting configurations are arbitrarily rotated, translated, and scaled, we performed a Generalized Procrustes Analysis (GPA) to standardize for those effects (Rohlf & Slice, 1990). This analysis was performed with the R (version 4.2.2 R Core Team) package Morpho, which allows for the removal of bilateral asymmetry (Schlager, 2017). The resulting superimposed configurations were subjected to a principal component analysis (PCA) for dimensionality reduction and data visualization.

To evaluate possible differences between *S. pacivorus* and the bush dog, we conducted a non-parametric multivariate analysis of covariance (npMANCOVA, Anderson, 2001) using size as a covariate, species as factor, and type II sum of squares. This analysis was performed only for the *Speothos* specimens to assess if differences among species can be explained only by allometric changes. If we find a significant effect of size, but not of species, that would be consistent with the existence of a single taxon with allometric differences among individuals. If we find a significant effect of species despite the presence of allometry, that would be consistent with non-allometric shape differences between both taxa. Size was measured as the log-transformed centroid size (logCS). The CS is calculated as the square-root of the sum of the distances among each landmark and the centroid of the configuration, which is the center of mass of the configuration.

Significance was tested using 9999 permutations of the species identities and calculating effect sizes using the R package geomorph (Adams et al., 2019). Because there is a single specimen of *S. pacivorus*, this would be equivalent to calculating the within-group variation only from bush dog and the between-group variation from the average of bush dog and the specimen of *S. pacivorus*. Permutations would then construct the null distribution of effect sizes by considering *S. pacivorus* as part of bush dog and randomly drawing a specimen of bush dog to be associated to *S. pacivorus*. Significance was calculated as the number of effect sizes greater than the ones observed through permutations. To visualize the allometric shape differences within the *Speothos* sample, we calculated the regression scores between shape and size (Drake & Klingeberg, 2008). This method calculates the projection score of individual shapes onto the coefficient of regression between size and shape (obtained from the npMAN-COVA), and thus describes the shape variation more associated with size (Drake & Klingeberg, 2008).

Finite Element Analysis

To understand the cranial functional properties in different hunting movements for both species of *Speothos*, we tested different extrinsic (i.e., 'external' forces, generated by a struggling prey) scenarios on the cranium of *S. pacivorus* and the bush dog (SMNS-Z-MAM-019136). The three-dimensional surfaces were composed of a single material, with no distinction between bone and teeth, as in Slater et al. (2009). These surfaces were then imported in the software Hypermesh 13.0 (Altair Engineering) and treated as isotropic and homogeneous (solid model consisting of approximately 800,000 tetrahedral elements per model). The material properties of cortical bones (E = 13.7
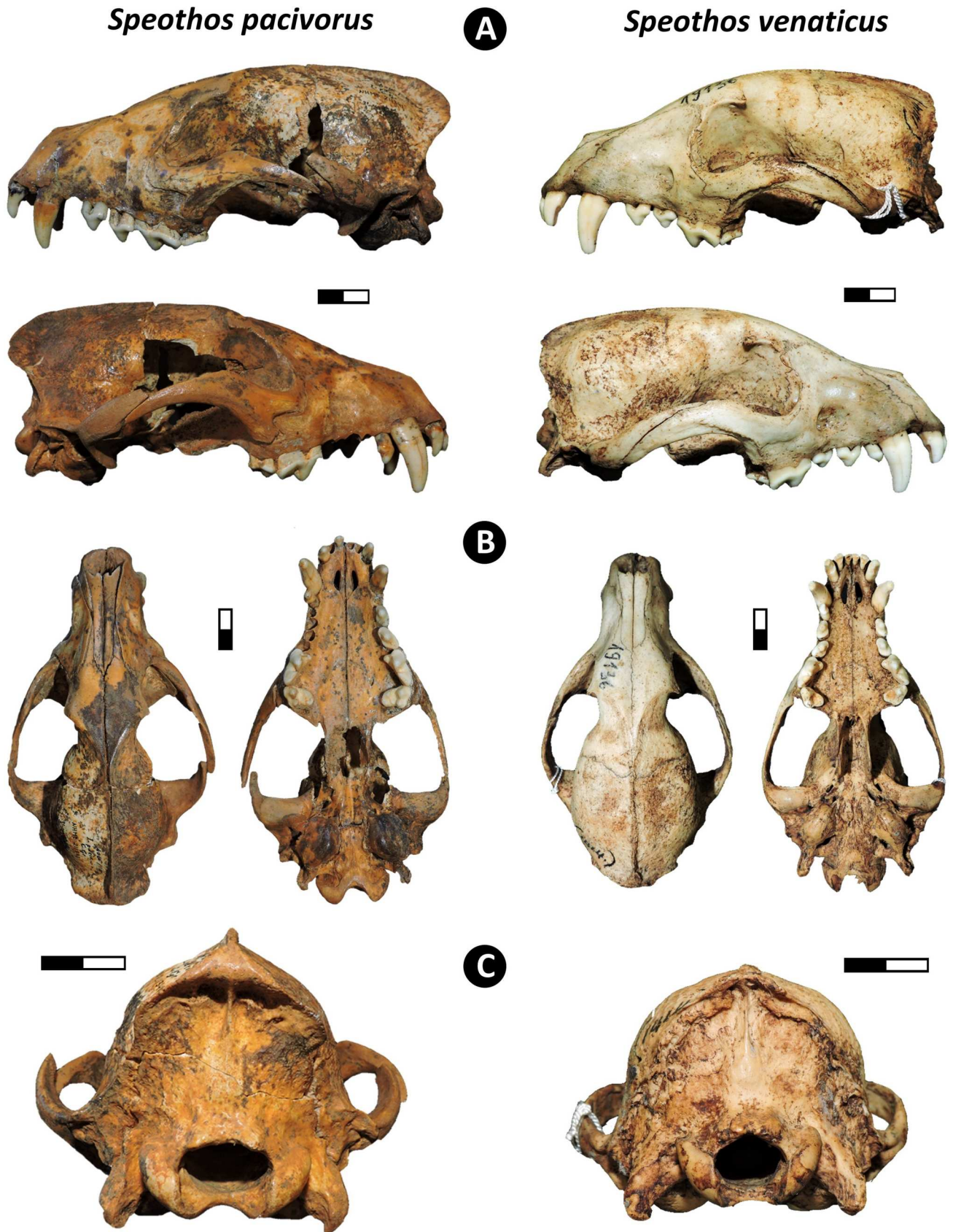
FIGURE 2. The crania of *Speothos pacivorus* (NHMD:211341) and *S. venaticus* (SMNS-Z-MAM-019136). **A**, left and right lateral views; **B**, dorsal and ventral views; **C**, occipital views. Scale bars equal 2 cm.

GPa, $\upsilon = 0.3$) were assigned based on previous works on carnivore mammals, including canids (Chamoli & Wroe, 2011; Figueirido et al., 2018; Slater & Van Valkenburgh, 2009; Slater et al., 2009). To avoid incongruities related to size difference, the cranium of *S. pacivorus* was scaled to the same volume of that of the bush dog (Sharp, 2015). Constraints were applied on the occipital condyle (10 nodes in total) and the temporomandibular joint (five on each side), with each node constrained in all directions (x, y, and z). Each modeled scenario was solved in the software Abaqus 6.14-1 (Simulia Engineering). The performance of each model was assessed via contour plots of von Mises stress distribution and mean von Mises stress per element and displacement value of the elements; to avoid individual stress singularities on nodes, 99% of the values were considered (Figueirido et al., 2018; Montefeltro et al., 2020).

Eight extrinsic scenarios with different load assignments were tested to understand the craniomandibular functional properties in different conditions, based on the application of an extrinsic load of 315 N on each canine and 530 N on each carnassial, according to the bite force estimated for the bush dog by Ruiz et al. (2022). Each scenario aims to investigate possible movements of prey capture, including bite and postcranial-guided head movements (Montefeltro et al., 2020). Six bilateral scenarios follow Figueirido et al. (2018) and Ruiz et al. (2022), and consist of: stabbing, in which a dorsally directed load was placed at the tip of the tooth; pulling back, in which an anteriorly directed load was placed at the posterior surface of the tooth; and head shaking, in which a laterally directed load was placed at the mid-left surface of the tooth.

Additionally, two unilateral, postcranially guided scenarios were tested following Montefeltro et al. (2020), the head twisting, in which a dorsally directed load was placed in the left tested tooth and a ventrally directed force was applied on the opposite, right tooth. This movement of grabbing a prey and twisting the skull laterally is characteristic for semiaquatic and aquatic vertebrates, being better known for crocodiles as the 'death roll' (Drumheller et al., 2019). It was not tested in canids through FEA in previous studies (e.g., Ruiz et al., 2022; Slater et al., 2009) and was included here due to the semiaquatic habits of the bush dog (Beisiegel & Zuercher, 2005).

Institutional Abbreviations—**NHMD**, Natural History Museum of Denmark, Copenhagen, Denmark; **SMNS-Z-MAM**, Stuttgart State Museum of Natural History, Mammal Collection, Stuttgart, Germany.

RESULTS

Comparative Description of the Skull

In this section we describe the anatomy of the preserved cranial and mandibular elements of *Speothos pacivorus* and its respective dentition (Fig. 3), comparing it with the bush dog (*S. venaticus*).

Cranium—overall, the cranium of *S. pacivorus* is a bit larger than those of the bush dog (Table S2), being longer and wider (at the zygomatic arches) in dorsal and ventral views (Fig. 2). In general, its shape is akin to that of the dhole (*Cuon alpinus*, Fig. S2), appearing to be less compact than the stumpy cranium of the bush dog.

The rostrum is superficially shorter in relation to the whole cranium than in the bush dog (Berta, 1984). In dorsal view, the contact of the nasals with the frontal has an acute shape, as in most bush dogs, although some specimens can present a blunt to square-shaped suture. The frontal of *S. pacivorus* has an anterior process situated between the nasal and maxilla, almost contacting the incisive and limiting the nasal-maxilla suture to a small segment. In the bush dog, the condition is usually similar but, in many specimens, the frontal and incisive contact each other, preventing a nasal–maxilla contact. The close proximity between the incisive and the anterior process of the frontal is a typical condition in short-rostrum species of living canids, being especially prominent in the hypercarnivorous painted dog (*Lycaon pictus*, Fig. S2). In dorsal and lateral views, the nasal does not reach the most posterior limit of the maxilla, a condition shared by *Speothos* with the short-eared dog (*Atelocynus microtis*), as noted by Berta (1984), and the crab-eating dog (*Cerdocyon thous*, Fig. S2).

