RESEARCH ARTICLE

The Mummified Brain of a Pleistocene Woolly Mammoth (*Mammuthus primigenius*) Compared With the Brain of the Extant African Elephant (*Loxodonta africana*)

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ABSTRACT

This study presents the results of an examination of the mummified brain of a pleistocene woolly mammoth (*Mammuthus primigenius*) recovered from the Yakutian permafrost in Siberia, Russia. This unique specimen (from 39,440–38,850 years BP) provides the rare opportunity to compare the brain morphology of this extinct species with a related extant species, the African elephant (*Loxodonta africana*). An anatomical description of the preserved brain of the woolly mammoth is provided, along with a series of quantitative analyses of various brain structures. These descriptions are based on visual inspection of the actual specimen as well as qualitative and quantitative comparison of computed tomography imaging data obtained for the woolly mammoth in comparison with magnetic resonance imaging data from three African elephant brains. In general, the brain of the woolly mammoth specimen examined, estimated to weigh between 4,230 and 4,340 g, showed the typical shape, size, and gross structures observed in extant elephants. Quantitative comparative analyses of various features of the brain, such as the amygdala, corpus callosum, cerebellum, and gyrnecephalic index, all indicate that the brain of the woolly mammoth specimen examined has many similarities with that of modern African elephants. The analysis provided here indicates that a specific brain type representative of the Elephantidae is likely to be a feature of this mammalian family. In addition, the extensive similarities between the woolly mammoth brain and the African elephant brain indicate that the specializations observed in the extant elephant brain are likely to have been present in the woolly mammoth. J. Comp. Neurol. 523:2326–2343, 2015.

INDEXING TERMS: Proboscidae; Elephantidae; Mammuthus; Pleistocene; permafrost; brain preservation; brain evolution

The brains of extinct Proboscideans, including mammoths, have not been the object of frequent study (Jerison, 1973; Cozzi et al., 2001). Even though several well-preserved frozen mummies of the large mammals, including woolly mammoths, have been found in the Siberian permafrost (Zalenskii, 1903; Zimmerman and Tedford, 1976; Vereschagin and Michelson, 1981), our current knowledge of the structure of the woolly mammoth brain is based solely on endocranial casts, and even these data are not extensively covered in the literature (Benoit et al., 2013; Manger et al., 2013). It is rare to find naturally preserved brains, even among mummified human remains, and these rarely exhibit

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any microscopically identifiable structures (Tkocz et al., 1979; Radanov et al., 1992; Gerszten and Martinez, 1995; Previgliano et al., 2003; Eklektos et al., 2006; Kim et al., 2008; Maixner et al., 2012). Similarly, frozen woolly mammoth mummies have revealed only featureless masses of nervous tissue remnants (Kreps et al., 1981). The Yuka woolly mammoth brain examined in the present study (Kharlamova et al., 2014) is a unique specimen, as the state of the mummified brain preserved in the Siberian permafrost allowed us to describe both the external morphology and internal structures using computed tomography (CT) imaging techniques. This in turn provides the opportunity to compare the brain morphology of the extinct woolly mammoth with the extant African elephant.

The woolly mammoth (*Mammuthus primigenius*, Blumenbach 1799) is the most recent known representative of the mammoth lineage (family Elephantidae, Gray, 1821). The extant elephants belong to the *Elephas* (Linnaeus, 1758) and *Loxodonta* (Anonymous, 1827) lineages, which are also within the family Elephantidae and are closely related to the *Mammuthus* (Brookes, 1828) (Maglio, 1973; Shoshani and Tassy, 2005), although the extant genus the mammoths are most closely related to is still debated. The *Elephas–Mammuthus* hypothesis is based on morphological evidence, whereas the *Loxodonta–Mammuthus* hypothesis is based on molecular analyses (Shoshani and Tassy, 2005).

The brains of extant elephants evince a generally Eutherian mammal structure, but there are several specific features found only in this group (Cozzi et al., 2001; Shoshani et al., 2006). The extant elephants have the largest terrestrial brains (Cozzi et al., 2001; Shoshani et al., 2006; Manger et al., 2009), and the cerebral cortex appears to have extensive parietal and temporal lobes (Cozzi et al., 2001; Shoshani et al., 2006). Although the cerebral cortex is extensively gyrencephalic, it is no more gyrencephalic than would be expected for its brain mass (Manger et al., 2012). It has been shown that the African elephant cerebral cortex lacks a layer IV (Jacobs et al., 2011), but in the case of the Asian elephants the presence or absence of a layer IV, or how clearly present this layer is, remains in doubt (Van't Hoog, 1920; Tower, 1954; Cozzi et al., 2000). Elephants have large olfactory bulbs, with extensive layering of the glomeruli, and the bulbs are connected to the brain by short, thick olfactory tracts; however, no accessory olfactory bulb is present (Ngwena et al., 2011). Elephants have the largest cross-sectional area of the corpus callosum of any mammal studied to date, but this is reflective of the size of the brain rather than a specialization of this commissure (Manger et al., 2010). In addition, there appears to be a sexual dimorphism in the corpus callosum area, with females having a larger cross-sectional area than males (Manger et al., 2010).

