The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2010, **159**, 988–1014. With 9 figures

Evolution and functional morphology of the frontal sinuses in Bovidae (Mammalia: Artiodactyla), and implications for the evolution of cranial pneumaticity

ANDREW A. FARKE*

Raymond M. Alf Museum of Paleontology, 1175 West Baseline Road, Claremont, CA 91711–2199, USA

Received 3 July 2008; accepted for publication 2 March 2009

The function and evolution of paranasal pneumaticity remains elusive, in part because of limited sampling and description. Here, the frontal sinuses from 62 species of bovids were investigated using X-ray computed tomography. This survey revealed hitherto undescribed diversity in the morphology of this sinus, and suggests that it was probably present in the common ancestor of Bovidae. Among extant bovids, the frontal sinuses were lost or reduced to recesses at least six different times. Quantitative analyses, when accounting for phylogeny using phylogenetically independent contrasts, did not find any link between the size or complexity of the frontal sinus and head-to-head ramming behaviour. Other analyses indicated that frontal sinus size was correlated most closely with the size of the frontal bone itself, rather than with the overall skull size or horn size. These results may be partially consistent with the hypothesis of sinuses being the result of 'opportunistic pneumatization', in which sinus size depends on the quantity of bone available for pneumatization as well as the mechanical demands placed on the skull. Additional evidence also indicates a strong phylogenetic correlation with sinus morphology, particularly with regard to the presence of paranasal diverticula, as well as the ability of sinuses to cross sutural boundaries.

doi: 10.1111/j.1096-3642.2009.00586.x

ADDITIONAL KEYWORDS: antelope – cattle – computed tomography – functional morphology – goats – opportunistic pneumatization – paranasal pneumaticity.

INTRODUCTION

Cranial sinuses, air-filled chambers resulting from the removal of bone by a pneumatic diverticulum, remain one of the most functionally enigmatic and debated structures within the vertebrate skull. Centuries of speculation have resulted in a host of functional hypotheses (see reviews in Blanton & Biggs, 1968; Blaney, 1990), although the current paradigm holds that the sinuses are simply functionless structures resulting from the interplay between bone resorption and deposition (e.g. Weidenreich, 1941; Edinger, 1950; Witmer, 1997). A number of descriptive studies have been published in support of one functional hypothesis or another, but quantitative and phylogenetically informed analyses have been comparatively rare. Furthermore, most quantitative studies have focused on primates, and thus represent only a limited phylogenetic diversity. The most comprehensive quantitative analysis of sinus morphology to date, in terms of number of taxa, included only 14 closely related species (Koppe & Nagai, 1999).

Hypotheses about sinus function are difficult to test without first obtaining information on sinus variation within and between species and higher level clades. With the exception of data for some primates, most information on variation in sinus form is purely qualitative or absent. In the present study, this situation will be addressed for the frontal sinuses of bovid mammals.

Bovidae, the clade of horned artiodactyls including cattle, sheep, goats, antelope, and their allies, is known to have extremely variable morphology of the

*E-mail: afarke@webb.org

frontal sinuses. These paranasal sinuses occupy the frontal bone, and occasionally extend up into the horncores. Their presence, size, and internal complexity are extremely variable, and thus these attributes have been used as characters for cladistic analyses (e.g. Gentry, 1992; Vrba & Schaller, 2000). Some authors (Schaffer, 1968; Schaffer & Reed, 1972) have suggested that the enlarged frontal sinuses of species such as bighorn sheep are an adaptation for head butting or ramming (common behaviours in many bovids), developed in order to protect the brain from impacts to the horns. Thus, the sinuses of bovids are a topic of considerable interest both from phylogenetic and functional viewpoints; however, morphological variability in the sinuses of bovids has been documented in only a handful of (mostly domesticated) taxa.

On a broader scale, the tremendous diversity of the frontal sinuses in bovids indicates their importance for understanding the evolution of paranasal pneumaticity. Numerous studies have documented the appearance or loss of certain paranasal sinuses, particularly for the maxillary sinus within cercopithecoid primates (e.g. Rae & Koppe, 2003; Rae, 2008). Yet hypotheses on factors contributing to the origin or loss of a sinus have been difficult to test, because of a lack of quantitative data as well as the limited taxonomic scope of most previous investigations.

If sinuses are primarily functionless structures, resulting as a by-product of the removal of structurally unnecessary bone within the skull (Weidenreich, 1924; Witmer, 1997), it is predicted that a strong relationship should exist between the size of the frontal bone and the size of the frontal sinus in bovids. It is assumed that, with some variation resulting from the loads placed upon the skull, a relatively larger frontal (as compared with skull size) should have a greater proportion of 'structurally unnecessary' bone. The relationship between the size of the frontal sinus and size of the skull and horns should be much less strong than that with the frontal bone itself. Farke (2007) found just such a relationship between frontal bone size and frontal sinus size in the hartebeest antelope, *Alcelaphus buselaphus*, but, no large-scale statistical analysis has yet been undertaken. Bovidae is a clade particularly suited for testing hypotheses of sinus function and evolution for several reasons. First, bovids exhibit a wide range of adult body sizes: from 3 kg in *Madoqua* up to 1200 kg in *Bubalus* (Silva & Downing, 1995). Second, bovids display a diversity of cranial morphologies with concomitant diversity of craniocentric behaviours, including display, head-butting and horn-rubbing. Finally, clade-wide phylogenies are available, allowing the use of phylogenetically-based analytical methods, such as independent contrasts.

This contribution will describe the frontal sinus anatomy across Bovidae, apply quantitative approaches to study the factors influencing frontal sinus morphology, and examine these data within a phylogenetic and behavioural context. It presents the largest quantitative examination of paranasal pneumaticity ever attempted.

Abbreviations: AMNH, American Museum of Natural History (New York, USA); cd, cornual diverticulum; fr, frontal recess; fs, frontal sinus; ls, lacrimal sinus; ms, midline strut; mxs, maxillary sinus; o, orbit; ss, supraorbital strut; YPM, Yale Peabody Museum of Natural History (New Haven, CT, USA).

PREVIOUS WORK ON BOVIDS

Descriptions of the frontal sinuses (and indeed any of the cranial sinuses) of bovids are scattered sparsely throughout the literature. Most publications typically note only the presence or absence of frontal sinuses, with little or no comment on their form. With few exceptions, the frontal sinuses of bovid taxa are generally unillustrated, unquantified, and undescribed.

The morphology of the frontal sinuses has been well-described for domesticated taxa, including domesticated sheep (*Ovis aries*), goats (*Capra hircus*), and cattle (*Bos taurus*), from the early days of comparative study (Zuckerkandl, 1887; Paulli, 1900). Heyne & Schumacher (1967) measured the volume of the cranial sinuses in a sample of domesticated sheep, *Ovis aries*, by filling the sinuses with wax. Their study was one of only a handful to quantify sinus volume in nonprimates. No significant correlation was found between the volume of the frontal sinus and various other cranial measurements.

One of the only comprehensive descriptions of frontal sinus morphology in nondomesticated bovids was undertaken by Schaffer & Reed (1972), for Caprinae, the clade including sheep and goats. Schaffer and Reed posited that the enlarged frontal sinuses were associated with an 'advanced' skull shape, in which the horncores were placed more caudally on the braincase relative to those animals that displayed a 'primitive' skull shape. Also, it was noted that the complexity of the sinuses (i.e. the number of bony septa subdividing the sinuses) varied between taxa and sexes, and the extent of the cornual diverticulum of the frontal sinus varied similarly. Finally, Schaffer and Reed suggested that the morphology of the sinuses in caprines is an adaptation for protecting the skull from the forces of impact during fighting. Specifically, they inferred that a blow to the horns could be translated into deformation of the calvaria. This deformation results in a shear within the brain tissue, with obvious deleterious effects. This hypothesis was built on an observation by Geist (1966), who

noted that many animals engaging in head-butting or ramming behaviour have a pneumatized skull roof. Alternatively, it might be suggested that thickened frontals are more important for protecting the brain, by separating the brain from the forces applied to the skull, and that the frontal sinuses are only coincidental. Kingdon (1982a, b), who documented, at least in passing, the presence and extent of the frontal sinuses in a variety of African bovids, also hypothesized that the frontal sinuses buffer the brain and contents of the orbit from impact forces to the horns.

Jaslow (1987) analysed a suite of measurements believed to be correlated with the mode of horn use (e.g. horn clashing vs. head butting) for sheep, goats and their close relatives. The maximum cross-sectional area of the frontal sinus was measured in lateral view from radiographs. Jaslow found that sinus area (a proxy for the total size of the sinus) correlated neither with skull size nor with the calculated impact force to the horns. An alternative hypothesis was proposed, that 'the size of the sinus is simply correlated with relative growth rates of the inner and outer tables of the frontal bone' (Jaslow, 1987: 43). Because brain size scales negatively with skull size, a thicker frontal bone was inferred to result, and thus there is more space for a frontal sinus. Another alternative hypothesis is that the thickness of the frontal bone was related to the dimensions of the horns: this was not tested. Additionally, no adjustments were made for phylogenetic effects. Although the results of Jaslow's study contradict the oft-cited hypothesis of Schaffer & Reed (1972), that increased frontal sinus size is associated with greater forces to the skull during horn use, and the true meaning of the results is debatable, given the shortcomings of the methodology available at the time of study.

Frontal sinus occurrence and morphology are often used as characters for phylogenetic analyses of extant and extinct bovids. Vrba (1979) was one of the first to apply cladistic methods to bovids. In her analysis of alcelaphine taxa, she included a character for the frontal sinus, either as 'absent to poorly developed' or 'extensive (i.e. past supraorbital canals and into orbital rims) with a single large smooth-walled sinus which extends into basal horn core'. She considered the latter condition to be autapomorphic for alcelaphines. Gentry (1992) scored the frontals as '(a) without, (b) with moderate or (c) with extensive internal sinuses'. Vrba & Schaller's (2000) analysis utilized two characters to describe the frontal sinus morphology: frontal sinus extent and the presence of bony struts within the frontal sinuses. Although these analyses represent a useful first step, they do not completely describe the morphology observed within Bovidae, nor the full range of potential characters, as outlined later in this paper.

PREDICTIONS

Enlarged and/or complex frontal sinuses are associated with ramming behaviour

Previous workers (e.g. Schaffer & Reed, 1972) have suggested that taxa exhibiting ramming behaviour may have enlarged or especially complex frontal sinuses to protect the brain, by absorbing the energy of impact, and maintain the structural integrity of the skull. If this is true, it is predicted that rammers should have sinuses that are larger, relatively more complex, and cover a greater proportion of the endocranial cavity. Ramming, rather than other bovid behaviours, such as horn clashing or stabbing, is the focus of this study, because it was assumed that this behaviour would result in the highest accelerations and compressive forces applied to the skull, and hence would result in the greatest chance of a structural manifestation in the bone of the skull, and the strongest selection for enlarged or complex sinuses.

The frontal sinus volume most closely tracks the volume of the frontal bone, rather than skull size or horn size

If sinuses are the result of 'opportunistic pneumatization', the process by which osteoclasts associated with a pneumatic epithelium remove 'unnecessary' bone, it is predicted that frontal sinus volume should more closely track the size of the frontal bone itself, rather than the overall skull size (Farke, 2007).

Phylogeny influences sinus morphology

If phylogeny is more important than cranial architecture in determining the size of the sinus (or, alternatively, if phylogeny determines the architecture that in turn controls the sinus morphology), it is predicted that any correlations should be nonsignificant, after accounting for the effects of phylogeny.

MATERIAL AND METHODS

Taxon selection

Of the 120 plus currently recognized species of extant wild bovids, 63 were sampled in this study, in order to represent the full range of body size, skull size, cranial morphology, and taxonomic variability within this clade (Figs 1, 2; Appendix 1). Skulls from individuals (shot in the wild, whenever possible) were borrowed from collections at the AMNH and YPM. Only the skulls of adult males were considered, in order to control for effects of sexual dimorphism and ontogeny. Specimens were considered adult if the third molar was fully erupted. Samples for each species were limited to a single subspecies whenever

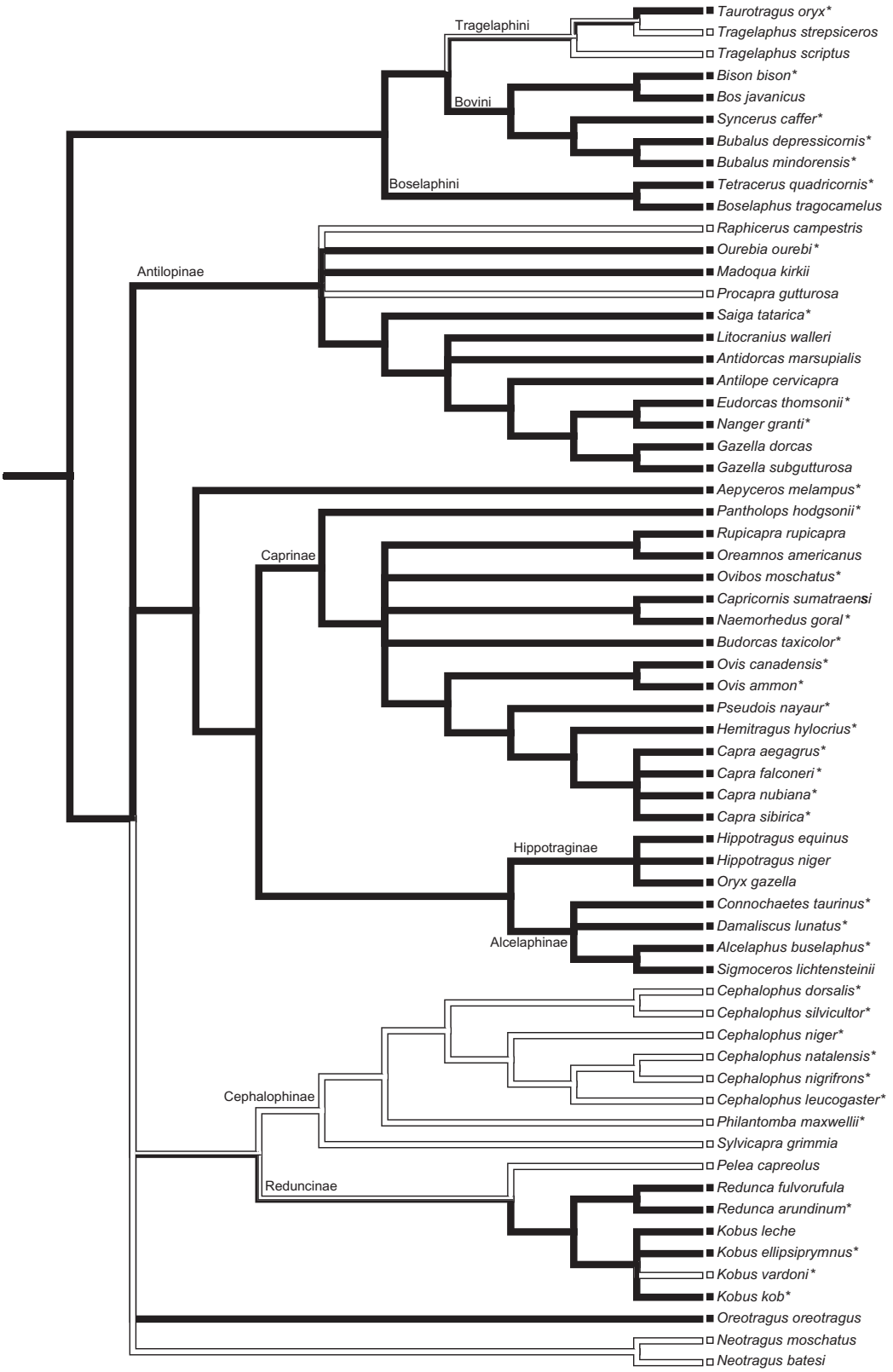

Figure 1. Phylogeny of Bovidae based on a supertree published by Fernández & Vrba (2005). Taxa with frontal sinuses are in black; taxa without sinuses are in white. States between nodes were inferred using ancestral parsimony state reconstruction. *Taxa that engage in ramming behaviour (data from Caro *et al.*, 2003).