Apart from the dentition (see below), the palatal region of both species of *Speothos* is very similar. Compared with any other living canid, it is proportionally shorter and wider. At the widest point (the contact of M1–M2), the width of the palate of *S. pacivorus* comprises about 30% of the condylobasal length of the cranium; in the studied bush dog specimens, the proportional width is similar, ranging from 26% to 33% (Table S4). Most of the pterygoid-palatine fossa and the nasopharyngeal region is missing in NHMD:211341.

The basicranium of NHMD:211341 is noteworthy by presenting unfused contact between the sphenoid (basisphenoid part) and the occipital (basioccipital part); the sphenoid (alisphenoid part) and temporal (squamous part), anteriorly to the tympanic bullae; and the occipital (basioccipital part) and temporal (tympanic part), around the medial and posterior margins of the tympanic bullae, as seen in ventral view (Fig. 2B). In posterior view (Fig. 2C), the temporal (tympanic and petrosal parts) is also unfused to the occipital (especially with the exoccipital but also with a small part of the supraoccipital). Apart from this, the basicranium of this specimen does not present any considerable deformation or displacement and looks very similar to the basicranium of the bush dog. In this species, the overall shape of the paracondylar process and the position of the jugular and hypoglossal foramina, as well as the overall shape of the occipital condyles in ventral view, differ among the analyzed specimens.

Although Berta (1984) attested that the tympanic bullae of *S. pacivorus* are larger than that of the bush dog, due to the great variety of size of this structure in the latter species, it is difficult to assume that an enlarged bulla is characteristic for *S. pacivorus* or if it is only a condition of this specimen. As cubs and juveniles of South American canids present larger bullae compared with older individuals (Segura et al., 2021), the large, globulous bullae of the holotype of *S. pacivorus* reinforces the possibility of it representing a young adult (A1) specimen; however, given the absence of additional specimens of *S. pacivorus* with a preserved basicranium, considerations on this anatomical trait and aging cannot be made with certainty.

The clearest difference between both species is the proportion of the braincase. In *S. pacivorus* it is considerably smaller in relation to the cranium as a whole (being approximately 42% of the cranium total length and with a width, at its widest point, of 57% compared with the cranium's widest point at the zygomatic arches), while the bush dog possesses a much more developed braincase (being approximately 50% of the cranium total length and with a width at widest point of 68.4% compared with the cranium's widest point at the zygomatic arches in SMNS-Z-MAM-019136). This enlarged braincase in the bush dog is even enhanced by a postorbital constriction more accentuated in *S. pacivorus*, which reduces the area of the anterior portion of the braincase in dorsal and ventral views (Fig. 2B). Although some specimens of bush dog also possess a considerable compression of the postorbital region, the degree of this compression is not so extreme as seen in *S. pacivorus*.

The sagittal crest of *S. pacivorus* is more developed than that of most bush dog specimens, which show crests of different sizes. In Carnivora, the sagittal crest tends to increase in size with age, allowing the attachment of the powerful adductor muscles (Garcia-Perea, 1996; Segura, 2013; Van Valkenburgh, 2007). However, considering that our sampling of *Speothos*
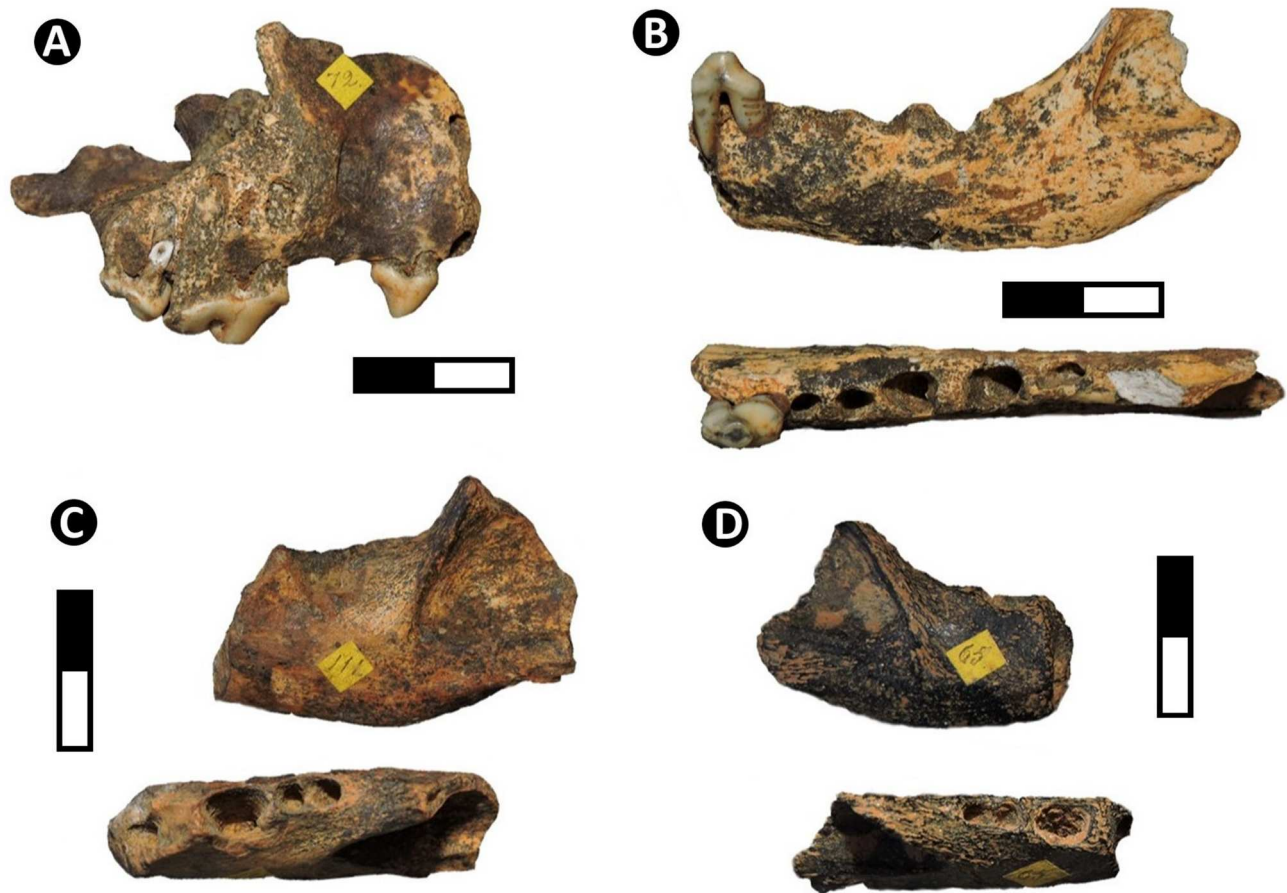
FIGURE 3. The fragmentary skull elements of *Speothos pacivorus*. **A**, right maxilla NHMD:72 in lateral view; **B**, partial left hemimandible NHMD:159 in labial and dorsal view; **C**, partial left hemimandible NHMD:711 in labial and dorsal view; **D**, partial right hemimandible NHMD:65 in labial and dorsal view. Scale bars equal 2 cm.

(*S. pacivorus* included) represents adults of different ages, it may indicate that the development of the sagittal crest in the members of this genus can also be related to other factors, such as sexual dimorphism or demographic variations. Finally, as with the tympanic bullae, the fact that only one complete cranium is known for *S. pacivorus* limits any inference on the relatively larger sagittal crest of the holotype and its possible association with aging.

The nuchal crest is mildly developed compared with other canids and is anteroventrally directed in *S. pacivorus*, with a concave margin that follows the lateral limits of the occipital region of the braincase, in lateral view. As with the sagittal crest, in the bush dog this trait is variable but, overall, it is less concave and more dorsoventrally directed, being almost straight in some specimens. In both species, the ventral limit of the nuchal crest ends on a small eminence almost contacting the external acoustic meatus. The more developed nuchal crest of *S. pacivorus* prevents the visualization of the occipital region of the cranium in lateral view, a condition present in some bush dog specimens.

The occipital region of *S. pacivorus* has a squared shape on its dorsal portion, with its lower limits (outlined by the nuchal crest) ventrolaterally directed, while in the bush dog it appears to be more rounded (Fig. 2C). The scars of the cervical muscles are marked by deeper depressions when compared with the blunter surface of the bush dog, a condition exaggerated by the larger nuchal crests of *S. pacivorus*. The foramen magnum of

S. pacivorus is oval and dorsoventrally compressed in posterior view, being larger in relation to the cranium than that of the bush dog (Fig. 2C). The dorsal margin of the foramen magnum bears a crest that is present in both *Speothos* species, but it is far more developed in the bush dog, notably seen in lateral view, just above the occipital condyles. The foramen magnum region, including the occipital condyles, is more posteriorly displaced in the bush dog than in *S. pacivorus*, a condition noted by Langguth (1980) and Berta (1984).

Mandible—there are three fragmentary mandibular specimens preserved for *S. pacivorus* (Fig. 3): NHMD:159 (a partial left hemimandible preserved from pm2 to the anterior half of the masseteric fossa), NHMD:65 (a small fragment of the right hemimandible preserved from the posterior wall of the anterior alveoli of m1 to the anterior portion of the masseteric fossa), and NHMD:711 (same as NHMD:65, but on the left hemimandible). The morphology of the preserved portions is very similar to that seen in the mandibles of the bush dog, being short and deep and possessing a slightly developed subangular lobe (Berta, 1984). The masseteric fossa extends to the level of m2, a condition that is also present in most bush dog specimens included in this study.

By estimating the length of the molar section of the mandible, we can suggest that the mandible of the bush dog is proportionally deeper than that of *S. pacivorus*. While in the latter the height of the mandibular ramus at the level of m1 is about 65–80% of

the length from the anterior part of the m1 to the posterior part of the m2, in the five largest bush dog specimens, it represents about 98–108% (Table S5). A shorter and deeper mandible can be directly related to the stumpy condition of the cranium of the bush dog, with its shorter rostrum and reduced dentition.