In terms of the hippocampal formation, it is large in size, but is what would be expected for a mammal with an approximately 5-kg brain. The volume of the elephant amygdala, although large, is what would be expected for a mammal with a 5-kg brain (Patzke et al., 2015), with a similar observation being made regarding the volume of the lateral ventricles (Maseko et al., 2011). Elephants have the relatively largest cerebellum among mammals (Maseko et al., 2012, 2013a), with approximately 251×10^9 neurons, which is substantially more than in any other mammal studied to date (Herculano-Houzel et al., 2014). All the typical mammalian cerebellar lobules can be described in the anterior, posterior, and caudal lobes of the cerebellar hemispheres and vermis (Ariens-Kappers et al., 1936; Larsell, 1947; Nieuwenhuys et al., 1998), but the large fifth lobule of the anterior lobe and simplex lobule (sixth cerebellar lobule) are features specific to the elephant brain (Nieuwenhuys et al., 1998). There are also several specialized features within the brainstem and diencephalon that have been identified at the histological level (Maseko et al., 2013b). The pars compacta of the substantia nigra, the inferior olivary nuclear complex, and the motor nucleus of the facial nerve are all specialized, and this is most likely correlated with control of trunk movement (Maseko et al., 2013b). Five features related to sound production and reception are specific for elephants, including the nucleus ellipticus of the periaqueductal gray matter of the midbrain (Precechtel, 1925; Maseko et al., 2013b), the enlarged lateral superior olivary nucleus (Maseko et al., 2013b), the transverse infrageniculate nucleus of the dorsal thalamus (Precechtel,1925; Abe, 1952; Maseko et al., 2013b), and the enlarged dorsal column nuclei and the ventral posterior inferior nucleus of the dorsal thalamus (Maseko et al., 2013b). In addition, two novel nuclei related to arousal and sleep in the orexinergic (a parvocellular hypothalamic cluster) and noradrenergic (a medial locus coeruleus nucleus) systems have been observed (Maseko et al., 2013b).

Given this range of typically mammalian and elephant-specific features in the brains of extant elephants, the study of the preserved woolly mammoth brain is of interest, as it will be able to inform us, within the limits of the preservation state of the specimen, whether these features were present or absent in the earlier stages of Elephantidae brain evolution, or whether they have been acquired more recently. In addition, the potential similarities and differences in these structures may reveal insights into the behavior and life history of the extinct mammoths that have yet to be revealed and what might be accurately inferred about woolly mammoths from behavioral observations of extant elephants.

MATERIALS AND METHODS

The naturally preserved brain of a woolly mammoth (*Mammuthus primigenius*, Blumenbach, 1799) from the Yakutian permafrost (Kharlamova et al., 2014) and three brains of adult male African elephants (*Loxodonta africana*) (Manger et al., 2009) were used in this study. The mummified carcass of the woolly mammoth, informally named Yuka, was found in August 2010 on the coast of the Laptev Sea in Siberia. Radiocarbon dating of the sampled Yuka mammoth bone revealed estimated dates of existence between 39,440 and 38,850 years BP (GrA_53289) (Boeskorov et al., 2013). Based on the state of the cranial sutures, as well as teeth generation and wear (DP4.M1), as observed in Asian elephants (Roth and Shoshani, 1988), the estimated age of the Yuka mammoth is 6–9 years. The estimated body mass of the Yuka woolly mammoth is 460 kg, as determined from the estimated height from the foot circumference (160 cm; Boeskorov et al., 2013) in accordance with the data on the correlation of height to weight in Asian elephants (Sukumar et al., 1988). This value is larger than the value defined from the estimated body size (350–400 kg), but smaller than the approximation from the mummified carcass (540–700 kg), which weighed 240 kg. The Yuka mammoth specimen was an adolescent female; thus we might expect that its brain may be somewhat smaller than that of adult woolly mammoths, but it is likely to be very close, as the estimated upper age of 9 years is only 1–3 years from the age of sexual maturity observed in Asian elephants (Sukumar, 1994). For details of the fixation and handling of the woolly mammoth brain, see Kharlamova et al. (2014), and for details of the three brains of the adult male African elephants, see Manger et al. (2009).

The CT scanning data of the woolly mammoth brain and magnetic resonance imaging (MRI) of three African elephant brains were used for the volumetric analysis. The CT scanning of the Yuka woolly mammoth brain was undertaken while the brain was still inside the cranium, and was done using a Somatom Emotion 16 CT machine (Seimens, Munich, Germany; 512×512, $0.56 \times 0.56 \times 1.5$ mm, $n = 256$) (see Kharlamova et al., 2014 for details of the scanning process). The three African elephant brains were scanned after removal from the skull in coronal, sagittal, and horizontal planes on a Philips 1.5 Tesla Intera System (Eindhoven, The Netherlands) (for details of the scanning process, see Manger et al., 2010).