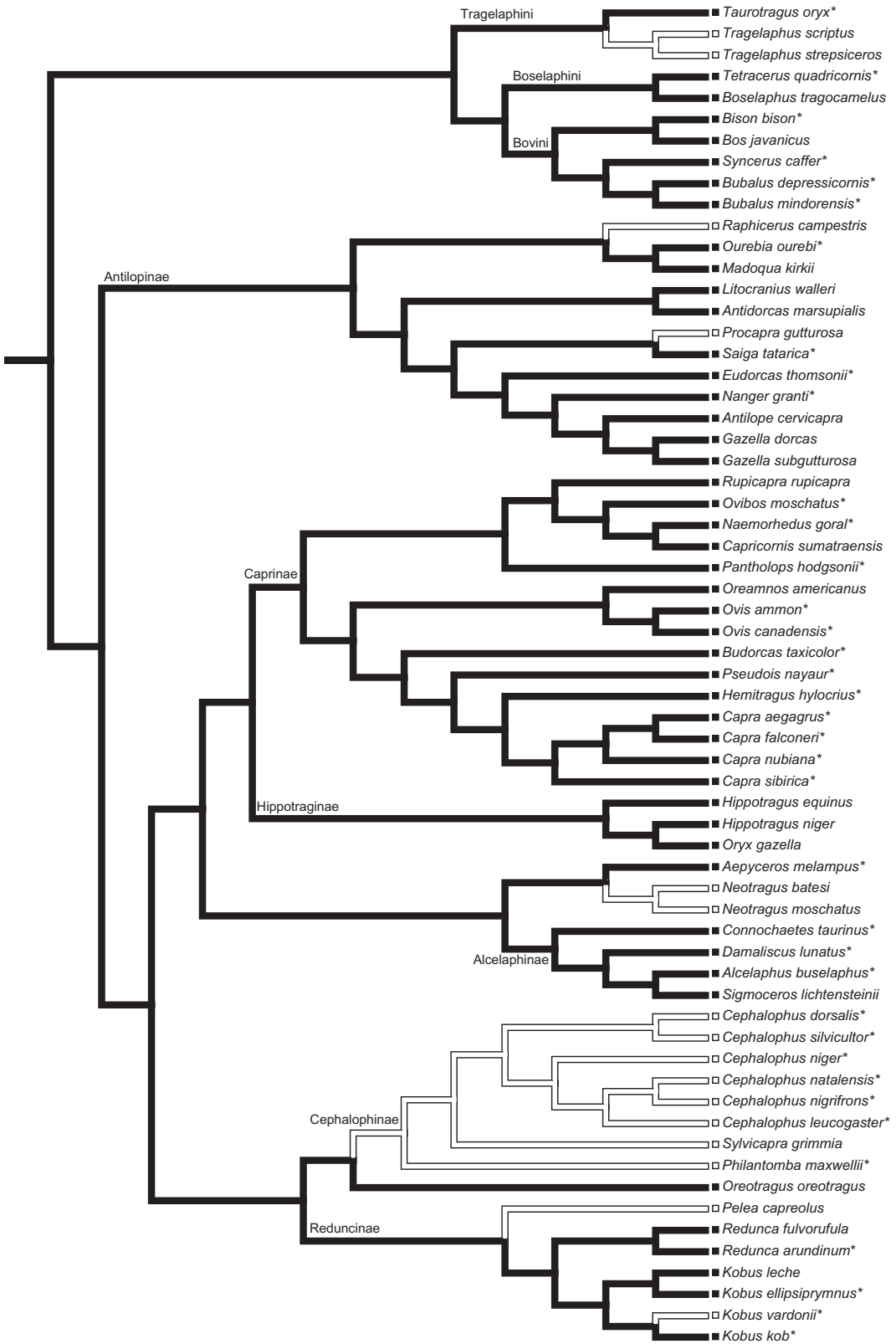

Figure 2. Phylogeny of Bovidae based on a composite supertree constructed as indicated in the text. Taxa with frontal sinuses are in black; taxa without sinuses are in white. States between nodes were inferred using ancestral parsimony state reconstruction. *Taxa that engage in ramming behaviour (data from Caro *et al.*, 2003).

possible. Most species were represented in the sample by two or three individuals.

Data acquisition

All skulls were scanned on a GE Lightspeed 16 medical computed tomography (CT) scanner. The slice spacing depended on the specimen size, but the main body of the skull (exclusive of the horns) was typically sampled with 400–600 slices. The in-plane pixel resolution also varied by specimen: specimens were reconstructed at the minimal reconstruction diameter necessary to include the entire width of the skull, exclusive of the unpneumatized portion of the horns. A lower resolution set of scans was reconstructed to include the entire extent of the horns, along with the rest of the skull. Skulls were scanned in a coronal orientation when possible, but some skulls (e.g. those of *Syncerus caffer*) were too large to scan in this orientation, and instead were scanned in the parasagittal plane.

Volumetric measurements

The CT data were exported in DICOM format and reconstructed using 3D Slicer 2.7 (http://www.slicer.org). The bone surrounding the frontal sinuses was thresholded using a modified half-maximum height protocol (Coleman & Colbert, 2007), with ten samples of the bone–air transition within the sinus measured on several slices from each specimen. After thresholding, the frontal sinuses were segmented by a combination of automatic and manual segmentation. Volumes of the reconstructed sinuses were measured to the nearest milliliter using the MeasureVol module in 3D Slicer 2.7 (Table S1). Additionally, the volume of the cornual diverticulum of the frontal sinus (the portion extending into the horncore) was measured separately from the rest of the sinus. The proximal end of the cornual diverticulum was delineated as coplanar with the burr (the prominent change of texture between the horncore and the rest of the skull) on the external surface of the base of the core.

Although linear measurements of horn dimensions (e.g. basal length and width) may capture some aspects of horn size, they are not directly comparable across all taxa because of the range of variation in horn morphology. Thus, the horn volume was used to represent horn size. The volume of the keratinous horn sheath was also defined, following a similar thresholding and segmentation protocol, and the volume of the horncore was estimated as the volume enclosed inside the hollow portion of the sheath. All volumetric measurements were converted to linear variables (in millimetres) by taking the cube roots of the original volumes.

Linear cranial measurements

A suite of external cranial measurements for each specimen was captured using digital calipers, to within 0.1 mm (see Tables S1 and S2). Additional measurements related to the coverage of the endocranial cavity by the sinuses and horns were measured from the CT data (also see Tables S1 and S2). All linear measurements were taken in millimetres.

Cranial size, instead of body mass, was the scaling variable used in this study, because skull size, and not body mass, was of most interest. As defined here, cranial size is the geometric mean of various cranial variables for each specimen. The variables selected focus on the dimensions of the tooth rows, calvaria, and splanchnocranium, excluding measurements on the horns and frontal. The horns and frontal were excluded from this geometric mean because they are the areas of focus in this study (following the recommendations of Coleman, 2008), and because of their extreme variability in size relative to the rest of the skull across taxa. Geometric means were used, rather than a standard measurement such as skull length, because they should represent a better measure of the overall size when examining a sample with variability in cranial proportions. For similar reasons, the frontal size was described using a geometric mean of the frontal maximum length, width, and thickness.

Calculation of sinus complexity

The complexity, or number of struts subdividing the chamber of the frontal sinus, was calculated in a manner analogous with the approaches used for quantifying the architecture of trabecular bone (e.g. Hildebrand & Rüegsegger, 1997; Hildebrand *et al.*, 1999). Farke (2007) found that a direct measurement of strut number did not accurately represent the density of struts within the sinus, especially for specimens that have a relatively low density of struts (as seen in many bovids). Instead, he found that a sinus complexity index (SCI) provided a better estimate. This index is calculated as strut spacing divided by the cube root of sinus volume. Strut spacing (referred to as trabecular spacing, or Tb.S., by other authors) measures the average diameter of multiple spheres fitted into the empty spaces between struts of the sinus. A sinus with relatively large spacing between struts would have a relatively high SCI, and would thus be considered to be noncomplex. A sinus with relatively small spacing between struts would have a relatively low SCI, and would thus be considered to be relatively complex. Strut spacing was calculated with the program CT Analyzer v1.7 (SkyScan, http://www.skyscan.be). Further details of this methodology are provided elsewhere (Farke, 2007).

Behavioural data

Data on the presence or absence of ramming (headbutting) behaviour were taken from the matrix published by Caro *et al.* (2003). Although data on the frequency of each behaviour is desirable, it is not available for most species.

Phylogenies and character mapping

Two alternative, but largely similar, phylogenies were used for the calculations of contrasts, and for mapping the evolution of sinus morphology (Figs 1, 2). The first was based on a supertree published by Fernández & Vrba (2005), which was trimmed to include only the taxa used in this analysis. The second supertree was assembled based on a combined molecular and morphological analysis published by Gatesy & Arctander (2000), with additional data from other studies (Rebholz & Harley, 1999; Schreiber *et al.*, 1999; Matthee & Davis, 2001; van Vuuren & Robinson, 2001; Buntjer *et al.*, 2002; Lalueza-Fox *et al.*, 2005; Willows-Munro, Robinson & Matthee, 2005; Pidancier *et al.*, 2006). The latter tree was used in order to reflect the most recent phylogenetic hypotheses concerning bovids (i.e. those published in the past 10 years), whereas the former relied on over 30-years worth of trees obtained through cladistic and noncladistic methodology. Two trees were used instead of one in order to see how robust the results were in the face of competing phylogenies. Branch lengths were assigned using the method of Nee (cited in Purvis, 1995), which, in the present data set, was found to best meet the assumption of no significant relationship between the contrast and the standard deviation (Garland, Harvey & Ives, 1992). Branch lengths provided by Fernández & Vrba (2005) were initially used for that tree, but it was found that the data violated the aforementioned assumption. Character history was traced on both trees in Mesquite v2.1 using parsimony ancestral state reconstruction.

Statistical tests and hypotheses

The influence of ramming behaviour on SCI, relative sinus volume, and coverage of the endocranium was compared between taxa divided into ramming and nonramming categories. For raw data, the two categories were compared using a Mann–Whitney *U*-test. In order to account for the effects of phylogeny, data were analyzed using the BRUNCH algorithm in the program CAIC v2.6.9, with a sign test.

Because of the strong correlation between frontal size and skull size ($r > 0.90$ in all data sets, regardless of phylogeny), partial correlation coefficients were calculated in order to better examine the relationships between skull size, frontal size, and frontal sinus size. Additionally, the relationship between sinus morphology and cranial morphology (skull size, frontal size, and horn size) was examined using reduced major-axis regression (RMA). The RMA method was chosen in order to account for the fact that the variables were both measured with error. Each variable was tested for normality using an Anderson–Darling test, and the data were log-transformed to the base 10 in order to more closely approximate a normal distribution. Independent contrasts for this analysis were calculated in the PDAP module v1.11 of Mesquite. Statistical analyses were completed in R v2.6.2, using the SMATR module v2.1. A value of 1 was added to the sinus volumes, so that logarithms could be calculated for taxa with a sinus volume of 0. Plots of the contrasts vs. standard deviation did not uncover a significant relationship ($P > 0.05$ for all variables). Additionally, a sign test was used to determine if the SCI was significantly associated with skull, horn, sinus, or frontal size.

Taxa were analyzed in two batches: one including all taxa, and a second one including only the taxa with sinuses. This was done because regardless of the quantity of bone available for pneumatization, no pneumatization should occur if a pneumatic recess from the nasal cavity is not present (outlined in greater detail in the discussion section). Thus, mixing taxa with and without sinuses could prevent a clear interpretation of the relationship between sinus size and the size of other cranial features. Therefore, it was desirable to exclude taxa without sinuses for some of the analyses.

Recognizing sinuses

Previous authors have pointed out the difficulty in distinguishing between a paranasal sinus and a paranasal recess (e.g. Rossie, 2006). A recess is simply a concavity of the nasal cavity, not associated with the active removal of bone. By contrast, the tissues associated with a paranasal sinus actively remove trabecular bone, thus resulting in an air-filled cavity placed between two layers of cortical bone. The identification of a sinus is comparatively easy for very large sinuses, but distinguishing between a sinus and a recess becomes more difficult for small sinuses or large recesses. Ideally, an ontogenetic series or soft-tissue histological sections would be needed in order to make this distinction. Unfortunately, either these data do not exist or it is not practicable to collect such data for this study. Sinuses were recognized as such in practice if they visibly and markedly impinged on the trabecular bone between the internal and external cortices of the frontal, and if they could be traced for at least a short extent between the two layers (i.e. the space was separated from the main

nasal cavity by a bony wall for at least a short distance; see Fig. 3C; Rae, 2008). Recesses were simply impressed into the internal layer of the cortex, perhaps creating a small depression, but not actually pneumatizing trabecular bone (see Fig. 3E).

QUANTITATIVE RESULTS

Behaviour and sinus morphology

The species values for sinus volumes and sinus complexity are listed in Appendix 1. The results of statistical comparisons are given in detail in Table 1. Prior to accounting for the effects of phylogeny in the sample including only taxa with sinuses, ramming and nonramming taxa differed in relative sinus volume and SCI, but not in the coverage of the endocranium. Regardless of which tree topology was used, none of these variables differed significantly between the two groups when accounting for phylogeny using the BRUNCH algorithm.

Prior to accounting for the effects of phylogeny in the entire sample (with and without sinuses), ramming and nonramming taxa differed only in cornual sinus size. This correlation only held for phylogenetically independent contrasts (PICs) based on the composite tree (although the data violated the assumption that the nodal value vs. the contrast slope was not significant; several attempts at branch-length transformation or data transformation were unsuccessful in resolving this problem).