Dentition—the dentition in the holotype of *S. pacivorus* is relatively complete, and without extensive wear on the crowns (Fig. 2). Teeth are also preserved in the maxillary fragment (NHMD:72) and in the right hemimandible (NHMD:159); there are also 54 isolated teeth assigned to the species (Ruiz et al., 2024). For a detailed description of the dentition, see Berta (1984).

Overall, the dentition of *S. pacivorus* is very similar to that of the bush dog (Fig. 2A, B), with specific differences. Of the four proposed autapomorphies of *S. pacivorus*, three are related to its molars (Berta, 1984). First, the M1 of *S. pacivorus* presents well-developed metaconule and hypocone, thus appearing larger and more developed, square-shaped in ventral view (Fig. 4C). In the bush dog, the metaconule and hypocone are absent (Berta, 1984), and the tooth has a more delicate, triangular appearance in ventral view (Fig. 4D). Second, unlike most bush dogs, *S. pacivorus* presents a M2, as there is an alveolus posterior to M1. In the holotype, it is single-rooted in the left side, but double-rooted in the right side (Fig. S3); in the maxillary fragment preserved it is also double-rooted (Fig. 4E). Usually, bush dogs do not possess M2: of the five specimens analyzed by Gudinho and Weksler (2021), only one had it (20% of the sampling). In our dataset of 59 specimens, the M2 is present in 11 specimens (about 18% of the sampling); of these, only three bear the additional molar in both sides of the toothrow. In general, this extra tooth is small and peg-like, circular in cross section, unlike the larger and wider alveolus present in *S. pacivorus* (Fig. 4F, G). Finally, the m2 in *S. pacivorus* is double rooted, as seen in the alveoli of NHMD:65 and NHMD:711 (Fig. 4H, I), but difficult to interpret in NHMD:159 due to its preservation. In bush dogs, this tooth is very reduced, presenting a single root (Winge, 1895; Fig. 4J). However, it is important to note that root number in molars is not a reliable character, especially in carnivorans with a specialized diet (DeMers, 2023).

Cranial Shape

The two first Principal Components (PCs) explain 68.8% of the total variation in the sample (Fig. 5; for higher PCs, see Fig. S4). The PC1 describes an overall contrast between a greater contribution of molar teeth (M1–2) in the overall length of the toothrow and a narrower braincase and zygomatic arches with negative values and a greater contribution of the carnassial (PM4) in relation to the overall length of the toothrow and a wider braincase and zygomatic arches with positive values. The PC2 mostly describes changes in the length of the rostrum, with specimens with short, wider rostra at more negative values and those with longer, narrower rostra at more positive values. For the bush dog, specimens are concentrated on the positive values of PC1 highlighting the overall shortening and robustness of the rostrum, and reduction of the number of teeth. Within the non-*Speothos* sample, there is a contrast between *Chrysocyon brachyurus*, with a gracile cranium and elongated rostrum (PC1 −, PC2+), and *P. troglodyctes*, with a robust cranium and short rostrum (PC1+, PC2−). '*Canis' gezi* is the only species positioned closer to the negative quadrant of both PCs (PC1−, PC2−), which refers to a gracile cranium with a relatively short rostrum. On the PC1 vs. PC2 morphospace, *S. pacivorus* is positioned between the bush dog and the remaining species.

The npMANCOVA showed a significant effect of both size and species on shape variation, suggesting that the differences observed between *S. pacivorus* and bush dog cannot be explained by allometric differences alone (Table 1). Shape differences between small and large individuals are subtle, with smaller individuals having proportionally shorter rostra and larger individuals having longer rostra (Fig. 6). Nevertheless, the regression scores illustrate the result of the npMANCOVA, showing that, despite being larger in size, the type specimen of *S. pacivorus* does not follow the allometric expectation of bush dog.

Finite Element Analysis

In relation to the distribution of von Mises stress, the differences between the species are more related to the degree of stress (i.e., how the magnitude varies in the same affected area) than to difference in the foci of stress through the cranium (i.e., distinct points of stress between the species). In all extrinsic scenarios tested, both species presented minor differences regarding the average von Mises stress per element, with the bush dog stressing slightly less than *S. pacivorus*, especially in the stabbing and head-shake scenarios (Fig. 7); these differences, albeit small, might be explained by the more stocky and higher cranium of the bush dog. Loads on the carnassials yielded more stress than on the canines. It is noteworthy, however, that the differences in mean values between both teeth in all scenarios are not considerable, even considering that the loads on the carnassial are about 170% that of the canines.

The head-shake scenarios were the most stressful of all tests, a condition also recovered for bush dogs in Ruiz et al. (2022), a study conducted with different models with distinct volumes, material properties, and loads. In these scenarios, the carnassial bites were slightly more stressful. Conversely, the difference of stress average between canines and carnassials in the stabbing scenarios are minimal. In the head-shake, the stress is more anteriorly distributed, especially at the orbital, lateral palatine surface, and zygomatic arch, with the rostrum being also affected but to a lesser degree. In the stabbing scenarios, the stress is distributed mainly on the braincase, orbital region, and lateral surface of the palatines, with minor focus of stress on the dorsal surface of the rostrum (in the canine scenarios).

The pull-back scenario stands out as the less stressed movement, similar to previous studies with canids (Ruiz et al., 2022; Slater et al., 2009). Compared with the other scenarios, the differences between the mean values of the canines and carnassials are higher, albeit only slightly. The stress distribution in the pull-back scenarios is limited mainly to the ventral portion of the cranium, with minor areas of stress at the anterior portion of the rostrum (in the canine tests), and in the posterior portion of the rostrum and at the frontal (in the carnassial tests).

The head-twist scenarios are also characterized by lower stress, responding very similarly, on average, to the pull-back scenario. These lower values can be attributed to it being a unilateral scenario. Although the bush dog shows similar mean values between the canine and carnassial tests, in *S. pacivorus* the canine-driven model is markedly less stressed than the carnassial one. This comprises the only remarkable, albeit subtle, difference between both species in all scenarios tested. The stress distribution is quite similar to that of the pull-back scenario, with less stress on the lateral surface of the palatines and more stress on the zygomatic arch.

DISCUSSION

Speothos venaticus as a Distinct Species

The identification of canid species by osteological and external features is difficult, especially when considering recent species (Machado & Teta, 2020). Morphological similarities may not be determinant of conspecifics, but subtle morphological
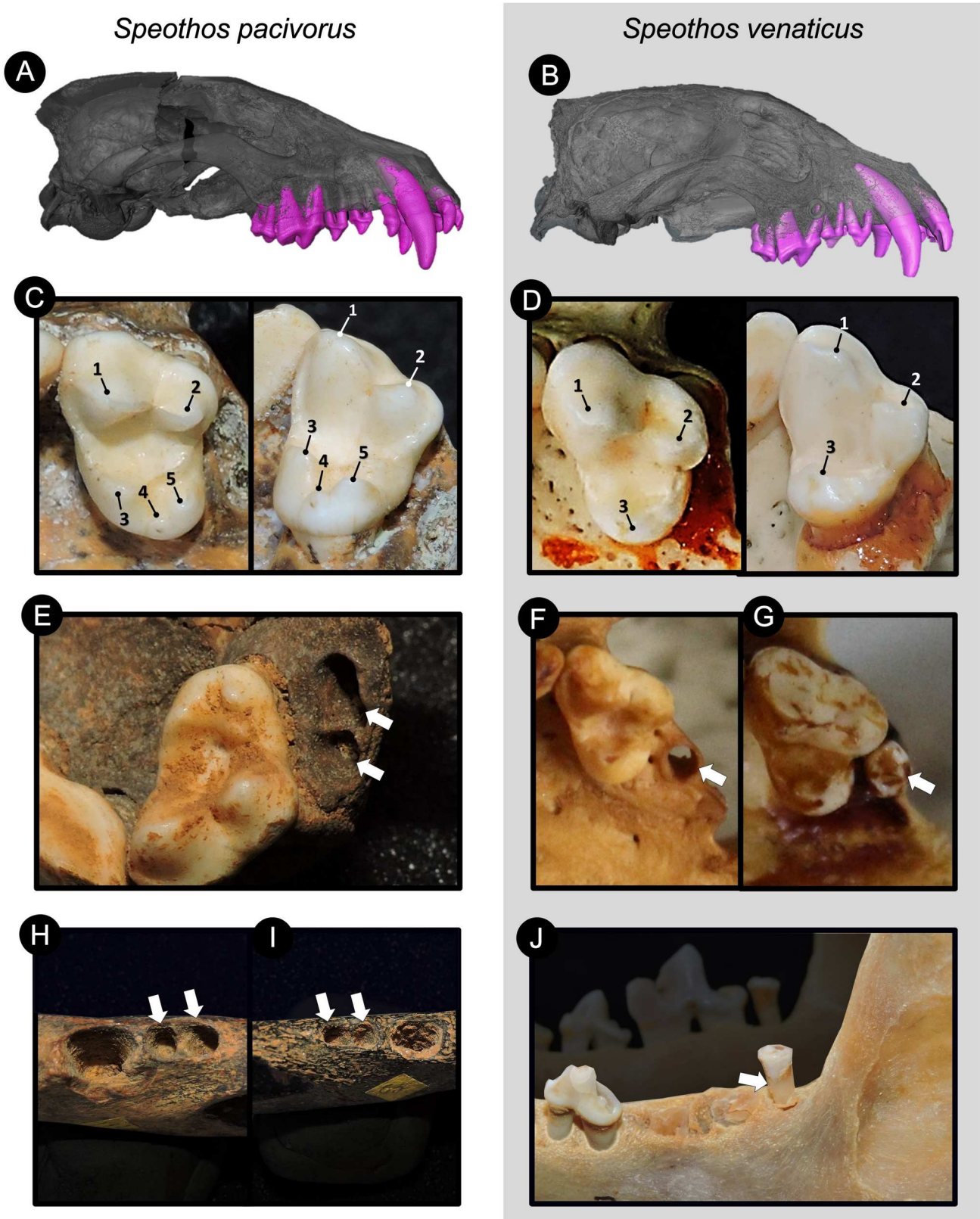
Speothos pacivorus