Sinus morphology and skull morphology

For the sample including all taxa, the partial correlation coefficient of frontal sinus size and frontal size was only significant (i.e. the 95% confidence interval excluded 0, indicating a correlation between the variables) for the raw sample. When calculated from PICs, this correlation did not differ significantly from zero (Table 2).

Partial correlations between frontal sinus size and skull size, or horn size, regardless of phylogeny, were never significant (indicating a lack of correlation between the variables). For the sample including only taxa with sinuses, the partial correlation coefficients of sinus size and frontal size were always significantly different from 0, but never so for sinus size and skull size, regardless of phylogeny.

All regressions of frontal sinus volume onto frontal size, skull size, and horn size were significant, regardless of the scope of the sample or phylogeny (Table 3). Of the three latter variables, the frontal sinus volume was mostly highly correlated with frontal size, but never outside the 95% confidence interval for the correlation coefficients for the other variables (even after accounting for phylogenetic effects). Thus, in the case of correlation coefficients (unlike partial correlation coefficients), it cannot be said that any particular variable considered here is more strongly correlated with frontal sinus volume. Frontal sinus volume displays strong positive allometry relative to all of the other variables, and the 95% confidence intervals of the slopes for the PICs data all overlap.

A sign test on PICs for SCI against sinus, skull, and frontal size indicates a significant relationship between these variables ($P < 0.03$ in all cases, regardless of phylogeny). No such relationship exists between SCI and horn size, however ($P > 0.18$ for both phylogenies).

MORPHOLOGY OF THE FRONTAL SINUSES

Frontal sinuses display considerable variation among bovid species in size relative to the skull, extent within the frontal bone, pneumatization of other cranial bones, and extent within the horncore. In the following section, the frontal sinuses of bovids are described clade-by-clade. Where necessary, details for certain species are noted. The general classication scheme follows that of Gatesy & Arctander (2000), which is relatively consistent with clades recovered by most recent phylogenetic analyses and the tree topologies used in the present paper. Species of historically problematic affiliation (*Aepyceros melampus*, *Neotragus* spp., *Oreotragus oreotragus*, and *Pantholops hodgsonii*) are discussed within their own sections.

The terminology follows that previously proposed by Farke (2007). The midline strut is that formed between the left and right frontal sinuses, coinciding with the interfrontal suture. The supraorbital strut is that running from the bony supraorbital canal, usually towards the medial wall of the sinus. Finally, the cornual diverticulum of the frontal sinus is that portion extending into the bony horncore.

Alcelaphinae

The frontal sinuses of *Alcelaphus buselaphus* and *Sigmoceros lichtensteinii* were described recently in detail elsewhere (Farke, 2007), so they will not be considered further here (except where necessary for comparison). In general, the sinuses in *Damaliscus lunatus* (Fig. 4A, B) and *Connochaetes taurinus* are broadly similar to those of *Alcelaphus buselaphus* and *Sigmoceros lichtensteinii*. In all of these taxa, the strut containing the supraorbital canal joins the medial wall of the frontal sinus (along the midline strut), well rostral to the base of the horncore. In *Damaliscus lunatus*, the sinus extends up to the frontoparietal suture, but the parietal has no involvement in the sinus (contrasting with the condition in *Alcelaphus buselaphus* and *Sigmoceros lichtensteinii*,

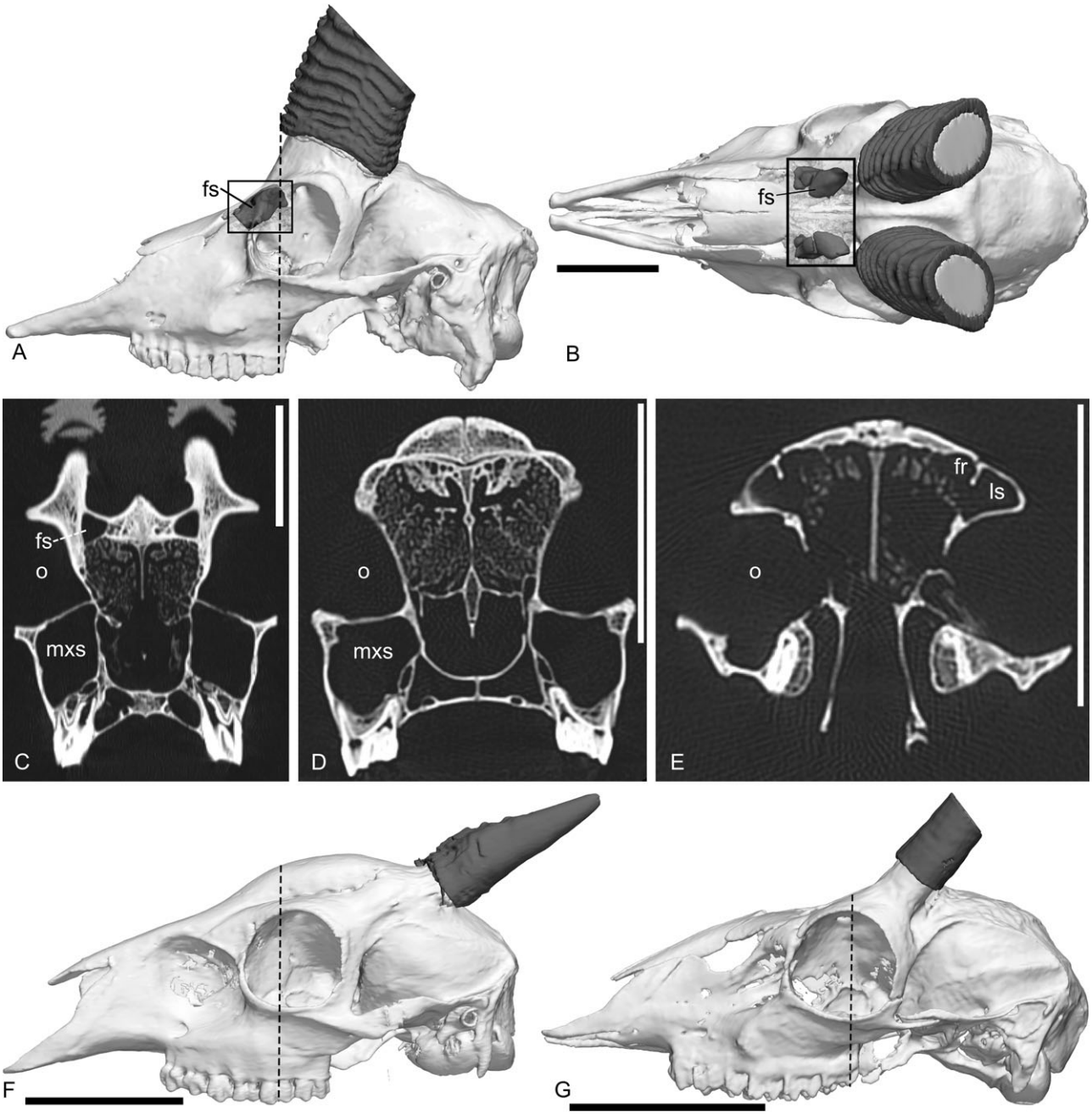

Figure 3. Digital reconstructions and computed tomography (CT) slices of bovid skulls, illustrating the frontal sinuses and related anatomy, in *Nanger granti* (A–C; YPM 11526), *Cephalophus leucogaster* (D, F; AMNH 52802), and *Raphicerus campestris* (E, G; YPM 10276). In C, note the distinct frontal sinus that invades the trabecular bone, is bounded by cortical bone on all sides, and is distinctly separated from the olfactory turbinals below. This contrasts with the condition in E, in which a distinct recess above the olfactory turbinals is pressed into the frontal bone, but does not actually invade the trabecular bone. In D, no recess exists at all, and the space beneath the frontals is entirely occupied by turbinals. The dashed lines in A, F, and G indicate the approximate positions of the coronal CT slices in C, D, and E, respectively. The boxed areas in A and B indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. Scale bars: 5 cm.

Table 1. Results of analyses comparing relative sinus volume (normalized for skull size) and coverage of the endocranium by the frontal sinus in ramming and nonramming bovids

Phylogeny	Sample	Variable	Mean (rammers, nonrammers)	*N*	*P*
None	All	Relative sinus volume	0.45, 0.29	63	0.053
None	SO	Relative sinus volume	0.57, 0.42	47	0.040*
C	All	Relative sinus volume		19	0.153
C	SO	Relative sinus volume		13	0.390
F&V	All	Relative sinus volume		15	0.147
F&V	SO	Relative sinus volume		12	0.525
None	All	Endocranial coverage	0.26, 0.15	63	0.067
None	SO	Endocranial coverage	0.33, 0.21	47	0.080
C	All	Endocranial coverage		19	0.286
C	SO	Endocranial coverage		13	0.546
F&V	All	Endocranial coverage		15	0.431
F&V	SO	Endocranial coverage		12	0.908
None	SO	SCI	0.27, 0.35	47	0.022*
C	SO	SCI		13	0.367
F&V	SO	SCI		12	0.890

*Indicates significance at $P < 0.05$.
For analyses without phylogenetically independent contrasts (PICs), the mean for each category is given. Under the phylogeny column, 'none' refers to analyses on the raw data, 'C' refers to analyses calculated using the composite phylogeny, and 'F & V' refers to analyses calculated using the phylogeny from Fernández & Vrba (2005). Under the sample column, 'all' refers to the analyses in which all taxa were used (regardless of sinus presence or absence) and 'SO' refers to the analyses using taxa with sinuses only. Note that the latter category is not included for the sinus complexity index (SCI), because this required a sinus in order to be calculated.

Table 2. Partial correlation coefficients for frontal sinus size on several variables

Phylogeny	Sample	v_1	v_2	v_3	v_4	$r_{12 \bullet 34}$
None	All	Sinus	Frontal	Skull	Horn	0.38*
None	SO	Sinus	Frontal	Skull	Horn	0.59*
C	All	Sinus	Frontal	Skull	Horn	0.09
C	SO	Sinus	Frontal	Skull	Horn	0.35*
F&V	All	Sinus	Frontal	Skull	Horn	0.19
F&V	SO	Sinus	Frontal	Skull	Horn	0.38*
None	All	Sinus	Horn	Skull	Frontal	0.14
None	SO	Sinus	Horn	Skull	Frontal	–0.16
C	All	Sinus	Horn	Skull	Frontal	0.09
C	SO	Sinus	Horn	Skull	Frontal	–0.07
F&V	All	Sinus	Horn	Skull	Frontal	–0.06
F&V	SO	Sinus	Horn	Skull	Frontal	0.00
None	All	Sinus	Skull	Frontal	Horn	–0.19
None	SO	Sinus	Skull	Frontal	Horn	–0.12
C	SO	Sinus	Skull	Frontal	Horn	0.11
C	All	Sinus	Skull	Frontal	Horn	0.04
F&V	SO	Sinus	Skull	Frontal	Horn	0.09
F&V	All	Sinus	Skull	Frontal	Horn	0.06

*Indicates significance at $P = 0.05$. Refer to the legend of Table 1 for the phylogeny and sample conventions.
All data were logged prior to analysis. The final column presents the partial correlation coefficient between the first two variables (v_1 and v_2) while holding the second two variables (v_3 and v_4) constant.

Table 3. Results of reduced major-axis (RMA) regressions for frontal sinus size on several variables

Phylogeny	Sample	*Y*	*X*	Slope	Intercept	r^2	*N*
None	All	Sinus	Frontal	2.82 (2.41–3.31)	–8.54 (from –10.33 to –6.75)	0.61	63
None	SO	Sinus	Frontal	1.90 (1.63–2.21)	–4.41 (from 1.63 to –3.21)	0.74	47
C	All	Sinus	Frontal	2.64 (2.14–3.25)	0	0.33	62
C	SO	Sinus	Frontal	1.58 (1.28–1.94)	0	0.51	46
F&V	All	Sinus	Frontal	2.67 (2.16–3.30)	0	0.31	62
F&V	SO	Sinus	Frontal	1.66 (1.37–2.01)	0	0.58	46
None	All	Sinus	Horn	2.27 (1.92–2.69)	–6.42 (from –7.98 to –4.86)	0.56	63
None	SO	Sinus	Horn	1.81 (1.46–2.24)	–4.21 (from 1.46 to –2.57)	0.49	47
C	All	Sinus	Horn	2.00 (1.62–2.47)	0	0.31	62
C	SO	Sinus	Horn	1.26 (1.00–1.59)	0	0.39	46
F&V	All	Sinus	Horn	2.08 (1.66–2.60)	0	0.23	62
F&V	SO	Sinus	Horn	1.34 (1.08–1.66)	0	0.47	46
None	All	Sinus	Skull	4.44 (3.70–5.32)	–15.94 (from –19.34 to –12.54)	0.49	63
None	SO	Sinus	Skull	2.94 (2.43–3.55)	–9.12 (from 2.43 to –6.72)	0.59	47
C	All	Sinus	Skull	3.74 (3.03–4.63)	0	0.31	62
C	SO	Sinus	Skull	2.18 (1.73–2.73)	0	0.42	46
F&V	All	Sinus	Skull	3.72 (3.00–4.61)	0	0.29	62
F&V	SO	Sinus	Skull	2.25 (1.81–2.80)	0	0.47	46

All data were logged prior to regression. The numbers in parentheses indicate the 95% confidence intervals. Refer to the legend of Table 1 for the phylogeny and sample conventions.

in which the parietal is involved, even if covered by a veneer of frontal bone; Farke 2007). In *Connochaetes taurinus* specimens, in which the sutures are open (e.g. YPM unnumbered), the sinus clearly invades at least part of the parietal. In all of the taxa, the very base of the horncore is invaded by the sinus, but the cornual diverticulum is not extensive. Other struts within the sinus are relatively sparse, although they do occur consistently.

Antilopinae

The morphology of the sinus is quite variable within this clade, ranging from absent to extensive, so the sinuses are described by species or by groups of species.

Antidorcas marsupialis

This species has the largest and most extensive frontal sinuses of any antilopine, extending into the base of the horncores and to the very edge of the orbital margin (Fig. 4C, D). The supraorbital strut displays the typical bovid condition, extending from the caudal edge of the supraorbital canal and then trending caudomedially. It terminates on the wall of the midline strut just rostral to the base of the horn and its associated cornual diverticulum. Other struts are relatively widely spaced. The frontal sinus in this species is contained completely within the frontal bone.

Antilope cervicapra, Eudorcas thomsonii, Gazella subgutturosa, Litocranius walleri, Madoqua kirkii, Nanger granti, and *Saiga tatarica*

The frontal sinuses in these taxa are relatively small and restricted rostrally, terminating rostral to the supraorbital canal in most cases (Fig. 3A, B). In *Saiga tatarica*, and one specimen of *E. thomsonii* (YPM 11526), the sinus extended up to the lateral portion of the supraorbital canal, within the supraorbital pits. Regardless, the canal is never surrounded completely by the sinuses, as seen in some other bovids (e.g. *Alcelaphus buselaphus*). The sinus on each side is restricted to the lateral portion of the frontal bone and separated from the lacrimal sinus by a thin lamina of bone. In nearly all individuals examined of these species, the sinus was completely unstrutted. The only exceptions were specimens of *Antilope cervicapra* (AMNH 54486) and *Nanger granti* (YPM 11526; Fig. 3B), which displayed a single strut at the middle of each sinus. In one specimen each of *L. walleri* (AMNH 81170) and *Nanger granti* (YPM 9480), only one of the two sinuses was strutted. One specimen of *M. kirkii* (YPM 9600) exhibited strong asymmetry in the shape and extent of the frontal sinuses. The left frontal sinus was quite well developed, extending to the lateral portion of the supraorbital canal, whereas the right frontal sinus was poorly developed, and terminated rostral to its ipsilateral supraorbital canal. Similar, although less extreme, asymmetry in the frontal sinuses was observed in the

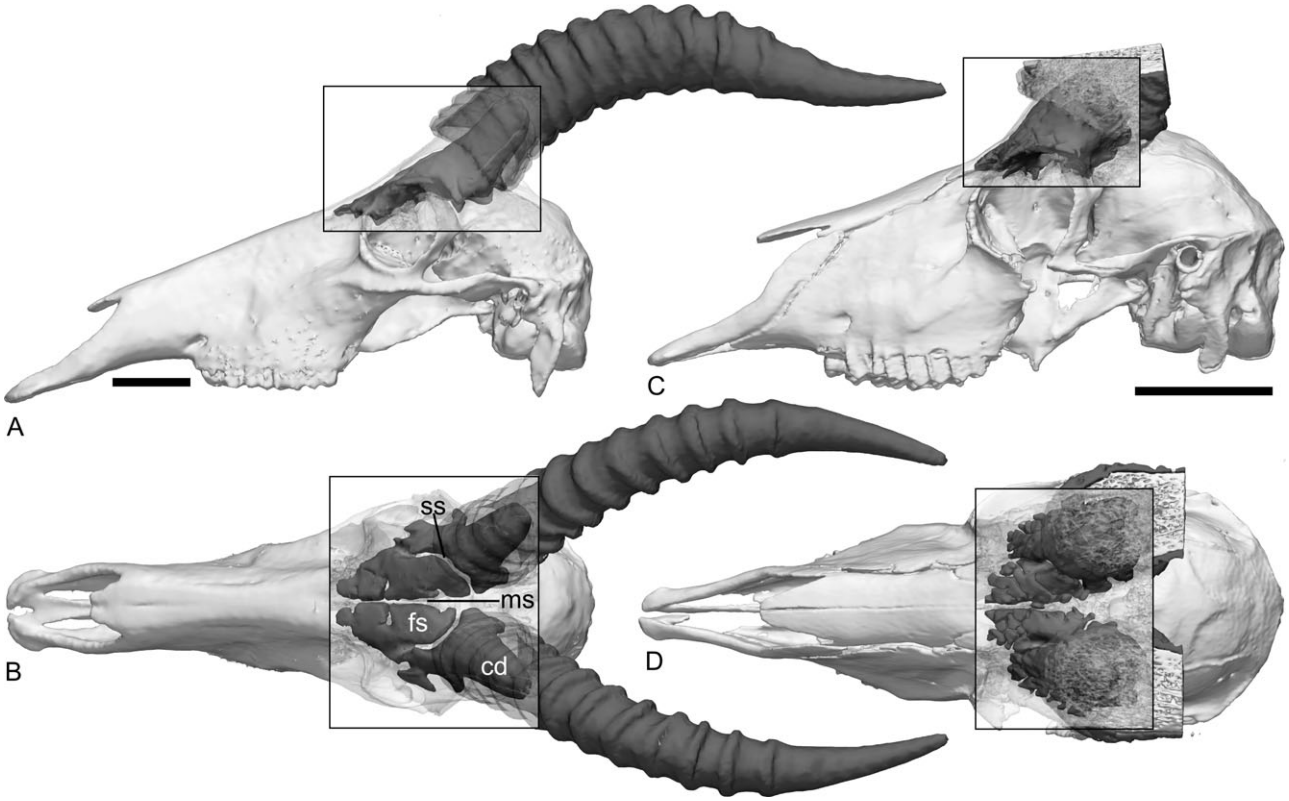

Figure 4. Digital reconstructions from computed tomography (CT) scan data of the skulls of *Damaliscus lunatus* (A–B; YPM 9586) and *Antidorcas marsupialis* (C–D; AMNH 233055), illustrating the frontal sinuses and related anatomy. Skulls are shown in lateral (A, C) and dorsal (B, D) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. The horns have been truncated in C and D. Scale bars: 5 cm.

other *M. kirkii* specimens, and in two specimens of *Nanger granti* (YPM 9480 and 9605).

Other antelopines

Ourebia ourebi lacks frontal sinuses as well as a distinct frontal recess on the internal surface of the frontal bone. *Gazella dorcas*, *Procapra gutturosa*, and *Raphicerus campestris* (Fig. 3E–G) also lack frontal sinuses, but do have a distinct frontal recess in nearly all cases (although no distinct recess was observed in the *Procapra gutturosa* specimen AMNH 85235). In some specimens the recess arguably borders on a true sinus in its degree of depression into the ventral surface of the frontal.

Boselaphini

Both extant boselaphines possess extensive frontal sinuses.

Boselaphus tragocamelus

The frontal sinuses extend through the entire length and breadth of the frontal, up into the bases of the horncores, and out to the lateral margins of the orbital rim (Fig. 5C, D). The sinuses are extensively strutted throughout. The supraorbital strut heads nearly directly caudally, and can be traced only to the plane including the rostral ends of the horncores. The interfrontal suture is well fused in all of the specimens examined here, and the midline strut has an undulating appearance in cross section, perhaps as a result of extensive remodelling. However, the left and right frontal sinuses do not communicate at any point.

Tetracerus quadricornis

The frontal sinuses of this taxon (Fig. 5A, B) are similar to those of *Boselaphus tragocamelus* in most morphological aspects, except those listed as follows. The supraorbital strut is more distinct (unlike in *Boselaphus tragocamelus*), and trends caudomedially from the caudal end of the supraorbital canal towards the midline strut. The bases of both the rostral pair of horncores as well as the caudal pair of horncores are pneumatized. The left and right sinuses are well-separated along the caudal third of their length

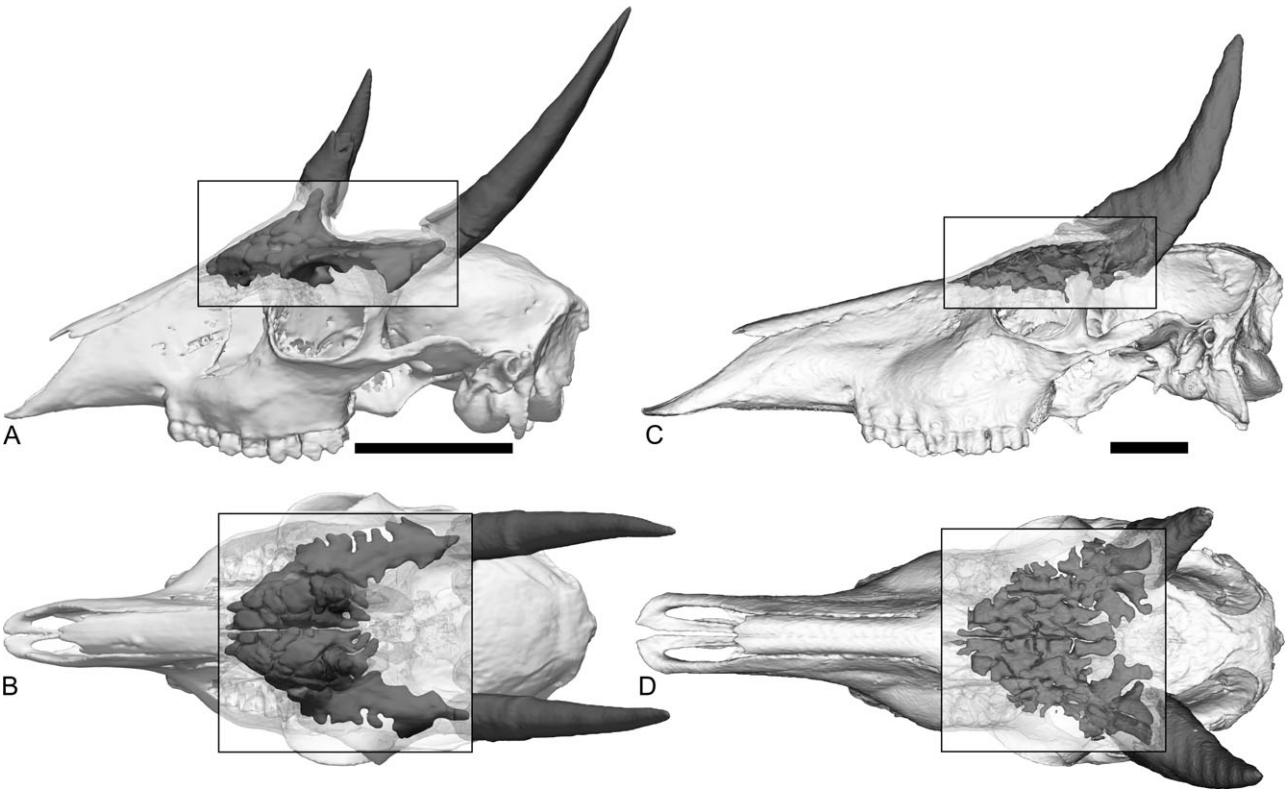

Figure 5. Digital reconstructions from computed tomography (CT) scan data of the skulls of *Tetracerus quadricornis* (A–B; YPM 7396) and *Boselaphus tragocamelus* (C–D; AMNH 22842, image reversed), illustrating frontal sinuses and related anatomy. Skulls are shown in lateral (A, C) and dorsal (B, D) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. Scale bars: 5 cm.

(without the thin midline strut), concomitant with the lateral placement of the horncores. The portion of the sinus in the base of the caudal horncores is unstrutted in all of the specimens studied here.

Bovini

All bovines have relatively large frontal sinuses, differing somewhat in their extent and complexity.

Bison bison

The frontal sinuses (Fig. 6C, D) pneumatize the entire frontal bone in this taxon, as well as the entire parietal. The sinus extends immediately up to the suture between the squamous temporal and the parietal. The occipital receives a pneumatic diverticulum from the parietal portion of the frontal sinus in some specimens, although most of this bone remains unpneumatized in ontogenetically younger specimens (YPM 9022, as determined by sutural fusion and tooth wear). In the oldest specimens (YPM 9023, as indicated by the degree of sutural fusion and tooth wear), the frontal sinus extends up to the foramen magnum and the base of the paroccipital process, but not into the occipital condyles. The midline strut may be heavily remodelled and indistinct caudally. This condition is apparently associated with fusion of the interfrontal suture. No distinct supraorbital strut exists beyond the immediate area of the supraorbital canal. The sinus extends to the distal tip of the horncores in the specimens examined here, and is heavily strutted throughout.

Bos javanicus

The extent and morphology of the sinuses in this taxon are quite similar to those seen in *Bison bison*. The occipital sutures were not fused completely in the specimen that was studied here (AMNH 113755, although it did have complete eruption of the third molar), indicating that the supraoccipital, but not the exoccipital portion of the occipital bone, was pneumatized in this individual.

Bubalus

Bubalus depressicornis (Fig. 6A, B) and *Bubalus mindorensis* both have frontal sinuses of variable extent,

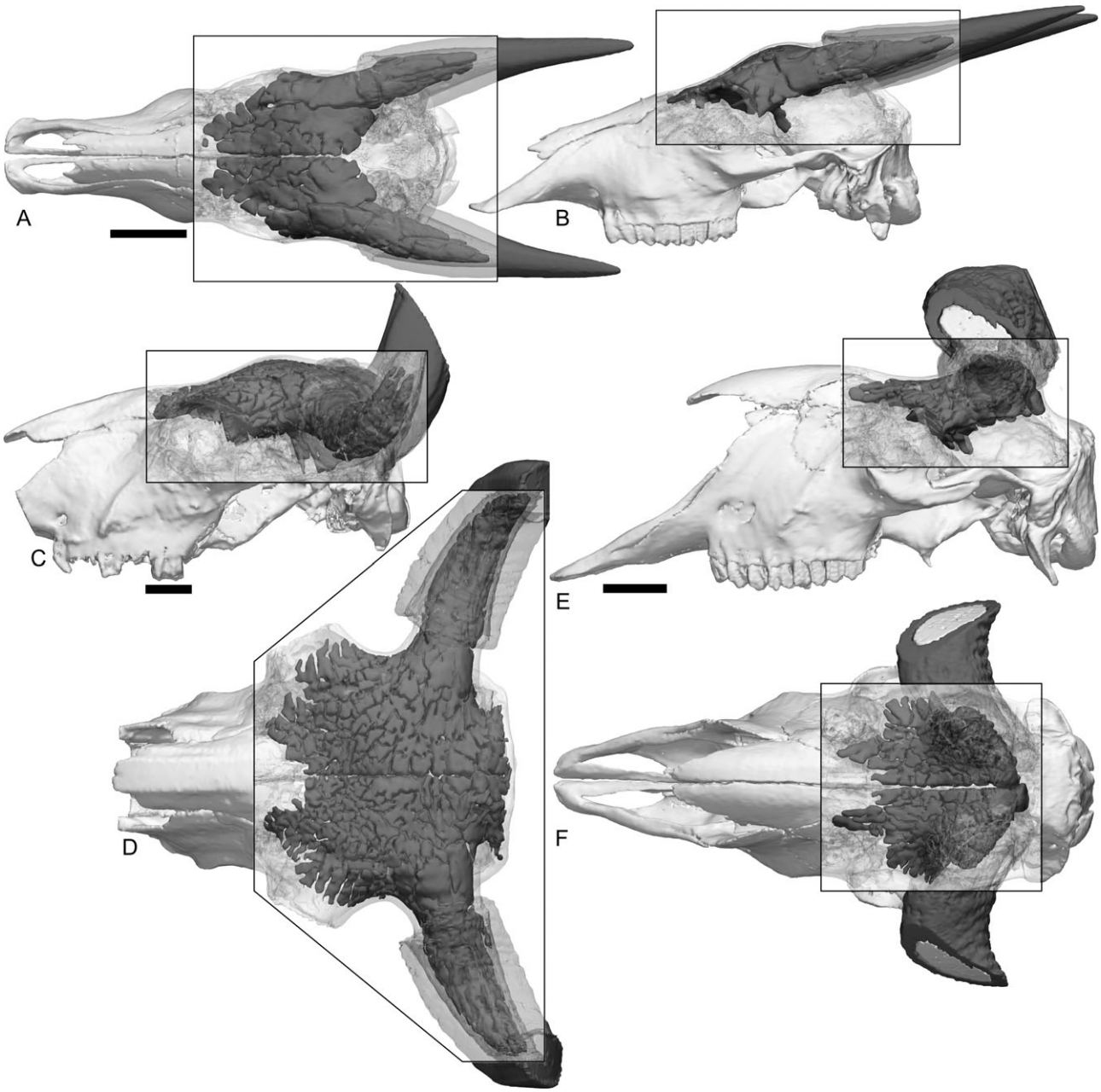

Figure 6. Digital reconstructions from computed tomography (CT) scan data of the skulls of *Bubalus depressicornis* (A–B; AMNH 152684), *Bison bison* (C–D; YPM 9023), and *Budorcas taxicolor* (E–F; AMNH 110476), illustrating frontal sinuses and related anatomy. Skulls are shown in lateral (B, C, E) and dorsal (A, D, F) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. The horns have been truncated in C–F. Scale bars: 5 cm.

possibly depending on age. The supraorbital canal is entirely enclosed by bone, but the supraorbital strut is not traceable for a great distance before it merges with a number of other, unrelated struts. Variability was seen in the pneumatization of the parietal and the extent of the pneumatization of the horncore in *Bubalus mindorensis*. In one specimen (AMNH 40046), only the basal portion of the horncore was pneumatized, and the sinus did not cross the frontoparietal suture into the parietal. In the other specimen (AMNH 99339), over two-thirds of the length of the horncore and the rostralmost portion of the parietal were pneumatized. The frontoparietal suture was somewhat less distinct in the latter specimen, as

visualized through CT and on the original specimen. In *Bubalus depressicornis*, the sinus extended right up to the suture (Fig. 6A), but did not pneumatize the parietal in either of the specimens observed here.