Speothos venaticus

FIGURE 4. Diagnostic dental characters in *Speothos pacivorus* (left column) and *S. venaticus* (right column). **A** and **B**, digital reconstruction of the upper dentition. **C** and **D**, left M1 in ventral (left) and lingual (right) views, in which: **1**, paracone; **2**, metacone; **3**, protocone; **4**, hypocone; and **5**, metaconule (following Berta, 1984); **E**, alveoli of the right M2 in *S. pacivorus*, showing the double rooted anatomy of the tooth (indicated by the arrows). Left M2 in *S. venaticus*, showing: **F**, the single alveolus for the tooth (USNM270370) and **G**, the preserved M2 (MPEG8794), both indicated by the arrows. Double alveoli for m2 (indicated by the arrows) in: **H**, left hemimandible (NHMD:711), and **I**, right hemimandible of *S. pacivorus* (NHMD:65). **J**, detached m2 of *S. venaticus*, showing its single root, indicated by the arrow (MZUSP35732).
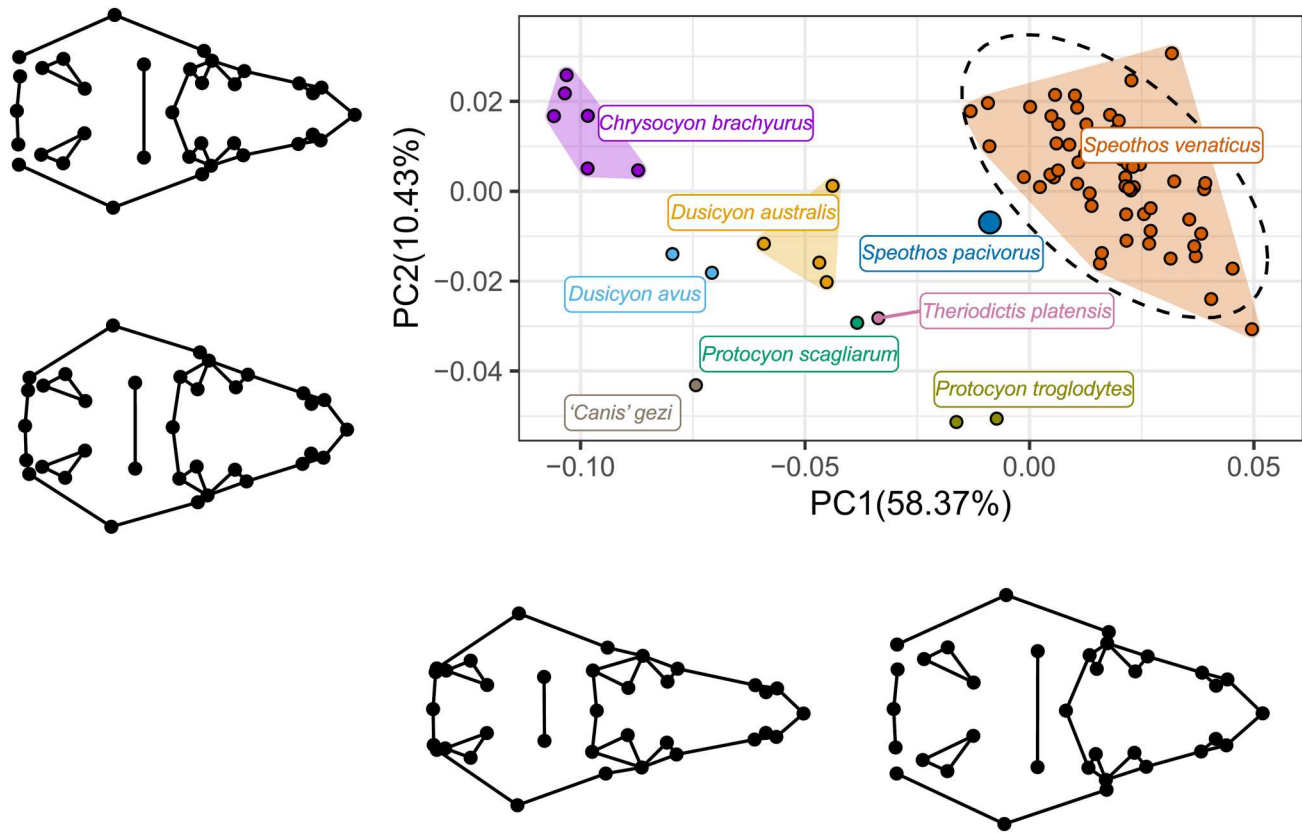
FIGURE 5. Morphospace occupation of nine species of the *Speothos–Chrysocyon* clade. PC1 vs PC2 plot of cranial shape variation in ventral view, with different colors representing different species and polygons (minimum convex hulls) used for species with multiple specimens included in the sample. The dashed line represents the 95% confidence ellipse representing the covariance among *S. venaticus* specimens.

discontinuities are a common criterion to distinguish species (Diersing & Wilson, 2017; Gaubert & Antunes, 2005; Machado & Teta, 2020). Although, overall, the crania and dentition of *S. pacivorus* and the bush dog are very akin, close inspection shows that (a) the proportions, especially regarding the rostrum and braincase, are different; and (b) the series of distinct cranial characters used to distinguish both species—such as the number of teeth, shape of tooth crown, and number of roots—are not consistent with the intraspecific variation found within our sample of the bush dog. Finally, postcranial elements also show distinct characters, as listed by Berta (1984).

Among living canids, the bush dog has arguably the most peculiar cranium in terms of proportion, resembling those of mustelids (Vieira, 1948). Our geometric morphometrics analysis showed that the shortening of the rostrum (the most extreme within the sampled species) occurs together with hypercarnivory-related dental adaptations (i.e., reduced number of molars and the development of a carnassial tooth PM4), with shorter rostra in individuals with a more hypercarnivorous dentition (Fig. 5). Larger, hypercarnivorous Cerdocyonina also present a shorter rostrum and, in the case of *Protocyon troglodytes*, also a noticeably wide cranium, while *S. pacivorus* appears closer to the bush dog as an intermediate condition between *P. troglodytes* and *S. venaticus*. Because only a single specimen of *S. pacivorus* with a complete cranium is known, it is difficult to confirm its distribution in relation to the other included hypercarnivorous taxa. However, the results of our npMANCOVA (see also Fig. S5) highlight that the difference between the *S. pacivorus* and the *S. venaticus* specimens is greater than the

TABLE 1. Non-parametric MANCOVA table of species differences with log(size) as a covariate. **Abbreviations**: **Df**, Degrees of freedom; **F**, Fisher's F; **MS**, Mean Squares; **Pr(>F)**, P-value: proportion of the non-parametric null-distribution that is as extreme or more than the observed value; **R²**, Percentage of variation explained by a factor, after accounting for the variation on other factors; **SS**, Sum of Squares; **Z**, Effect size.

	Df	SS	MS	R^2	F	Z	Pr(>F)
log(size)	1	2.46E + 00	2.46E + 00	0.038	2.321	2.081	0.019
Species	1	2.46E + 00	2.46E + 00	0.037	2.318	1.995	0.022
Residuals	57	6.05E + 01	1.06E + 00	0.922			
Total	59	6.56E + 01					

distances among *S. venaticus*, supporting the hypothesis of them being distinct but closely related species.

Additionally, one of the proposed diagnoses of *S. pacivorus* is its larger size. Allometric scaling led to significant morphological differences in canids, with large individuals of a species being sometimes misleadingly classified as different taxa (Machado & Teta, 2020; Wayne, 1986). However, our npMANCOVA results clearly showed that the specimen of *S. pacivorus* is not within the expected shape of an oversized bush dog. Most bush dogs analyzed have a similar age to *Speothos pacivorus* (A1; Table S2), so its position in the morphospace cannot be interpreted
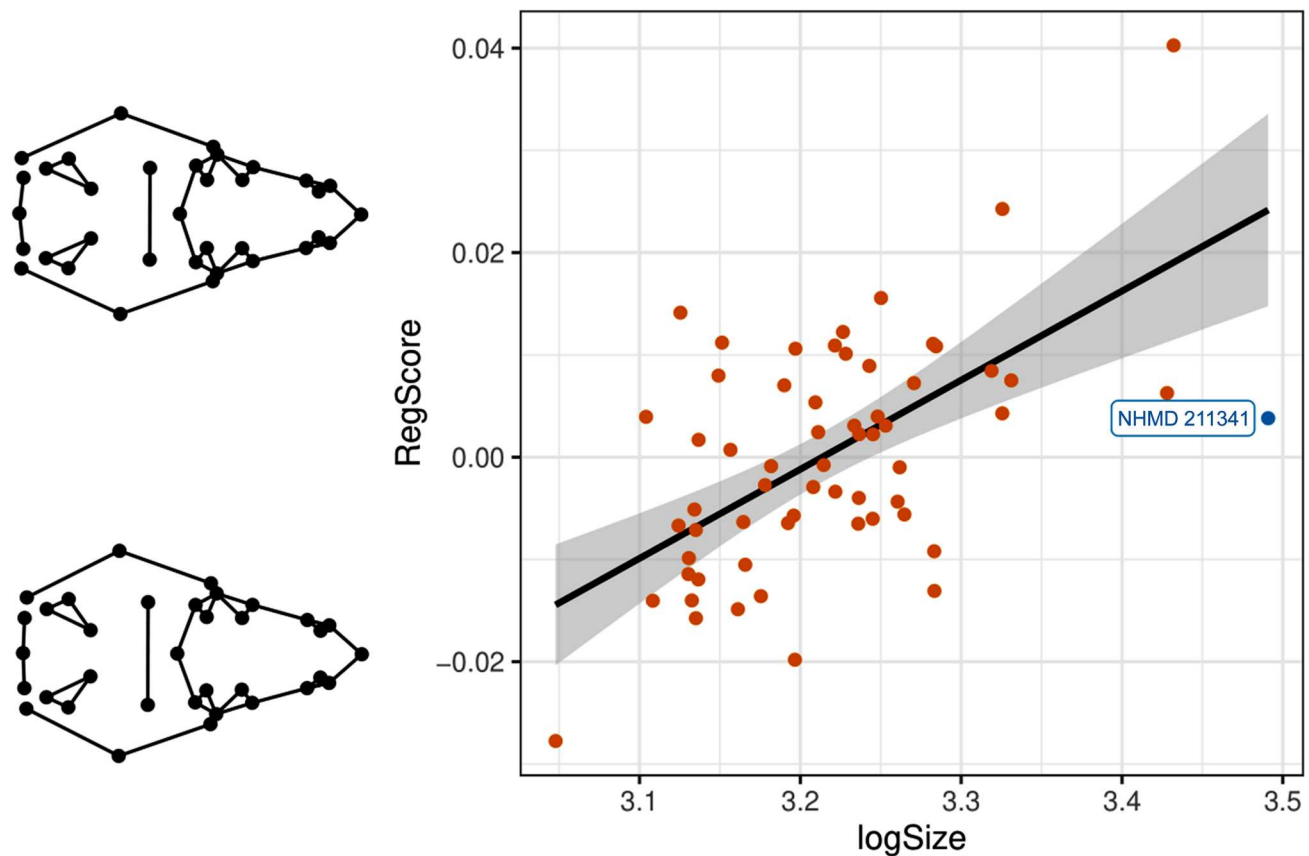
FIGURE 6. Relationship between the shape regression scores (RegScore) and size (logSize) in *Speothos* (*S. venaticus* represented by orange dots and the type specimen of *S. pacivorus* represented by the blue dot). Configurations represent shape changes associated with size differences on the ventral view of the crania.

due to ontogenetic differences (i.e., a refutation to the interpretation of the holotype of *S. pacivorus* as an abnormally large adult bush dog). In light of these results and considering that *Speothos pacivorus* and the bush dog are distinguished from each other by discrete morphological characters, we endorse the 'conventional view' of *Speothos* taxonomy, rejecting *S. venaticus* as a junior synonym of *S. pacivorus*.

Speothos as Pleistocene Predators

Although morphologically distinct, the cranium of both *Speothos pacivorus* and the bush dog present very similar biomechanical performances. Our results do not suggest different hunting movements for capturing prey for each taxon. With both *Speothos* species being slightly different in size and form, and assuming a sympatric distribution for it in the Pleistocene of Central Brazil, two main questions arose: (a) how such similar taxa could coexist temporally and spatially; and (b) why *S. pacivorus* became extinct but the bush dog did not. Different ecological, dietary, and reproductive strategies of extant canids can provide some insights into it.

Coexistence of canid species in modern ecosystems occurs with similar sized but generalist species (Di Bitetti et al., 2009; MacDonald et al., 2004; Novaro et al., 2004), species with different sizes, or species with different diets and other ecological traits as habitat use (Fowler et al., 2022; Kozlowski et al., 2008; Petroelje et al., 2021). In the case of the Pleistocene *Speothos*, our results suggest that both species were highly specialized

hypercarnivores, indicating a similar diet and, consequently, ecological niche. In modern ecosystems, such examples do not usually overlap in their distribution (Castelló, 2018) and, when they do, such as in the case of the gray wolf (*Canis lupus*) and the dhole (*Cuon alpinus*), they are antagonists and usually avoid each other spatially at the microhabitat scale (Heptner & Naumov, 1998, but see Ghaskadbi et al., 2021). Although some canid communities show evidence of species displacement, black-backed jackals (*Lupulella mesomelas*), side-striped jackals (*Lu. adusta*), and African golden wolves (*Canis lupaster*), three species of generalist feeders of similar sizes, coexist in Kenya (Sillero-Zubiri, 2009). Could this be the case of *Speothos* in the Brazilian Intertropical Region (BIR)? Comparing modern and Pleistocene ecosystems, however, is not simple since the faunal compositions are substantially different.

A factor that could allow the spatial coexistence of *S. pacivorus* and bush dogs is a richer community of herbivorous mammals in the Pleistocene. Modern bush dogs are pack-hunters that eat small to medium-sized prey, especially caviomorphs and armadillos (Lima et al., 2009; Zuercher et al., 2005), also appearing to be specialized in some prey in certain regions (e.g., armadillos in Pantanal, Lima et al., 2009). Their robust skulls also allow the bush dogs to occasionally hunt bigger prey (Ruiz et al., 2022), such as brocket deer, peccaries, capybaras, and even tapirs (Beisiegel, 1999; Beisiegel & Zuercher, 2005; Wallace et al., 2002). In the Pleistocene, the Lagoa Santa region supported a rich community of herbivorous mammals, with at least 21 species of rodents, xenarthrans, and ungulates registered to date (Cartelle, 2020).
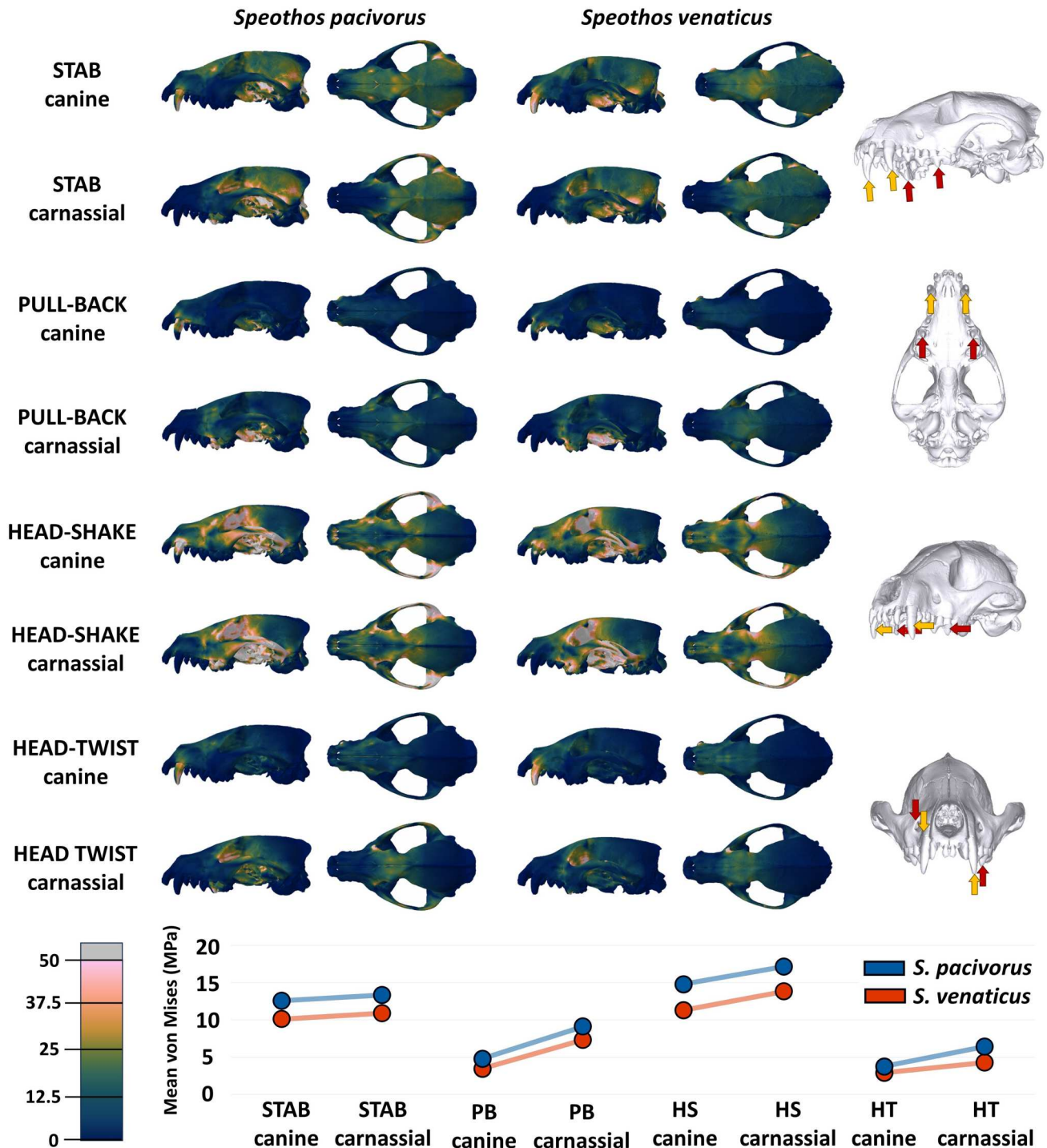
FIGURE 7. von Mises stress contour plots from finite element analysis of the extrinsic scenarios modeled to the crania of *Speothos pacivorus* and *S. venaticus*, with reconstruction of the loads of each scenario illustrated on the right, and relation among the mean von Mises values per element in the tested scenarios. **Abbreviations**: **HS**, head-shake; **HT**, head-twist; **PB**, pull-back.

Many of these species are larger relatives of known prey of modern bush dogs, such as the armadillos *Propraopus* spp. and the rodents *Brasiliochoerus stenocephalus*, *Neochoerus sulcidens*, and, noteworthy, the large paca *Cuniculus rucigeps* (Cartelle, 2020).

Since the modern, slightly smaller *Speothos* hunts extensively on modern pacas—also smaller than their extinct relatives—it is reasonable to think that part of the diet of the larger *S. pacivorus* was based on the larger, contemporaneous pacas. The specific epithet of *S. pacivorus* means 'paca eater,' in allusion to the large bed of bones of those rodents in the same caves where the remains of *S. pacivorus* were found (Paula-Couto, 1979). The collector and describer of the species, Peter Lund, attributed both *S. pacivorus* and *Protocyon troglodytes* as being mainly responsible for the accumulation of paca carcasses in these caves (Lund, 1839; Mouchard, 2019). The skull morphology

of *S. pacivorus*, in addition, suggests it could have preyed on even larger prey when hunting in packs, occasionally pursuing species that could not be targeted by the smaller bush dogs, avoiding an extensive overlap in dietary niche between both species. Although there is no direct evidence of pack hunting in *S. pacivorus*, it is a behavior also postulated for *Theriodictis* (Prevosti & Palmqvist, 2001) and known for bush dogs and extinct *Protocyon* (Beisiegel & Zuercher, 2005; Dantas et al., 2022), as well as non-Cerdocyonina extant hypercarnivorous canids such as gray wolves, painted dogs, and dholes (Sillero-Zubiri, 2009).