Syncerus caffer
The frontal sinuses are quite extensive in this taxon, pneumatizing the parietal and potentially the occipital (the sutures were nearly completely fused on the specimen examined here, so it cannot be determined for certain). The basal third of the horncores are pneumatized. The midline strut remains sharply defined along most of its length, up until the former location of the frontoparietal suture. A distinct, enclosed supraorbital canal is present, but a discrete supraorbital strut cannot be identified because of the abundance of other struts within the sinus.

Caprinae

All taxa within this clade possess a frontal sinus. Tremendous variation in the morphology of this structure necessitates a taxon-by-taxon description.

Budorcas taxicolor
The entire extent of the frontal is pneumatized, up to the basal portion of the horncores (Fig. 6E, F). The sinus crosses the frontoparietal suture (which is still patent in both specimens examined here) to pneumatize the proximal portion of the parietal bone, but not the occipital bone. Numerous struts subdivide the sinus, and, consequently, a distinct supraorbital strut cannot be traced away from the supraorbital canal.

Capra
The morphology of the frontal sinus is relatively uniform across the four species of *Capra* studied here (*Capra aegagrus*, *Capra falconeri*, *Capra nubiana*, and *Capra sibirica*). The entire extent of the frontal is pneumatized, nearly up to the frontoparietal suture. A discrete supraorbital strut is not always present, although when it can be traced, it trends medially for a short distance before joining the medial wall of the sinus. In *Capra falconeri*, there is no distinct supraorbital strut. The horncores are pneumatized for their entire length in the oldest individuals (e.g. *Capra sibirica*, AMNH 54906; Fig. 7A, B), although in younger adults, only the basal half is pneumatized (e.g. *Capra sibirica*, AMNH 57317). The sinuses are strutted, but less prominently than seen in *Ovis*.

Capricornis sumatraensis and Naemorhedus goral
These two species (which are closely related) are similar in most details of the sinus, and are described together. The frontal is pneumatized along nearly its entire extent (not quite to the frontoparietal suture; Fig. 7E, F), with no pneumatization of the parietal, but only the basal third of the horncore is pneumatized. A supraorbital strut extends caudal to the supraorbital canal for a short distance, ending on the medial wall of the sinus rostral to the horncore. Relatively thin struts occur throughout the rest of the sinus.

Hemitragus hylocrius
The entire frontal is pneumatized in this taxon, up to (but not across) the frontoparietal suture, and through at least three-quarters of the length of the horncore. The sinus is well strutted, and consequently a discrete supraorbital strut cannot be traced beyond the supraorbital canal.

Oreamnos americana
The frontal sinus fills the body of the frontal bone, but ends at the bases of the horncores well before reaching the frontoparietal suture (Fig. 7G, H). Only the base of the horncores is pneumatized. The strutting within the sinus is relatively infrequent, particularly compared with *Ovis*. A distinct supraorbital strut can be traced running from the caudal edge of the supraorbital canal back to the medial surface of the sinus, terminating approximately at the base of the horncore.

Ovibos moschatus
The frontals are pneumatized entirely in this taxon, but only the very base of the horncore contains a sinus. In one specimen (AMNH 80095), both halves of the parietal and the portion of the occipital bordering the frontoparietal suture (unilaterally) are pneumatized. In the other (AMNH 29949), the parietal is not pneumatized. One major difference between the specimens appears to be the degree of fusion between the sutures: in AMNH 80095, the sutures are much more fused in this region than in AMNH 29949. A distinct supraorbital canal is present within the sinus, but no supraorbital strut is discernible because of the high number of other struts.

Ovis
An extensive frontal sinus occupies the entire frontal bone in both species of *Ovis* examined here (*Ovis ammon* and *Ovis canadensis*), with some differences between the two. A cornual diverticulum extends to the very tip in *Ovis canadensis* (Fig. 7C, D), but only along half to three quarters of the length of the horncore in *Ovis ammon*. The sinuses are subdivided into a large number of small chambers by numerous bony struts. Some of these struts contain neurovascular canals that communicate with foramina on the external surface of the horncore and dorsum of the skull. The origin of most of these canals cannot be

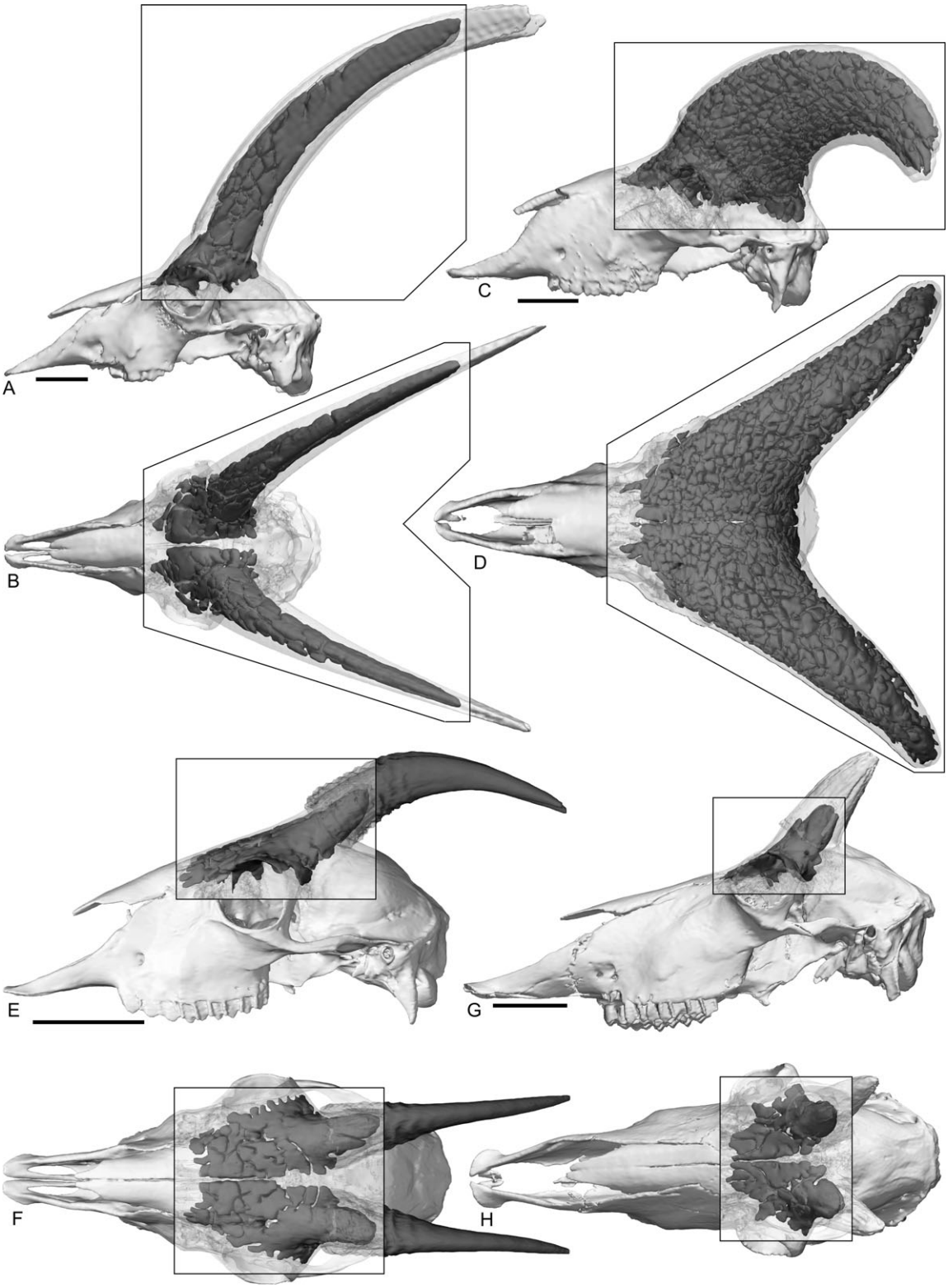

Figure 7. Digital reconstructions from computed tomography (CT) scan data of the skulls of *Capra sibirica* (A–B; AMNH 54906), *Ovis canadensis* (C–D; YPM 7376), *Naemorhedus goral* (E–F; AMNH 43033), and *Oreamnos americanus* (G–H; AMNH 128105), illustrating frontal sinuses and related anatomy. Skulls are shown in lateral (A, C, E, G) and dorsal (B, D, F, H) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. The horn sheaths have not been rendered in A–D and G–H. Scale bars: 5 cm.

traced, because of structural discontinuities. The midline strut is well defined, although it is not perfectly flat in the sagittal plane. A 'wavy' surface is created by occasional pneumatic diverticula excavated into the side of the septum. The supraorbital canal is fully contained within a strut, but the strut is not traceable for any great distance because of the numerous septa within the sinus.

The parietal is pneumatized by the frontal sinus in all individuals of *Ovis canadensis* examined here (but not in *Ovis ammon*), and the sinus clearly crosses sutural boundaries, even in specimens in which the sutures are not completely ossified (e.g. YPM 6682, *Ovis canadensis*). In YPM 6682, the one specimen of *Ovis canadensis* for which the sutures could be traced reasonably well on CT scans, the frontal portion of the sinus is separated from the parietal portion of the sinus by a strut that seems to conform to the contours of the frontoparietal suture. On one side in this specimen the strut is completely continuous (i.e. there is no communication between the frontal and parietal portions of the sinus). On the other side, there is a wide communication between these portions of the sinus. Thus, it appears that the pneumatic diverticulum that pneumatized the parietal entered only on one side. In other specimens, the pneumatic diverticulum appears to be bilateral. By comparison with external landmarks on the skulls with fused sutures, it is apparent that the parietal is pneumatized in all of the specimens considered here. The sinus does not invade the occipital. Unlike the condition seen in the frontal, no midline strut divides the parietal portion of the frontal sinus into left and right halves (perhaps corresponding to the early fusion of the parietal in bovids). In tracing the structural continuity of the parietal portion, it has no relation to any pneumatic diverticula from the middle ear.

Pseudois nayaur

The sinuses of *Pseudois nayaur* are similar in morphology and extent to those seen in *Ovis*. Although sutures are fused on the specimens examined here, topological relationships indicate that the parietal is pneumatized. The horncore is pneumatized along approximately three-quarters of its length.

Rupicapra rupicapra

In this species, the sinuses occupy the frontal bone exclusively, extending slightly behind the base of the horncore, but not up to the frontoparietal suture. The base of the horncore is also pneumatized. The sinuses are relatively undivided, but no supraorbital strut is associated with the supraorbital canal in either specimen examined here.

Cephalophinae

This clade (including *Cephalophus*, *Philantomba*, and *Sylvicapra*) is remarkable in its consistent lack of frontal sinuses, or apparently even a frontal recess (no well-developed depression is evident at any point on the ventral surface of the frontals; Fig. 3D). This morphology is invariant, whether in the smallest (e.g. *Philantomba maxwelli*) or largest (*Cephalophus sylvicultor*) species examined here.

Hippotraginae

The sinuses of *Hippotragus niger* and *Hippotragus equinus* are quite similar in all respects, so they are described together. Based on an examination of a skull of *H. niger*, in which the sutures are not completely fused (AMNH 83606; Fig. 8A, B), the sinus is contained exclusively within the frontal bone. Caudally, it extends up to the frontoparietal suture and into the base of the horncore. The strut coincident with the supraorbital canal continues for some distance caudomedially past the termination of the canal, ending at the medial base of the horncore, but not entering the horncore itself. The sinus is subdivided by bony struts, although the chamber leading into the base of the horncore is relatively open.

In *Oryx gazella*, the extent of the frontal sinus is similar to that seen in *Hippotragus*. The sinuses of *Oryx gazella* have comparatively more struts, and the supraorbital strut does not continue caudally beyond the end of the supraorbital canal.

Reduncinae

None of the specimens of *Pelea capreolus* displayed frontal sinuses, although one (AMNH 80920) displayed a clear frontal recess. The occurrence of a frontal sinus is variable within other reduncines, but the sinus is small when it is present.

Kobus

In the single specimen of *Kobus leche* examined here (YPM 11524), the frontal sinuses are present and strongly asymmetrical. The left sinus extends to the rostral end of the supraorbital canal, and the right sinus extends around the lateral margin of the canal, nearly to the caudal end of the orbit. Similar asymmetry was seen in a specimen of *Kobus ellipsyprymnus* (YPM 9101; Fig. 8C, D). In other specimens of *K. ellipsiprymnus*, the sinuses extend to the lateral margin of the supraorbital canal. In *Kobus kob*, the sinuses extend to the rostral ends of the supraorbital canals. The sinuses in all of these species typically have a few struts within them. *Kobus vardonii* lacks a frontal sinus, but does have a frontal recess.

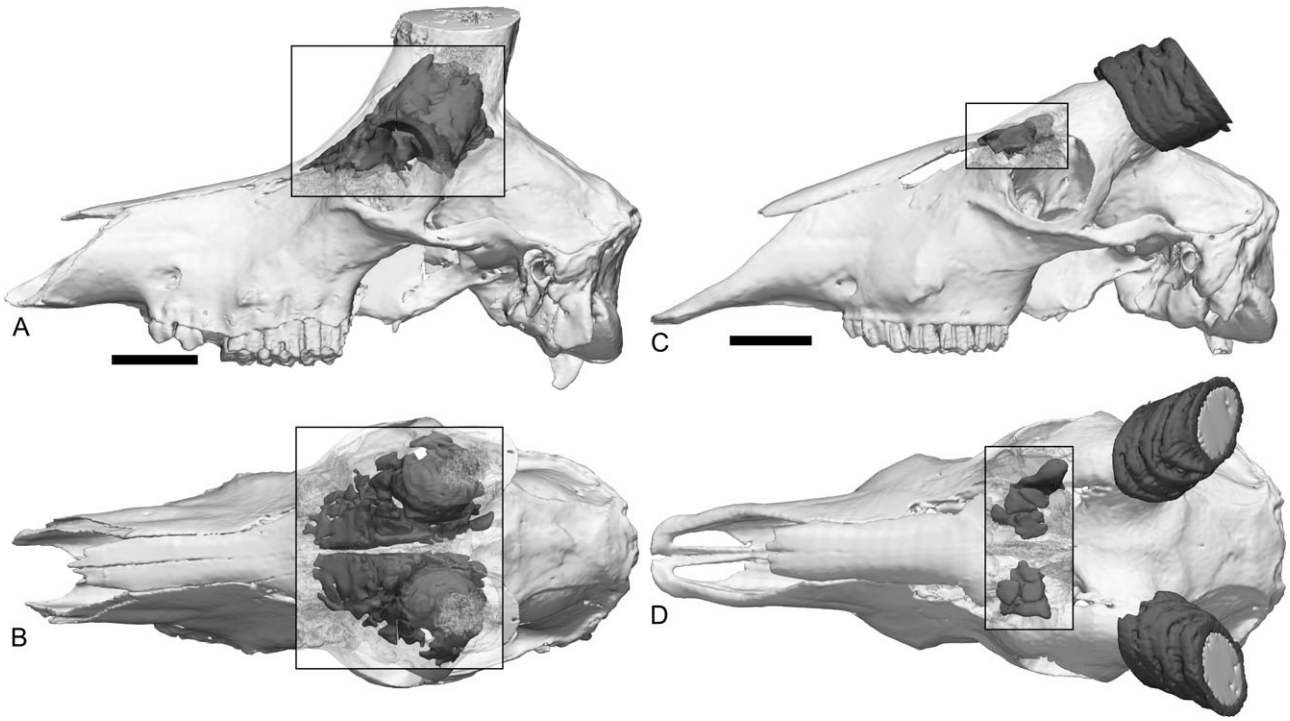

Figure 8. Digital reconstructions from computed tomography (CT) scan data of the skulls of *Hippotragus niger* (A–B; AMNH 83606) and *Kobus ellipsyprymnus* (C–D; YPM 9101), illustrating frontal sinuses and related anatomy. Skulls are shown in lateral (A, C) and dorsal (B, D) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. The horn sheaths have not been rendered on A and B, and the horns were truncated on all images. Scale bars: 5 cm.

Redunca

The presence of a sinus was highly variable within both species examined, although at least a recess was present in all cases. Two out of three specimens of *Redunca arundinum* had frontal sinuses, and one out of three specimens of *Redunca fulvorufula* also had them. In *Redunca arundinum*, the sinuses are extremely small, unstrutted, and restricted to the lateral- and rostralmost portions of the frontal bone. The single specimen of *Redunca fulvorufula* with a sinus had similar morphology, but the sinus was developed only on one side.

Tragelaphini

Of the three taxa examined from this clade, only one displayed evidence of a true frontal sinus (*Taurotragus oryx*; Fig. 9A, B). In this taxon, the frontal sinus is extremely restricted in size and extent. It originates from a large recess in the caudodorsal portion of the nasal cavity, is bordered by a distinct bony wall, and excavates a small volume of trabecular bone. The sinus does not extend to even the rostral border of the supraorbital canal, and is situated medial to the parasagittal plane containing the canal. The right and left sinuses do not meet along the midline. *Tragelaphus strepsiceros* shows a small recess in the equivalent region, but *Tragelaphus scriptus* lacks even this feature.

Tragelaphines are unique in the presence of a separate 'cornual sinus' within the very base of the horncores, extending only as far forward as the caudal margin of the orbits. All individuals of all three taxa examined for this study preserved this feature, which was observed both in CT scans and in sectioned horns. This sinus is not connected to the nasal cavities, and thus was almost certainly not pneumatic in origin. Instead, it may have been filled with fat or marrow in life. Rostrally, the cavities are lined by relatively smooth bone, but the bone surface becomes trabecular towards the caudal end. This contrasts sharply with the completely smooth bone lining of the pneumatic frontal sinus in other bovids.

Taxa of uncertain affinity

Aepyceros melampus

In this taxon (Fig. 9C, D), the frontal sinus is contained strictly within the frontal, and extends only into the most basal portion of the horncores. The cornual diverticulum has a peaked distal end, with struts running parallel with the long axis of the

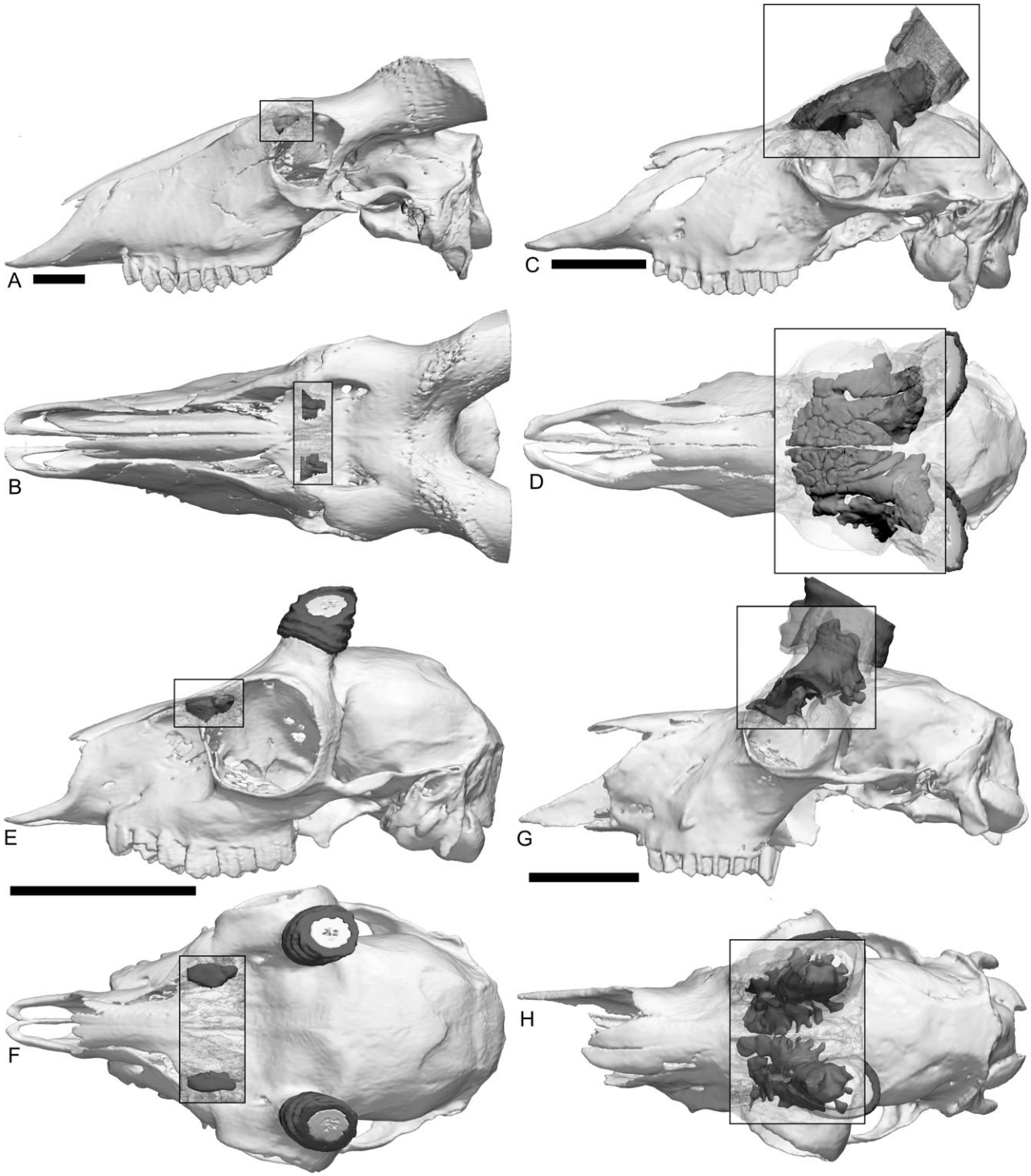

Figure 9. Digital reconstructions from CT scan data of the skulls of *Taurotragus oryx* (A–B; YPM 10471), *Aepyceros melampus* (C–D; YPM 9597), *Oreotragus oreotragus* (E–F; AMNH 27827), and *Pantholops hodgsonii* (G–H; AMNH 55819), illustrating frontal sinuses and related anatomy. Skulls are shown in lateral (A, C, E, G) and dorsal (B, D, F, H) views. The boxed areas indicate the region of the skull that has been rendered partially transparent in order to visualize the anatomy of the frontal sinuses. The horn sheaths have not been rendered in A and B, and they are truncated in C–H. Scale bars: 5 cm.

horncore. In all specimens examined, the supraorbital strut runs from the caudal border of the supraorbital canal to the very base of the cornual diverticulum. Unlike the condition in other bovids, the strut trends caudolaterally to terminate on the lateral wall of the sinus, rather than caudomedially to terminate on the midline strut. The dorsal and caudodorsal margins of the orbit are pneumatized by the frontal sinus. The main body of the sinus is subdivided into numerous chambers by a series of bony struts.

Neotragus spp.
Neither of the species of *Neotragus* examined here (*Neotragus batesi* and *Neotragus moschatus*) exhibited frontal sinuses, or even a prominent recess along the internal surface of the frontal bone.

Oreotragus oreotragus
All specimens of this taxon possessed a small, unstrutted frontal sinus, which is restricted to the frontal bone well rostral to the supraorbital canal (Fig. 9E, F). The frontal sinus is immediately adjacent to the lacrimal sinus, and is separated from it by a thin lamina of bone.

Pantholops hodgsonii
The frontal sinuses extend into the bases of the horncores, but not to the frontoparietal suture (Fig. 9G, H). Relatively few struts occur within the sinus, and the most prominent is a supraorbital strut that extends from the supraorbital canal medially and caudally, back to the very base of the horncore.

EVOLUTION OF THE FRONTAL SINUSES

As inferred from ancestral parsimony-state reconstruction on the two phylogenetic hypotheses used here, the presence of a frontal sinus was the ancestral condition for Bovidae. Depending on the tree topology, frontal sinuses were lost or reduced to a recess independently up to seven times (Figs 1, 2). These instances were within tragelaphines, reduncines (*Kobus* and *Pelea*), antilopines (*Raphicerus* and *Procapra*), *Neotragus*, and cephalophines. The tree topology of Fernández & Vrba (2005) has several polytomies, and thus results in a more ambiguous reconstruction (Fig. 1). In this case, a frontal sinus is still present in the common ancestor of all bovids, but the sinus may have been initially lost and then re-evolved within reduncines.

DISCUSSION

Sinuses and behaviour

After accounting for phylogenetic effects, the analyses do not support the claim that enlarged frontal sinuses or bony struts within the sinuses are an adaptation for head-butting. Although the use of the BRUNCH algorithm greatly reduces the effective sample size (down to 12 data points, in some cases), and hence reduces the power of the statistical tests, the *P*-values are well above 0.05 in all cases (Table 1). So, it is probably not simply a case of significance masked by small sample size. Instead, the analysis indicated that variables such as relative frontal sinus size or complexity, as well as ramming behaviour, have a strong phylogenetic component. In the raw sample, much of the pattern may be driven by caprines (sheep, goats, and their allies) and bovines (cattle and their allies). As a whole, these two groups have the lowest SCI (indicating greatest complexity) and the largest relative sinus volumes of any of the groups considered (even though not all members butt heads). Furthermore, frontal sinuses are completely absent in cephalophines, which do butt heads (Estes, 1991). Outside of Bovidae, frontal sinuses are absent in a number of taxa that also use cranial appendages (horns or antlers) for vigorous combat behaviour (head butting or otherwise). The examination of CT scans of various cervids (*Alces alces* and *Odocoileus virginianus*) and *Antilocapra americana* (A.A. Farke, pers. observ.) indicates that the frontal sinuses are extremely restricted or absent in these taxa. Paulli (1900) presented further data that are in agreement with this observation. Such observations indicate that enlarged frontal sinuses are not absolutely necessary to protect the brain from forces applied to the horns or antlers.

The statistical results indicating no link between sinus morphology and head-butting behaviour are consistent with results from the finite-element modelling of a goat skull under loads to the horns (Farke, 2008). These simulations varied the morphology of a goat skull, including filling the frontal sinuses with bone or removing the sinuses and altering the overall morphology of the frontal bone, and examined the effects on shock absorption (as measured through strain energy density and principal strains). In general, it was found that the frontal sinuses only had a minor role in protecting the endocranial cavity and its contents from blows to the horns. Thus, the results of the comparative analysis are consistent with these modelling results.

Computer modelling of sinus growth suggests that structural complexity within the space of the sinus may result from intrinsic features of the growth process itself, rather than any particular mechanical function of the sinus within the skull (Zollikofer & Weissmann, 2008). When sinuses were modelled using Laplacian and Poisson growth equations, the variation in 'viscosity' of the system was found to replicate the variation in sinus complexity. Within

bovids, this variation in sinus complexity perhaps reflects differential growth rates within the skull. Species with a rapidly expanding frontal bone over the course of ontogeny (analogous with the low-viscosity runs of the simulation), and thus a rapidly expanding sinus, might be expected to have very complex sinuses, whereas species with a slowly expanding frontal bone (analogous with high-viscosity simulations) would be expected to have simpler sinuses. Comparative ontogenetic studies are needed to test this hypothesis.

Sinuses and cranial morphology

The results of the partial correlations are at least partially consistent with the 'opportunistic pneumatization' hypothesis, which implies that paranasal sinuses are primarily functionless, resulting from the removal of structurally unnecessary bone (although because correlation and causation cannot be separated here, the results are not definitive). This hypothesis predicts that among frontal size, horn size, and skull size, sinus size should logically be most correlated with frontal size. Here, it was found that the frontal sinus size was only significantly correlated with frontal size (but not with skull or horn size) when considering partial correlations (except for the sample including all taxa, when accounting for phylogeny; see below). No previous interspecific comparisons have so directly examined the relationship between a sinus and the bone it occupies. Thus, no previously published analysis is completely comparable with the present study, in terms of variables considered, number of species, or types of statistical analyses.