By also presenting longer leg bones (Berta, 1984), *S. pacivorus* could have had different hunting strategies that are not suggested by its skull biomechanics. The short legs of the bush dog are one of its most striking characters, and it was assumed to be an adaptation to facilitate its moving in narrow spaces (Beisiegel & Zuercher, 2005; Kleiman, 1972), presumably allowing it to pursue prey through thick vegetation. It could also be related to digging behavior, since it is known to chase prey in their burrows (Fleck & Voss, 2016; Lima et al., 2012), presenting also wider forepaws with strong claws, characters that enable a better digging performance (Lima et al., 2009). Shorter legs, in contrast, did not allow bush dogs to maintain high speed for long periods when compared with longer legged pack hunters such as gray wolves and painted dogs (Ruiz et al., 2022). The short legs of bush dogs, thus, can indicate a specialization to prey capture in conditions better suited for smaller bodies (i.e., undercover and riparian thick vegetation, burrows) when compared with the sympatric *S. pacivorus* and *P. troglodytes*.

The Pleistocene of the BIR had a community of land mammals with comparatively more herbivores than modern ecosystems, which could handle a more complex carnivore assembly as well. Today, similarly rich faunal compositions in other parts of the world accommodate more than one species of canid specialized in hypercarnivory. For example, there is an overlap in the distribution of the dhole and the gray wolf in certain parts of India, Nepal, Bhutan, and China (Boitani et al., 2023; Castelló, 2018; Kamler et al., 2015). In the Pleistocene, however, dholes were far more widespread, having a distribution very similar to that of the modern Eurasian wolf, with several records in Europe (Petrucci et al., 2012; Ripoll et al., 2010). Paleoclimatic range reconstructions indicate also its presence in the Levant, where the dhole has coexisted and admixed with the very similar painted dog (Rocha et al., 2022). Finally, its presence in North America is attested by fossils found in Mexico, a region with Pleistocene records not only for gray wolves and red wolves (*Canis rufus*) but also for the larger *Aenocyon dirus* (Bravo-Cuevas et al., 2018; Ceballos et al., 2010; Hodnett et al., 2009) and the similar-sized *P. troglodytes* (although the temporal and spatial coexistence with this species is unclear, see Schubert et al., 2019).

Assuming that the extinction of different-sized hypercarnivore predators can be directly related to the extinction of the megaherbivores after the Pleistocene (Berta, 1987, 1988), the same reason could also explain why the smaller bush dog was the only South-American hypercarnivorous canid to cross the Pleistocene–Holocene boundary. There are no data to confirm how exactly the process of extinction of megafauna has occurred in the Lagoa Santa region, but a study conducted in the Brazilian Pampas region showed that, after a major extinction event of megaxenarthrans, smaller rodents and carnivorans became the most abundant mammals in Holocene deposits (Lopes et al., 2020). Modern large canids are usually associated with habitats in which prey are at least abundant (e.g., Ethiopian wolves, *Canis simensis*) and, more generally, abundant and large (e.g., painted dogs, gray wolves, Sillero-Zubiri, 2009). Considering the size and hunting habits of Pleistocene Cerdocyonina, Berta (1987) noted that larger, pack-hunting 'wolflike' forms (i.e., *Protocyon*, *Theriodictis*) became extinct along with the

megaherbivores, while smaller, 'foxlike' solitary hunters (i.e., *Cerdocyon*, *Lycalopex*), increased in diversity in the Pleistocene–Holocene transition. The bush dog has a mixture of these traits: it is a hypercarnivorous pack-hunter but with fox size, and can deal with small prey, as observed today.

Hypercarnivory in canids is correlated to an increase of body size and the specialization on large prey with, at least, half their body weight (Van Valkenburgh, 2007), a trend observed in both living and extinct lineages (Van Valkenburgh, 1991; Van Valkenburgh et al., 2004). The bush dog is the only extant small-sized hypercarnivorous canid, and it could be precisely this trait that led to its survival through the Pleistocene–Holocene boundary. Three of the four species of extant hypercarnivorous canids are not only larger than their sister species, but also the larger canids in their ecosystems (Castelló, 2018; Sillero-Zubiri, 2009). The only exception is the small-bodied bush dog, smaller than most sympatric, non-hypercarnivorous species (Castelló, 2018; Chavéz et al., 2022; Sillero-Zubiri, 2009).

CONCLUSIONS

Although superficially similar, the skull of *Speothos pacivorus* bears considerable differences when compared with that of the bush dog, especially regarding the proportions of the rostrum and braincase, the width of the cranium, the morphology of the molars M1 and m2, and the presence of a well-developed M2, which sums with differences in postcranial elements reported before. Our quantitative data from the GMM gives further support to the descriptive information, and we therefore argue the 'conventional view' of *S. pacivorus* and *S. venaticus* as different species.

Both species performed very similarly in all tested extrinsic FEA scenarios, suggesting similar biting movements to capture prey. The coexistence of these similarly specialized hypercarnivorous canids in both space and time could be explained by a richer community of prey, already described to the Lagoa Santa Karst. A better performance of the bush dog in hunting smaller prey than *S. pacivorus* and other larger hypercarnivores from the BIR might explain its survival through the Pleistocene–Holocene boundary. This hypothesis could also clarify one of the most remarkable characters of the bush dog: its small size, unique among living hypercarnivorous canids.

AUTHOR CONTRIBUTIONS

JVR (Conceptualization, FEA, formal analysis, data curation, investigation, writing original draft), GSF (Conceptualization, CT scanning, investigation, review and editing final draft), FAM (GMM, formal analysis, data curation, investigation, review and editing final draft), CK (CT scanning, data curation, investigation, review and editing final draft), PLG (investigation, review and editing final draft), CG (CT scanning, review and editing final draft), MCC (investigation, review and editing final draft), and FCM (project administration, conceptualization, investigation, review and editing final draft). All authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY STATEMENT

The high-resolution images of thin sections used in this study are available on Morphosource. *Speothos pacivorus* NHMD:211341 available at https://www.morphosource.org/concern/media/000616850?locale=en; *Speothos venaticus* SMNS-Z-MAM-019136 available at https://www.morphosource.org/concern/media/000616967?locale=en.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

ORCID

Juan V. Ruiz http://orcid.org/0000-0002-1482-1286
Gabriel S. Ferreira http://orcid.org/0000-0003-1554-8346
Fabio A. Machado http://orcid.org/0000-0002-0215-9926
Christina Kyriakouli http://orcid.org/0000-0002-9178-0238
Pedro L. Godoy http://orcid.org/0000-0003-4519-5094
Carsten Gundlach http://orcid.org/0000-0002-2895-1882
Mariela C. Castro http://orcid.org/0000-0002-5734-9639
Felipe C. Montefeltro http://orcid.org/0000-0001-6519-8546

SUPPLEMENTARY FILES

Supplementary files are available for this article for free at www.tandfonline.com/UJVP, with institutional abbreviations, list of analyzed specimens, skull measurements, GMM landmarks, and supplementary figures available in File S1; GMM dataset available in File S2; GMM commented script on File S3. The CT data are available at Morpho Source database (see Data Availability Statement).

LITERATURE CITED

Abràmoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International*, *11*(7), 36–42.

Adams, D., Collyer, M., Kaliontzopoulou, A., & Baken, E. (2019). Geomorph: geometric morphometric analyses of 2D/3D landmark data. *R package version 3.2, 1*. See: https://cran.r-project.org/package=geomorph

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46.

Auler, A. S. (2020). History of research in the Lagoa Santa Karst. In A. S. Auer, & P. Pessoa (Eds.), *Lagoa Santa Karst: Brazil's Iconic Karst Region* (pp. 1–11). Springer Nature.

Beisiegel, B. D. M. (1999). *Contribuição ao estudo da história natural do cachorro do mato, Cerdocyon thous, e do cachorro vinagre*, Speothos venaticus. Unpublished Doctoral thesis. São Paulo, Brazil: Universidade de São Paulo, 1-100.

Beisiegel, B. D. M., & Zuercher, G. L. (2005). Speothos venaticus. *Mammalian Species*, *783*(1), 1–6. doi:10.1644/783.1

Berta, A. (1984). The pleistocene bush dog *Speothos pacivorus* (Canidae) from the Lagoa Santa caves, Brazil. *Journal of Mammalogy*, *65*(4), 549–559. doi:10.2307/1380837

Berta, A. (1987). Origin, diversification, and zoogeography of the South American Canidae. *Fieldiana Zoology*, *39*, 455–471.

Berta, A. (1988). *Quaternary evolution and biogeography of the large South American Canidae (Mammalia, Carnivora), Vol. 132*. Univ of California Press.

Boitani, L., Phillips, M., & Jhala, Y. (2023). *Canis lupus* (amended version of 2018 assessment). *The IUCN Red List of Threatened Species* 2023: e.T3746A247624660. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T3746A247624660.en. Accessed on 07 February 2024.

Bravo-Cuevas, V. M., & Jiménez-Hidalgo, E. (2018). Advances on the paleobiology of late Pleistocene mammals from central and southern Mexico. In G. Huard, & J. Gareau (Eds.), *The Pleistocene: Geography, Geology, and Fauna* (pp. 277–314). Nova Science Publishers.

Cartelle, C. (2020). Cave Paleontology in the Lagoa Santa Karst. In A. S. Auer, & P. Pessoa (Eds.), *Lagoa Santa Karst: Brazil's Iconic Karst Region* (pp. 209–225). Springer Nature.

Castelló, J. R. (2018). *Canids of the world: wolves, wild dogs, foxes, jackals, coyotes, and their relatives*. Princeton University Press, 1-331.