Koppe & Nagai (1999) published regressions for maxillary sinus volume on skull length for hominoid primates (six species) and *Macaca* (eight species). The two clades were analysed separately, specimen data points rather than species means were used to calculate the regressions, and no confidence intervals are given, so it cannot be compared with the results presented here. A similar analysis of anthropoid primates (five genera) found an isometric relationship between maxillary sinus volume and facial volume or geometric mean, strong allometry relative to basicranial length, and similar correlation coefficients between all of those variables with maxillary sinus volume (Rae & Koppe, 2000). The isometric relationship between facial volume and maxillary sinus volume is interesting, but it cannot be compared directly with the strongly allometric relationship between frontal sinus size and frontal size for two reasons. First, the 'facial volume' included not only the size of the maxilla, but also the size of the nasal cavity. Nasal cavity size has previously been recognized to have an effect on maxillary sinus size in some taxa (Shea, 1977; Rae *et al.*, 2003). An alternative analysis might subtract out the size of the nasal cavity from facial volume in order to examine more directly the relationship between sinus volume and maxilla volume. A more important departure preventing a direct comparison between the present study and the previous ones is the use of specimen data points, rather than species means. Particularly because of the unequal sample numbers between genera (between six and 11), and the lack of information on the number of species represented in each genus of the sample, it is difficult to determine if the pattern of isometry is genuine or driven by the choice of specimens.

The inference of 'opportunistic pneumatization' is also consistent with the finite-element modelling of goat skulls mentioned above (Farke, 2008). In these models, it was found that the bone removed by the sinuses was generally unloaded.

The statistical analysis also indicates that a complex sinus is associated with large skull size (and its accompanying large frontal and frontal sinuses). Regardless of behaviour, a large sinus would need more struts within it in order to maintain structural integrity. Or, as described above, the complexity may simply be a byproduct of normal growth processes (Zollikofer & Weissmann, 2008).

It is important to note that significant correlations between frontal sinus size and frontal size were not found for the samples including all taxa (with and without sinuses), and accounting for phylogeny. This may indicate a phylogenetic influence upon the presence or absence of a recess capable of pneumatizing the frontal, as well as a detrimental statistical effect of including a large number of taxa with sinus volumes of '0'. Such a phylogenetic effect may counter the conclusion that pneumatization proceeds only within areas of unloaded bone (delimited in turn by the location, strength, and frequency of loads placed on the skull).

The strong positive allometry of sinus size relative to skull size (and frontal size) is also consistent with the role of the sinuses as weight-reducing structures in larger members of this group. It is expected that weight reduction would be a much more important factor at large body sizes; thus, large bovids should have proportionately larger sinuses. However, it does not yet explain the ultimate factors behind the origin of skeletal pneumaticity.

Prerequisites for sinuses

Witmer (1997) emphasized the necessity of air-filled epithelial diverticula for the formation of a sinus. However, he also noted that many taxa possess extracapsular epithelial diverticula, but lack cranial sinuses (e.g. *Varanus*). No explanation has been offered for this yet. Based on the results of the

present study, two conditions are hypothesized as prerequisites for paranasal sinus development: (1) presence of an extracapsular epithelial diverticulum of the nasal cavity; and (2) presence of bone that can be pneumatized by the diverticulum without structural compromise of the skull. If either condition is not met, a bony sinus will not develop. It is important to note here that bone development and sinus development proceed simultaneously (Koppe *et al.*, 2000). A similar hypothesis, although not explicitly stated, was implied by Rossie (2006), who also noted the importance of close spatial proximity between the diverticulum and the bone to be pneumatized.

The best support for the above hypothesis lies in groups that fulfill only one of the two above criteria, and thus lack sinuses. Among bovids, Cephalophinae perhaps represent one such clade. Here, the frontal bone is quite thick in some taxa, but there is no paranasal diverticulum associated with this bone, so the frontal is not pneumatized (Fig. 3D). Further examples are found in cercopithecoid primates: the Old World monkeys. All extant members of this clade, except for *Macaca*, lack maxillary sinuses. Rae *et al.* (2002) demonstrated that the loss of maxillary sinuses occurred near the origin of this clade. However, they could not offer an explanation for why this group lost them. Rae and Koppe proposed that the development of sinuses was 'suppressed' in cercopithecoids, but there is currently no good evidence of the precise mechanism by which this suppression would occur (Rae & Koppe, 2003; Rae, 2008). Detailed comparative histological studies of cercopithecoid nasal cavities are necessary to evaluate this hypothesis.

Other examples exist among bovids (e.g. *Gazella* and *Procapra*) in which there is apparently a diverticulum, but no pneumatization of the trabecular bone within the frontal (criterion one but not two). Rossie (2006) noted a similar lack of bone in the platyrrhine primates *Cacajao* and *Saimiri*, which both lack maxillary sinuses but possess maxillary recesses. The condition in these genera contrasts with that of closely related platyrrhines: which have a relatively deeper maxilla, with more trabecular bone, and therefore more potential space for a sinus to occupy, and thus have a sinus.

Sinus evolution in bovids

Although molecular phylogenies have played an increased role in reconstructing bovid evolution, the identification of valid morphological characters is necessary for placing most extinct taxa within a phylogenetic framework. The present study indicates that some characters are probably more useful than others, and also identifies previously unrecognized characters of potential importance. For instance, the presence or frequency of bony struts within the sinus has been used as a character (Vrba & Schaller, 2000). The data here found that although some taxa have many struts within their sinuses, and others have very few, there is no discrete cut-off between the two states. The most common character relating to the frontal sinuses concerns relative size. Many workers have simply specified whether the sinuses are large or small (e.g. Gentry, 1992). The approach taken by Vrba (1979), specifying the extent of the sinus relative to the supraorbital canal, seems to be most tractable in light of the data presented here. For a single ordered character related to sinus extent, the most logical states would include: (0) complete absence of frontal recess; (1) frontal recess present but no sinus; (2) frontal sinus present but does not extend caudal to supraorbital canal; and (3) frontal sinus present and extends caudal to supraorbital canal. An additional, hitherto undocumented character, concerns the pneumatization of the parietal and occipital bones by the frontal sinus. This character appears to be age-dependent in at least some taxa (only appearing in relatively old individuals), nonetheless it may be quite informative.

The data are partially consistent with opportunistic pneumatization as an influence upon sinus morphology in bovids. Yet, some aspects of the sinuses, such as sinus complexity or the absence of a frontal recess, are apparently correlated with phylogeny. Is this a direct link, in which a gene or set of genes directly influences sinus morphology? Or is it an indirect link, in which frontal architecture is determined genetically and the sinus morphology follows? The present study cannot address this. Further work is needed, for instance, on the factors that cause some taxa to completely lose a pneumatic recess associated with the frontal bone, or the factors that lead to pneumatization of the parietal and occipital. Is this development under genetic control or epigenetic control? More developmental and histological studies (along the lines of Hönig *et al.*, 2002; Smith *et al.*, 2005) are needed in order to answer this question.

Rather than indicating multiple origins of the frontal sinuses within Bovidae, the present data for bovids strongly suggest the presence of the sinus at the origin of the clade, with multiple losses instead (and possible re-evolution within reduncines in one tree topology; Fig. 1). This is consistent with the fact that one of the earliest known bovids, the boselaphine *Eotragus sansaniensis* from the mid-Miocene of France, apparently had small frontal sinuses of unknown extent (Solounias & Moelleken, 1992). The factors behind the loss of the frontal sinuses in some bovids are uncertain, but two possibilities exist. As suggested for the maxillary sinuses of *Cacajao* (in which the lateral recess of the nasal cavity is well

separated from trabecular bone within the maxilla; Rossie 2006), issues of spatial packing may have led to a loss of the frontal sinus in some bovids. In cephalophines, the nasal cavity is narrowed drastically internally, in association with an extremely enlarged preorbital gland on the external aspect of the skull. The spatial constraints imposed by this condition may have led to the loss of a recess capable of pneumatizing the frontal bone or the positioning of such a recess well away from the frontal. Alternatively, an extreme reduction in overall skull size may also explain the loss of a sinus, if sufficient bone is not then available for pneumatization (as proposed for bats; Moore, 1981). If the ancestor of a clade went through a 'dwarf' phase that resulted in the loss of a sinus, even descendants that became larger would also lack this sinus. However, some taxa with very small body size and skull size still exhibit frontal sinuses (such as *Madoqua*, with a maximum adult body mass of 5.5 kg, one of the smallest within Bovidae; Silva and Downing, 1995). Paleontological data are needed for other clades in order to support or refute this hypothesis.

Sinuses and sutures

Farke (2007) documented apparent but not direct pneumatization of the parietal by the frontal sinus in hartebeest (*Alcelaphus* and *Sigmoceros*). In these taxa, a thin 'veneer' of frontal bone was adhered to the parietal portion of the sinus, in at least some individuals. With age, this veneer was lost. Regardless of whether or not a thin portion of the frontal remained against the parietal, the internal morphology of the parietal was affected by the pneumatization. Based on this evidence, it was suggested that cranial sutures may have a role in restricting or influencing pneumatization.

The results of the present study are mixed in this regard. In at least some taxa, the frontal sinus extends up to the frontoparietal suture, and even conforms to its morphology in part, but does not cross the suture. The interfrontal suture also appears to be maintained relatively consistently across taxa, even when well fused.

In other taxa (e.g. *Bos javanicus*), the sinus crosses multiple patent sutures to pneumatize the parietal, and occasionally even the occipital bone. Thus, sutures may have a role in restricting the expansion of sinuses, but some taxa appear to circumvent this supposed restriction. Again, genetic factors, rather than the purely structural factors indicated by 'opportunistic pneumatization' may be more important here. Clearly, additional work is needed on the interactions between the pneumatic epithelium of the sinus and surrounding tissues. Why do the sutures apparently restrict sinus growth in some taxa, but not in others?

Sinuses and asymmetry

Strong asymmetry was observed between the left and right sinuses in several taxa (e.g. Fig. 8D). This manifested as marked development on one side and minimal development or absence on the other. This is not attributable to asymmetry in the frontal bone itself, as the frontals in these individuals seem to be symmetrical in cross section. Neither can it be attributed to pathology such as atelectasis, as no abnormal bone morphology is visible in the CT scans (Koppe *et al.*, 2006). This marked asymmetry only occurred in taxa with relatively small sinuses. Unfortunately, the sample size at present is too small to determine if this can be classified as fluctuating asymmetry or some other process.

Ontogenetic factors

Although documentation of ontogenetic variation was not a central aim of this study, some differences were observed among adult specimens that may be caused by ontogenetic changes occurring from early adulthood into old age. This is a consequence of the fact that adult status was judged by molar eruption, and sinus expansion apparently continued after the eruption of the third molar in some taxa. In particular, this was noted in *Capra sibiricus* and *Bison bison*. By contrast, relatively little change in frontal sinus extent occurs within *Alcelaphus buselaphus* and *Sigmoceros lichtensteinii* after the eruption of the third molar (Farke, 2007). Additional research, using large specimen samples, is needed in order to determine just how much change, if any, occurs in sinus morphology during adulthood (or throughout ontogeny in general).

CONCLUSIONS

This study presents the broadest and most comprehensive quantitative analysis of sinus morphology ever attempted. It was found that the frontal sinuses are closely tied to the size of the frontal bone, but are less tied to the overall cranial size or horn size. This is perhaps consistent with the 'opportunistic pneumatization' hypothesis, yet phylogenetic effects are also implicated in some cases. Thus, opportunistic pneumatization, or a purely structural role for the sinuses, cannot be the only factor determining the morphology of the sinuses (a conclusion reached independently by Rae & Koppe, 2008). Furthermore, the data integrating behaviour and relative sinus volume or complexity do not strongly support the role of the frontal sinuses as shock absorbers within Bovidae.

Within Bovidae, the sinuses hold clear promise as characters for morphological phylogenetic analysis. On a broader level, bovids offer an ideal opportunity for further study of the mechanisms behind cranial

pneumatization. What genetic or epigenetic factors lead to sinus loss? Or is sinus loss purely a structural phenomenon? Are all portions of the sinus within bovids derived from homologous nasal recesses? Ontogenetic, and particularly soft-tissue-based studies, are needed to clarify these issues.

Although the two-part criteria outlined above offer a framework in which to understand the range of morphologies observed in paranasal sinuses, they do not necessarily provide a prediction of the selective pressures (if any) that lead to paranasal recesses and sinuses. In the end, bovids provide a case study for the multiple loss of a sinus, and therefore an evolutionary test of sinus origins remains. Much work is necessary in this regard, especially including fossil taxa.

ACKNOWLEDGEMENTS

I thank my dissertation committee, including B. Demes, C. Forster, S. Judex, N. Kley, and J. Rossie, for numerous discussions and suggestions throughout the course of this research. Additional input by D. Boyer, M. Coleman, J. Georgi, S. Nichols, P. O'Connor, B. Patel, R. Racicot, M. Wedel, L. Witmer, E. Yoo, and numerous other individuals was also invaluable. Thanks are especially due to the Department of Mammalogy at the American Museum of Natural History and the Department of Vertebrate Zoology at the Yale Peabody Museum of Natural History, for access to specimens used in this research. E. Westwig (AMNH) and K. Zyskowski (YPM) offered invaluable support and assistance in borrowing specimens, and the CT scanning was completed in the Department of Radiology at Stony Brook University Hospital. Comments from an anonymous reviewer are acknowledged for improving the manuscript. This research was supported by a National Science Foundation Graduate Research Fellowship, and a grant from the Society of Integrative and Comparative Biology.

REFERENCES

Blaney SPA. 1990. Why paranasal sinuses? *Journal of Laryngology and Otology* **104:** 690–693.

Blanton PL, Biggs NL. 1968. Eighteen hundred years of controversy: the paranasal sinuses. *American Journal of Anatomy* **124:** 135–147.

Buntjer JB, Otsen M, Nijman IJ, Kuiper MTR, Lenstra JA. 2002. Phylogeny of bovine species based on AFLP fingerprinting. *Heredity* **88:** 46–51.

Caro TM, Graham CM, Stoner CJ, Flores MM. 2003. Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology* **55:** 32–41.

Coleman MN. 2008. What does geometric mean, mean geometrically? Assessing the utility of geometric mean and other size variables in studies of skull allometry. *American Journal of Physical Anthropology* **135:** 404–415.

Coleman MN, Colbert MW. 2007. Technical note: CT thresholding protocols for taking measurements on three-dimensional models. *American Journal of Physical Anthropology* **133:** 723–725.

Edinger T. 1950. Frontal sinus evolution (particularly in the Equidae). *Bulletin of the Museum of Comparative Zoology at Harvard College* **103:** 411–496.

Estes RD. 1991. *Behavior guide to African mammals*. Berkeley, CA: University of California Press.

Farke AA. 2007. Morphology, constraints, and scaling of frontal sinuses in the hartebeest, *Alcelaphus buselaphus* (Mammalia: Artiodactlya, Bovidae). *Journal of Morphology* **268:** 243–253.