Ceballos, G., Arroyo-Cabrales, J., & Ponce, E. (2010). Effects of Pleistocene environmental changes on the distribution and community structure of the mammalian fauna of Mexico. *Quaternary research*, *73*(3), 464–473. doi:10.1016/j.yqres.2010.02.006

Chamoli, U., & Wroe, S. (2011). Allometry in the distribution of material properties and geometry of the felid skull: why larger species may need to change and how they may achieve it. *Journal of Theoretical Biology*, *283*(1), 217–226. doi:10.1016/j.jtbi.2011.05.020

Chavez, D. E., Gronau, I., Hains, T., Dikow, R. B., Frandsen, P. B., Figueiró, H. V., … Wayne, R. K. (2022). Comparative genomics uncovers the evolutionary history, demography, and molecular adaptations of South American canids. *Proceedings of the National Academy of Sciences*, *119*(34), e2205986119. doi:10.1073/pnas.2205986119

Dantas, M. A. T., Bernardes, C., Asevedo, L., Rabito Pansani, T., De Melo França, L., Santos De Aragão, W., … Ximenes, C. (2022). Isotopic palaeoecology (δ 13C) of three faunivores from Late Pleistocene of the Brazilian intertropical region. *Historical Biology*, *34*(3), 507–514. doi:10.1080/08912963.2021.1933468

DeMers, A. C. (2023). Functional Significance of the Mandible, Tooth Roots, and Tooth Crowns, and their Implications for Fossil Dietary Inference. Doctoral dissertation. Columbus, EUA: The Ohio State University, 68-118.

DeVries, R. P., Sereno, P. C., Vidal, D., & Baumgart, S. L. (2022). Reproducible digital restoration of fossils using Blender. *Frontiers in Earth Science*, *10*, 833379. doi:10.3389/feart.2022.833379

Di Bitetti, M. S., Di Blanco, Y. E., Pereira, J. A., Paviolo, A., & Pírez, I. J. (2009). Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and pampas foxes (Lycalopex gymnocercus). *Journal of Mammalogy*, *90*(2), 479–490. doi:10.1644/08-MAMM-A-113.1

Diersing, V. E., & Wilson, D. E. (2017). Systematic status of the rabbits *Sylvilagus brasiliensis* and *S. sanctaemartae* from northwestern South America with comparisons to Central American populations. *Journal of Mammalogy*, *98*(6), 1641–1656. doi:10.1093/jmammal/gyx133

Drake, A. G., & Klingenberg, C. P. (2008). The pace of morphological change: historical transformation of skull shape in St Bernard dogs. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1630), 71–76. doi:10.1098/rspb.2007.1169

Drumheller, S. K., Darlington, J., & Vliet, K. A. (2019). Surveying death roll behavior across Crocodylia. *Ethology Ecology & Evolution*, *31*(4), 329–347. doi:10.1080/03949370.2019.1592231

Evans H. E., & de Lahunta A. (2012). *Miller's Anatomy of the Dog*, 4th edn. Philadelphia: W. B. Saunders, 1-851.

Figueirido, B., Lautenschlager, S., Pérez-Ramos, A., & Van Valkenburgh, B. (2018). Distinct predatory behaviors in scimitar-and dirk-toothed sabertooth cats. *Current Biology*, *28*(20), 3260–3266. doi:10.1016/j.cub.2018.08.012

Fleck, D. W., & Voss, R. S. (2016). Indigenous knowledge about the greater long-nosed armadillo, *Dasypus kappleri* (Xenarthra: Dasypodidae) in northeastern Peru. *Edentata*, *17*, 1–7.

Fowler, N. L., Petroelje, T. R., Kautz, T. M., Svoboda, N. J., Duquette, J. F., Kellner, K. F., … Belant, J. L. (2022). Variable effects of wolves on niche breadth and density of intraguild competitors. *Ecology and Evolution*, *12*(2), e8542. doi:10.1002/ece3.8542

Garcia-Perea, R. (1996). Patterns of postnatal development in skulls of lynxes, genus *Lynx* (Mammalia: Carnivora). *Journal of Morphology*, 229(3), 241–254.doi:10.1002/(SICI)1097-4687(199609)229:3<241::AID-JMOR1>3.0.CO;2-1

Gaubert, P., & Antunes, A. (2005). Assessing the taxonomic status of the Palawan pangolin *Manis culionensis* (Pholidota) using discrete morphological characters. *Journal of Mammalogy*, 86(6), 1068–1074. doi:10.1644/1545-1542(2005)86[1068:ATTSOT]2.0.CO;2

Ghaskadbi, P., Das, J., Mahadev, V., & Habib, B. (2021). First record of mixed species association between dholes and a wolf from Satpura Tiger Reserve, India. *Canid Biology & Conservation*, 23(4), 15–17.

Gudinho, F. S., & Weksler, M. (2021). On the dental formulae of Brazilian terrestrial Carnivora (Mammalia). *Anais da Academia Brasileira de Ciências*, 93(3), e20191384. doi:10.1590/0001-3765202120191384

Heptner, V. G., & Naumov, N. P. (1998). Genus *Cuon* Hodgson, 1838. In V. G. Heptner, & N. P. Naumov (Eds.), *Mammals of the Soviet Union. Vol. II. Part 1A: Sirenia and Carnivora (Sea Cows, Wolves, and Bears)* (pp. 566–586). Smithsonian Institution and National science Foundation.

Hodnett, J. P. M., Mead, J. I., & Baez, A. (2009). Dire wolf, *Canis dirus* (Mammalia; Carnivora; Canidae), from the late Pleistocene (Rancholabrean) of east-central Sonora, Mexico. *The Southwestern Naturalist*, 54(1), 74–81. doi:10.1894/CLG-12.1

Holten, B., & Sterll, M. (2000). The Danish naturalist Peter Wilhelm Lund (1801-80): Research on early man in Minas Gerais. *Luso-Brazilian Review*, 33–45.

Holten B., & Sterll M. (2011). *Peter Wilhelm Lund e as grutas com ossos em Lagoa Santa*. Belo Horizonte: Editora UFMG, 1-336.

Jacob, T., Diniz, D., Kerber, L., Dentzien-Dias, P., & Francischini, H. (2024). A large-sized mammalian coprolite containing ground sloth osteoderms from the Upper Pleistocene Touro Passo Formation of Brazil. *Journal of South American Earth Sciences*, 133, 104715. doi:10.1016/j.jsames.2023.104715

Kamler, J. F., Songsasen, N., Jenks, K., et al. (2015). *Cuon alpinus. The IUCN Red List of Threatened Species*: e.T5953A72477893. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T5953A72477893.en. Accessed on 07 February 2024.

Kleiman, D. G. (1972). Social behavior of the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. *Journal of Mammalogy*, 53(4), 791–806. doi:10.2307/1379214

Kozlowski, A. J., Gese, E. M., & Arjo, W. M. (2008). Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. *The American Midland Naturalist*, 160(1), 191–208. doi:10.1674/0003-0031(2008)160[191:NOARPB]2.0.CO;2

Kraglievich, L. (1930). Craneometría y clasificación de los canidos sudamericanos especialmente los Argentinos actuales y fósiles. *Physis*, 10, 35–73.

Langguth, A. (1980). El origen del genero *Speothos* y la evolución hacia *Speothos venaticus*. In*: Anales de I Reunion Iberoamericana Zoologia de Vertebrados 1977*. La Rabida, 587-600.

Lima, E. D. S., Jorge, R. S. P., & Dalponte, J. C. (2009). Habitat use and diet of bush dogs, *Speothos venaticus*, in the Northern Pantanal, Mato Grosso, Brazil. *Mammalia*, 73(1), 13–19.

Lima, E. D. S., DeMatteo, K. E., Jorge, R. S., Jorge, M. L. S., Dalponte, J. C., Lima, H. S., & Klorfine, S. A. (2012). First telemetry study of bush dogs: home range, activity and habitat selection. *Wildlife Research*, 39(6), 512–519. doi:10.1071/WR11176

Lopes, R. P., Pereira, J. C., Kerber, L., & Dillenburg, S. R. (2020). The extinction of the Pleistocene megafauna in the Pampa of southern Brazil. *Quaternary Science Reviews*, 242, 106428. doi:10.1016/j.quascirev.2020.106428

Lösel, P. D., van de Kamp, T., Jayme, A., Ershov, A., Faragó, T., Pichler, O., … Heuveline, V. (2020). Introducing Biomedisa as an open-source online platform for biomedical image segmentation. *Nature Communications*, 11(1), 5577. doi:10.1038/s41467-020-19303-w

Lund, P. W. ((1839).Coup. d'oeil sur les espèces éteintes de Mammifères du Brésil, extrait de quelques mémoires présentés à l'Académie Royale des Sciences de Copenhague. *Annales des Sciences Naturelles*, 11, 214–234.

Lund, P. W. (1840). Blik paa Brasiliens Dyreverden för sidste jordomvaeltning. Tredje Afhandling: Fortsaettelse af Pattedyrene. *Danske Videnskabernes Selskabs Naturvidenskabelig og Mathematisk Afdelin*, 8, 27–144.

Lund, P. W. (1842). Blik paa Brasiliens Dyreverden för Sidste Jordomvaeltning. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelig og Mathematisk Afdeling*, 9, 201.

Lund, P. W. (1842/43). Modet den 17 de Juni. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 6, 77–82.

Macdonald D. W., Loveridge A. J., & Atkinson R. P. (2004). A comparative study of side-striped jackals in Zimbawe: the influence of habitat and congeners. In: Macdonald DW, Sillero-Zubiri C (eds.) *Biology and Conservation of Wild Canids*. Oxford University Press, 255-270.

Machado, F. A., & Teta, P. (2020). Morphometric analysis of skull shape reveals unprecedented diversity of African Canidae. *Journal of Mammalogy*, 101(2), 349–360. doi:10.1093/jmammal/gyz214

Mivart, S. G. J. (1890). *Dogs, jackals, wolves, and foxes: a monograph of the Canidae*. RH Porter.

Montefeltro, F. C., Lautenschlager, S., Godoy, P. L., Ferreira, G. S., & Butler, R. J. (2020). A unique predator in a unique ecosystem: modelling the apex predator within a Late Cretaceous crocodyliform-dominated fauna from Brazil. *Journal of Anatomy*, 237(2), 323–333. doi:10.1111/joa.13192

Mouchard A. (2019). *Etimología de los nombres científicos de los mamíferos de Argentina*. Buenos Aires: Fundación de Historia Natural Félix de Azara, 1-236.