Farke AA. 2008. Frontal sinuses and head-butting in goats: a finite element analysis. *Journal of Experimental Biology* **211:** 3085–3094.

Fernández MH, Vrba ES. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews of the Cambridge Philosophical Society* **80:** 269–302.

Garland T, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41:** 18–32.

Gatesy J, Arctander P. 2000. Hidden morphological support for the phylogenetic placement of *Pseudoryx nghetinhensis* with bovine bovids: a combined analysis of gross anatomical evidence and DNA sequences from five genes. *Systematic Biology* **49:** 515–538.

Geist V. 1966. The evolutionary significance of mountain sheep horns. *Evolution* **20:** 558–566.

Gentry AW. 1992. The subfamilies and tribes of the family Bovidae. *Mammal Review* **22:** 1–32.

Heyne K, Schumacher GH. 1967. Biometrische Untersuchungen an den Nebenhöhlen der Nase von Ovis aries. *Anatomischer Anzeiger* **120:** 433–443.

Hildebrand T, Laib A, Müller R, Dequeker J, Rüegsegger P. 1999. Direct three-dimensional morphometric analysis of human cancellous bone: microstructural data from spine, femur, iliac crest, and calcaneus. *Journal of Bone and Mineral Research* **14:** 1167–1174.

Hildebrand T, Rüegsegger P. 1997. A new method for the model-independent assessment of thickness in three-dimensional images. *Journal of Microscopy* **185:** 67–75.

Hönig JF, Merten HA, Schütte R, Grohmann UA, Cassisis A. 2002. Experimental study of the frontal sinus development on Goettingen miniature pigs. *Journal of Craniofacial Surgery* **13:** 418–426.

Jaslow CR. 1987. *A functional analysis of skull design in the Caprini*. Unpublished Ph.D. Dissertation, University of Chicago.

Kingdon J. 1982a. *East African mammals: an atlas of evolution in Africa. Volume III part C (Bovids)*. London: Academic Press.

Kingdon J. 1982b. *East African mammals: an atlas of evolution in Africa. Volume III Part D (Bovids)*. London: Academic Press.

Koppe T, Klauke T, Lee S, Schumacher G. 2000. Growth pattern of the maxillary sinus in the miniature pig (*Sus scrofa*). *Cells Tissues Organs* **167:** 58–67.

Koppe T, Nagai H. 1999. Quantitative analysis of the maxillary sinus in catarrhine primates. In: Koppe T, Nagai H, Alt KW, eds. *The paranasal sinuses of higher primates: development, function, and evolution*. Carol Stream, IL: Quintessence Publishing, 121–132.

Koppe T, Röhrer-Ertl O, Breier S, Wallner C. 2006. Maxillary sinus atelectasis in a wild born gibbon (*Hylobates moloch*). *Primates* **47:** 140–144.

Lalueza-Fox C, Castresana J, Sampietro L, Marques-Bonet T, Alcover JA, Bertranpetit J. 2005. Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. *BMC Evolutionary Biology* **5:** 70.

Matthee CA, Davis SK. 2001. Molecular insights into the evolution of the family Bovidae: a nuclear DNA perspective. *Molecular and Biological Evolution* **18:** 1220–1230.

Moore WJ. 1981. *The Mammalian Skull*. Cambridge: Cambridge University Press.

Paulli S. 1900. Über die Pneumaticität des Schädels bei den Säugerthieren. Eine morphologische Studie. II. Über die Morphologie des Siebbeins und die der Pneumaticität bei den Ungulaten und Probosciden. *Gegenbaurs Morphologisches Jahrbuch* **28:** 179–251.

Pidancier N, Jordan S, Luikart G, Taberlet P. 2006. Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): discordance between mitochondrial DNA and Y-chromosome phylogenies. *Molecular Phylogenetics and Evolution* **40:** 739–749.

Purvis A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions: Biological Sciences* **348:** 405–421.

Rae TC. 2008. Paranasal pneumatization in extant and fossil Cercopithecoidea. *Journal of Human Evolution* **54:** 279–286.

Rae TC, Hill RA, Hamada Y, Koppe T. 2003. Clinal variation of maxillary sinus volume in Japanese macaques (*Macaca fuscata*). *American Journal of Primatology* **59:** 153–158.

Rae TC, Koppe T. 2000. Isometric scaling of maxillary sinus volume in hominoids. *Journal of Human Evolution* **38:** 411–423.

Rae TC, Koppe T. 2003. The term 'lateral recess' and craniofacial pneumatization in Old World monkeys (Mammalia, Primates, Cercopithecoidea). *Journal of Morphology* **258:** 193–199.

Rae TC, Koppe T. 2008. Independence of biomechanical forces and craniofacial pneumatization in Cebus. *The Anatomical Record* **291:** 1414–1419.

Rae TC, Koppe T, Spoor F, Benefit B, McCrossin M. 2002. Ancestral loss of the maxillary sinus in Old World monkeys and independent acquisition in Macaca. *American Journal of Physical Anthropology* **117:** 293–296.

Rebholz W, Harley E. 1999. Phylogenetic relationships in the bovid subfamily Antilopinae based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **12:** 87–94.

Rossie JB. 2006. Ontogeny and homology of the paranasal sinuses in Platyrrhini (Mammalia: Primates). *Journal of Morphology* **267:** 1–40.

Schaffer WM. 1968. Intraspecific combat and the evolution of the Caprini. *Evolution* **22:** 817–825.

Schaffer WM, Reed CA. 1972. The co-evolution of social behavior and cranial morphology in sheep and goats (Bovidae, Caprini). *Fieldiana* **61:** 1–88.

Schreiber A, Seibold I, Notzold G, Wink M. 1999. Cytochrome b gene haplotypes characterize chromosomal lineages of anoa, the Sulawesi dwarf buffalo. *Journal of Heredity* **90:** 165–176.

Shea B. 1977. Eskimo craniofacial morphology, cold stress and the maxillary sinus. *American Journal of Physical Anthropology* **47:** 289–300.

Silva M, Downing JA. 1995. *Handbook of mammalian body masses*. Boca Raton: CRC Press.

Smith TD, Rossie JB, Cooper GM, Mooney MP, Siegel MI. 2005. Secondary pneumatization of the maxillary sinus in callitrichid primates: insights from immunohistochemistry and bone cell distribution. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology* **285A:** 677–689.

Solounias N, Moelleken SMC. 1992. Cranial restoration of *Eotragus sansaniensis* (Mammalia: Ruminantia), one of the oldest known bovids. *Journal of Vertebrate Paleontology* **12:** 250–255.

Vrba ES. 1979. Phylogenetic analysis and classification of fossil and recent Alcelaphini Mammalia: Bovidae. *Biological Journal of the Linnean Society* **11:** 207–228.

Vrba ES, Schaller GB. 2000. Phylogeny of Bovidae (Mammalia) based on behavior, glands and skull morphology. In: Vrba ES, Schaller GB, eds. *Antelopes, deer, and relatives: fossil record, behavioral ecology, systematics, and conservation*. New Haven, CT: Yale University Press, 203–222.

van Vuuren BJ, Robinson TJ. 2001. Retrieval of four adaptive lineages in duiker antelope: Evidence from mitochondrial DNA sequences and fluorescence in situ hybridization. *Molecular Phylogenetics and Evolution* **20:** 409–425.

Weidenreich F. 1924. Über die pneumatischen Nebenräume des Kopfes. Ein Beitrag zur Kenntnis des Bauprinzips der Knochen, des Schädels und des Körpers. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **72:** 55–93.

Weidenreich F. 1941. The brain and its role in the phylogenetic transformation of the human skull. *Transactions of the American Philosophical Society* **31:** 320–442.

Willows-Munro S, Robinson TJ, Matthee CA. 2005. Utility of nuclear DNA intron markers at lower taxonomic levels: Phylogenetic resolution among nine *Tragelaphus* spp. *Molecular Phylogenetics and Evolution* **35:** 624–636.

Witmer LM. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir* **3:** 1–73.

Zollikofer CPE, Weissmann JD. 2008. A morphogenetic model of cranial pneumatization based on the invasive tissue hypothesis. *The Anatomical Record* **291:** 1446–1454.

Zuckerkandl E. 1887. *Das Periphere Geruchsorgan der Säugethiere*. Stuttgart: Verlag von Ferdinand Enke.

APPENDIX 1

List of taxa, specimens and measurements used in this study

Taxon	Specimen	*N*	SV (ml)	SE	SCI	SE
Aepyceros melampus	YPM 9192, 9597, 11525	3	58.9	5.3	0.27	0.02
Alcelaphus buselaphus	YPM 7393, 9127, 9131, 9174, 9177, 9185, 10281, 10473, 11519, 11542	10	393.5	118.2	0.48	0.02
Antidorcas marsupialis	AMNH 165078, 165080, 233055	3	47.1	6.5	0.44	0.04
Antilope cervicapra	AMNH 19613, 54485, 54486	3	1.7	0.8	0.43	0.03
Bison bison	YPM 9021, 9022, 9023	3	2530.1	356.9	0.17	0.01
Bos javanicus	AMNH 113755	1	1626.0		0.21	
Boselaphus tragocamelus	AMNH 22842, 35520	2	104.3	5.8	0.21	0.00
Bubalus depressicornis	AMNH 61146, 152856, 152864	3	150.8	36.1	0.23	0.02
Bubalus mindorensis	AMNH 40046, 99339	2	499.6	316.6	0.21	0.03
Budorcas taxicolor	AMNH 110476, 110477	2	331.5	102.8	0.15	0.00
Capra aegagrus	AMNH 88691, 88697	2	302.2	113.5	0.21	0.04
Capra falconeri	AMNH 54610	1	451.3		0.16	
Capra nubiana	AMNH 82264	1	338.4		0.20	
Capra sibirica	AMNH 54906, 57317, 57318	3	364.1	211.5	0.25	0.08
Capricornis sumatraensis	AMNH 45348, 56981; YPM 7398	3	134.0	20.6	0.24	0.03
Cephalophus dorsalis	AMNH 52917, 52924, 52987	3	0.0	0.0		
Cephalophus leucogaster	AMNH 52799, 52802, 52804, 52843	4	0.0	0.0		
Cephalophus natalensis	AMNH 216376	1	0.0			
Cephalophus niger	AMNH 89402	1	0.0			
Cephalophus nigrifrons	AMNH 52949, 52989	2	0.0	0.0		
Cephalophus silvicultor	AMNH 55382, 55383, 170368	3	0.0	0.0		
Connochaetes taurinus	YPM 9537, 9585, 10282, unnumbered	4	357.1	73.2	0.33	0.03
Damaliscus lunatus	YPM 9482, 9586	2	156.9	15.8	0.38	0.01
Eudorcas thomsonii	YPM 9246, 9651, 10480	3	0.8	0.5	0.46	0.03
Gazella dorcas	AMNH 82283, 82285, 82288	3	0.2	0.4	0.47	
Gazella subgutturosa	AMNH 57263, 57272	2	0.6	0.7	0.48	0.01
Hemitragus hylocrius	AMNH 54755; YPM 7391	2	244.3	49.3	0.15	0.00
Hippotragus equinus	YPM 9141	1	220.9		0.28	
Hippotragus niger	AMNH 83606; YPM 9140	2	216.2	8.9	0.31	0.04
Kobus ellipsiprymnus	YPM 9101, 9183, 9193	3	15.6	9.4	0.32	0.06
Kobus kob	YPM 9164	1	3.4		0.30	
Kobus leche	YPM 11524	1	12.2		0.44	
Kobus vardonii	YPM 8975	1	0.0			
Litocranius walleri	AMNH 81170; YPM 9602, 10278	3	0.9	0.3	0.43	0.02
Madoqua kirkii	YPM 9600, 10561, 10563	3	0.1	0.1	0.50	0.03
Naemorhedus goral	AMNH 43033, 110485	2	34.6	5.9	0.26	0.00
Nanger granti	YPM 9480, 9605, 11526	3	2.6	1.9	0.44	0.03
Neotragus batesi	AMNH 53169, 53192, 53202	3	0.0	0.0		
Neotragus moschatus	YPM 3129	1	0.0			
Oreamnos americanus	AMNH 60793, 128105; YPM 11552	3	45.2	11.4	0.32	0.02
Oreotragus oreotragus	AMNH 27827; YPM 8399, 10275	3	0.2	0.2	0.43	0.12
Oryx gazella	AMNH 233035	1	227.8		0.24	
Ourebia ourebi	AMNH 90163, 118450; YPM 7389	3	0.0	0.0	0.00	
Ovibos moschatus	AMNH 29949, 80095	2	568.8	118.3	0.16	0.02
Ovis ammon	YPM 4295, 54885	2	973.4	10.1	0.11	0.02
Ovis canadensis	YPM 6682, 7376, 7377	3	1374.9	131.6	0.09	0.01
Pantholops hodgsonii	AMNH 55818, 55819; YPM 9554	3	27.8	1.5	0.34	0.02
Pelea capreolus	AMNH 80919, 80920; YPM 7386	3	0.0	0.0		
Philantomba maxwellii	AMNH 89432, 89625	2	0.0	0.0		
Procapra gutturosa	AMNH 57252, 57260, 85235	3	0.0	0.0		
Pseudois nayaur	AMNH 110494, 117401	2	645.4	380.5	0.12	0.03

APPENDIX 1 *Continued*

Taxon	Specimen	*N*	SV (ml)	SE	SCI	SE
Raphicerus campestris	AMNH 54186, 54193; YPM 10276	3	0.0	0.0		
Redunca arundinum	YPM 9180, 9186, 11545	3	0.1	0.1	0.46	0.09
Redunca fulvorufula	AMNH 54257; YPM 9594, 10277	3	0.0	0.0	0.56	
Rupicapra rupicapra	AMNH 90235, 90237	2	38.0	14.8	0.25	0.01
Saiga tatarica	AMNH 85301; YPM 7397	2	2.5	0.6	0.45	0.04
Sigmoceros lichtensteinii	YPM 8952, 8955, 8968, 9106, 11535	5	491.0	71.0	0.36	0.02
Sylvicapra grimmia	YPM 10523, 10524, 10525	3	0.0	0.0		
Syncerus caffer	YPM 11649	1	4461.8		0.12	
Taurotragus oryx	YPM 9549, 10471, 11549	3	10.3	4.3	0.38	0.02
Tetracerus quadricornis	AMNH 54941, 54983; YPM 7396	3	18.0	4.4	0.25	0.01
Tragelaphus scriptus	YPM unnumbered (3)	3	0.0	0.0		
Tragelaphus strepsiceros	YPM 8957, unnumbered	2	0.0	0.0		

Abbreviations: *N*, number of specimens; SV, sinus volume in milliliters; SE, standard error; SCI, sinus complexity index.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Measurements used in this study.
Table S2. Measurements of individual specimens.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.