Novaro A. J., Funes M. C., Jiménez J. (2004). Patagonian Foxes: Selection for introduced prey and conservation of culpeo and chilla foxes in Patagonia. In: Macdonald DW, Sillero-Zubiri C (eds.) *Biology and conservation of wild canids*. Oxford University Press, 243-254.

Okřinová I. (2013). *Paleoecology of fossil species of canids (Carnivora, Mammalia)*. Unpublished Master dissertation. České Budějovice: University of South Bohemia, 1-53.

Oliveira, ÉV, Prevosti, F. J., & Pereira, J. C. (2005). *Protocyon troglodytes* (Lund)(Mammalia, Carnivora) in the Late Pleistocene of Rio Grande do Sul and their paleoecological significance.

Paula-Couto C. (1979) *Tratado de Paleomastozoologia*. Rio de Janeiro: Academia Brasileira de Ciências, 1-590.

Perini, F. A., Russo, C. A. M., & Schrago, C. G. (2010). The evolution of South American endemic canids: a history of rapid diversification and morphological parallelism. *Journal of Evolutionary Biology*, 23(2), 311–322. doi:10.1111/j.1420-9101.2009.01901.x

Petroelje, T. R., Kautz, T. M., BeyerJrD. E., & Belant, J. L. (2021). Interference competition between wolves and coyotes during variable prey abundance. *Ecology and Evolution*, 11(3), 1413–1431. doi:10.1002/ece3.7153

Petrucci, M., Romiti, S., & Sardella, R. (2012). The Middle-Late Pleistocene *Cuon* Hodgson, 1838 (Carnivora, Canidae) from Italy. *Bollettino della Società Paleontologica Italiana*, 51(2), 138.

Porton, I. J., Kleiman, D. G., & Rodden, M. (1987). Aseasonality of bush dog reproduction and the influence of social factors on the estrous cycle. *Journal of Mammalogy*, 68(4), 867–871. doi:10.2307/1381569

Prevosti, F. J. (2010). Phylogeny of the large extinct South American canids (Mammalia, Carnivora, Canidae) using a "total evidence" approach. *Cladistics*, 26(5), 456–481. doi:10.1111/j.1096-0031.2009.00298.x

Prevosti, F. J., & Palmqvist, P. (2001). Análisis ecomorfológico del cánido hipercarnívoro *Theriodictis platensis* Mercerat (Mammalia, Carnivora), basado en un nuevo ejemplar del Pleistoceno de Argentina. *Ameghiniana*, 38(4), 375–384.

Prevosti, F. J., Zurita, A. E., & Carlini, A. A. (2005). Biostratigraphy, systematics, and paleoecology of *Protocyon* Giebel, 1855 (Carnivora, Canidae) in South America. *Journal of South American Earth Sciences*, 20(1-2), 5–12. doi:10.1016/j.jsames.2005.05.005

Prevosti, F. J., & Rincón, A. D. (2007). A new fossil canid assemblage from the late Pleistocene of northern South America: the canids of the Inciarte asphalt pit (Zulia, Venezuela), fossil record and biogeography. *Journal of Paleontology*, 81(5), 1053–1065. doi:10.1666/pleo05-143.1

Prevosti, F. J., Ubilla, M., & Perea, D. (2009). Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and paleoecological remarks. *Historical Biology*, 21(1-2), 79–89. doi:10.1080/08912960903249337

Prevosti, F. J., Santiago, F., Prates, L., & Salemme, M. (2011). Constraining the time of extinction of the South American fox *Dusicyon avus* (Carnivora, Canidae) during the late Holocene. *Quaternary International*, 245(2), 209–217. doi:10.1016/j.quaint.2011.02.010

Prevosti, F. J., & Schubert, B. W. (2013). First taxon date and stable isotopes (δ13C, δ15N) for the large hypercarnivorous South American canid *Protocyon troglodytes* (Canidae, Carnivora). *Quaternary International*, 305, 67–73. doi:10.1016/j.quaint.2012.07.003

Prevosti F. J., Forasiepi, A. M. (2018). South American fossil carnivorans (order Carnivora). In Prevosti F. J., Forasiepi, A. M. (eds) *Evolution of South American Mammalian Predators During the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies.* Springer Nature, 85-136.

Ripoll, M. P., Perez, J. V. M., Serra, A. S., Tortosa, J. E. A., & Montanana, I. S. (2010). Presence of the genus *Cuon* in upper Pleistocene and initial Holocene sites of the Iberian Peninsula: new remains identified in archaeological contexts of the Mediterranean region. *Journal of Archaeological Science*, 37(3), 437–450. doi:10.1016/j.jas.2009.10.008

Rocha, R. G., Goncalves, J., Tarroso, P., Monterroso, P., & Godinho, R. (2022). Multiple lines of ecological evidence support ancient contact between the African wild dog and the dhole. *Frontiers in Ecology and Evolution*, 10, 803822. doi:10.3389/fevo.2022.803822

Rohlf, F. J. (2015). The tps series of software. *Hystrix*, 26(1), 9–12.

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, 39(1), 40–59. doi:10.2307/2992207

Ruiz, J. V., Ferreira, G. S., Lautenschlager, S., Castro, M. C., & Montefeltro, F. C. (2022). Different, but the same: Inferring the hunting behaviour of the hypercarnivorous bush dog (*Speothos venaticus*) through finite element analysis. *Journal of Anatomy*, 242(4), 553–567. doi:10.1111/joa.13804

Ruiz, J. V., Kyriakouli, C., Hansen, K., Gundlach, C., Ferreira, G. S., Machado, F. A., Godoy, P. L., Castro, M. C., & Montefeltro, F. C. (2024). The Fossils of *Speothos pacivorus* (Carnivora: Canidae) at the Peter Lund/Quaternary Collection of the Natural History Museum of Denmark. *MorphoMuseuM*, e229. doi: 10.18563/journal.m3.229

Ruiz-Ramoni, D., Wang, X., & Rincón, A. D. (2022). Canids (Caninae) from the past of Venezuela. *Ameghiniana*, 59(1), 97–116. doi:10.5710/AMGH.16.09.2021.3448

Schlager, S. (2017). Morpho and Rvcg–Shape Analysis in R: R-Packages for geometric morphometrics, shape analysis and surface manipulations. In G. Zheng, S. Li, & G. Székely (Eds.), *Statistical shape and deformation analysis* (pp. 217–256). Academic Press.

Schubert, B. W., Chatters, J. C., Arroyo-Cabrales, J., Samuels, J. X., Soibelzon, L. H., Prevosti, F. J., … Erreguerena, P. L. (2019). Yucatán carnivorans shed light on the Great American Biotic Interchange. *Biology Letters*, 15(5), 20190148. doi:10.1098/rsbl.2019.0148

Segura, V. (2013). Skull ontogeny of *Lycalopex culpaeus* (Carnivora: Canidae): description of cranial traits and craniofacial sutures. *Mammalia*, 77(2), 205–214. doi:10.1515/mammalia-2012-0028

Segura, V., & Prevosti, F. (2012). A quantitative approach to the cranial ontogeny of *Lycalopex culpaeus* (Carnivora: Canidae). *Zoomorphology*, 131(1), 79–92. doi:10.1007/s00435-012-0145-4

Segura, V., Cassini, G. H., & Prevosti, F. J. (2021). Evolution of cranial ontogeny in south American canids (carnivora: Canidae). *Evolutionary Biology*, 48(2), 170–189. doi:10.1007/s11692-020-09529-3

Sharp, A. C. (2015). Comparative finite element analysis of the cranial performance of four herbivorous marsupials. *Journal of Morphology*, 276(10), 1230–1243. doi:10.1002/jmor.20414

Sillero-Zubiri, C. (2009). Family Canidae. In D. E. Wilson, & R. A. Mittermeier (Eds.), *Handbook of Mammals of the World Volume 1 - Carnivores* (pp. 352–446). Lynx Edicions.

Slater, G. J., & Van Valkenburgh, B. (2009). Allometry and performance: the evolution of skull form and function in felids. *Journal of evolutionary biology*, 22(11), 2278–2287. doi:10.1111/j.1420-9101.2009.01845.x

Slater, G., Dumont, E. R., & Van Valkenburgh, B. (2009). Implications of predatory specialization for cranial form and function in canids. *Journal of Zoology*, 278(3), 181–188. doi:10.1111/j.1469-7998.2009.00567.x

Van Valkenburgh, B. (1991). Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. *Paleobiology*, 17(4), 340–362. doi:10.1017/S0094837300010691

Van Valkenburgh, B. (2007). Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and comparative biology*, 47(1), 147–163. doi:10.1093/icb/icm016

Van Valkenburgh, B., Wang, X., & Damuth, J. (2004). Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, 306(5693), 101–104. doi:10.1126/science.1102417

Vieira, C. (1948). Carnívoros do estado de São Paulo. *Arquivos de Zoologia*, 5, 135–176. doi:10.11606/issn.2176-7793.19485135-176

Wallace, R. B., Painter, R. E., & Saldania, A. (2002). An observation of bush dog (*Speothos venaticus*) hunting behaviour. *Mammalia (Paris)*, 66(2), 309–311.

Wayne, R. K. (1986). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution*, 40(2), 243–261. doi:10.2307/2408805

Winge, H. (1895). Jordfundne og nulevende Rovdyr ("Carnivora") fra Lagoa Santa, Minas Geraes, Brasilien, med Udsigt over Rovdyrenes indbyrdes Slaegtskab, af Herluf Winge. *E Museo Lundii*, 2(4), 1–103.

Zrzavý, J., Duda, P., Robovský, J., Okřinová, I., & Pavelková Řičánková, V. (2018). Phylogeny of the Caninae (Carnivora): combining morphology, behaviour, genes and fossils. *Zoologica Scripta*, 47(4), 373–389. doi:10.1111/zsc.12293

Zuercher, G. L., Gipson, P. S., & Carrillo, O. (2005). Diet and habitat associations of bush dogs *Speothos venaticus* in the Interior Atlantic Forest of eastern Paraguay. *Oryx*, 39(1), 86–89. doi:10.1017/S0030605305000153

Handling Editor: Melissa Pardi.