The internal brain structures of the woolly mammoth could be identified on the serial CT scans, but in many instances the borders of these structures were not clearly visible due to the preservation state of the material. To avoid the inaccurate reporting of the size of specific brain structures, we limited our analysis to those structures with clearly visible borders. The total volume of the structures was calculated by summing each of the areas on each coronal slice from the most rostral to the most caudal slices in which the structure was present and multiplying this total area by the slice thickness (1.5-mm slice thickness for the woolly mammoth CT scans and 2 mm for the African elephant MR images). The images were processed by using the freely available open source software program OsiriX (Rosset et al., 2004; www.osirix-viewer.com). Calculation of the corpus callosum area, gyrencephalic index, amygdala volume, and cerebellar volumes was undertaken in accordance with previously published studies investigating these parameters in the African elephant (respectively, Manger et al., 2010, 2012; Zilles et al., 1989; Patzke et al., 2015; Maseko et al., 2012). To establish the brain mass of the Yuka mammoth, several different methods were tried, all appearing to converge on a similar result. The details of these methods are provided in the Results section, as the details of the methods are important to the calculation of brain mass. When some of the volumes and areas used for comparison were calculated, the data had to be corrected for shrinkage, and the details of these correction factors are provided in each case.

RESULTS

General appearance of the Yuka mammoth brain and calculation of brain mass

The Yuka mammoth specimen evinced the typical shape and size of the brain observed in modern elephants (Fig. 1). The central problem with direct comparisons was that, due to the preservation of the mammoth tissue, the Yuka mammoth brain had undergone extensive and differential shrinkage, such that the volume of the actual mummified Yuka mammoth brain was 54.83% of the volume of the endocranial cavity. This volume decrease appears to be the result of dehydration during the long-term mummification of the tissue in the permafrost. In contrast, the dura mater appeared to have shrunk minimally in comparison with the brain, probably because it was constituted of connective tissue composed mostly of collagen fibres (Kharlamova et al., 2014). Even so, a direct comparison

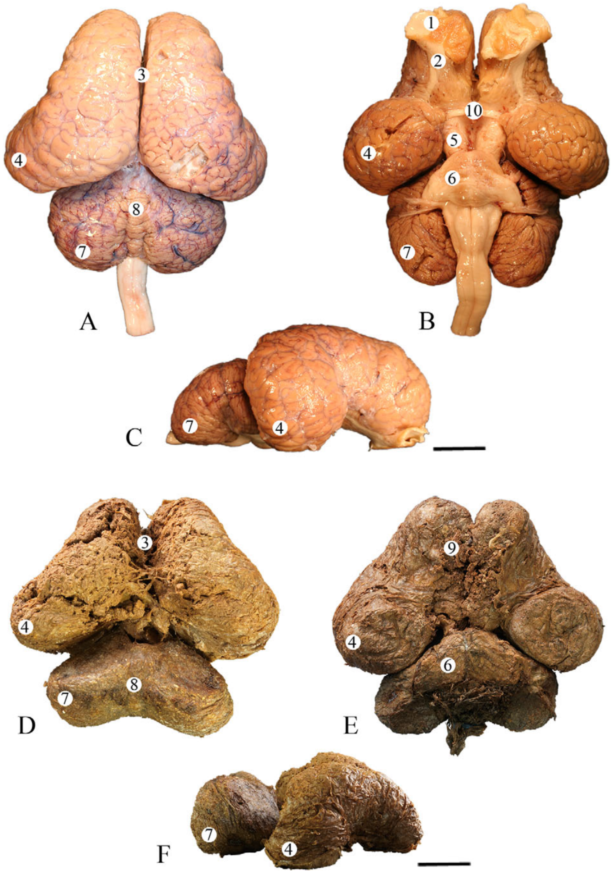

Figure 1. Brain of the African elephant in dorsal (**A**), ventral (**B**), and lateral (**C**) views and the mummified brain of the Yuka woolly mammoth specimen from the dorsal (**D**), ventral (**E**), and lateral (**F**) views. Note the overall similarity in size and shape of the cerebral hemispheres and the cerebellum, features that indicate the woolly mammoth has a typical Elephantidae brain structure. 1, olfactory bulb; 2, olfactory tract; 3, interhemispheric fissure; 4, temporal lobe; 5, cerebral peduncle; 6, pons; 7, cerebellar hemisphere; 8, cerebellar vermis; 9, damaged olfactory tubercle of the Yuka woolly mammoth specimen. (A–C are reproduced from Kharlamova et al., 2014, with permission from Elsevier Science Publishers.) Scale bar = 5 cm in C (applies to A–C) and F (applies to D–F).

with the African elephant brain (Fig. 1) revealed the presence of the interhemispheric fissure (Shoshani et al., 2006), the laterally expanded temporal lobes and rostrally gently tapering frontal lobes, the cerebral peduncles, the ventral pons, and the vermis and hemispheres of the large cerebellum (Fig. 1). Thus, in overall appearance, the gross morphology of the Yuka mammoth brain was very similar to that of the extant African elephant brain.

As mentioned above, the overall brain volume of the Yuka mammoth specimen only occupied approximately 55% of the total endocranial volume, having undergone substantial shrinkage during preservation. We calculated that the actual volume of the mummified Yuka mammoth brain specimen was 2,755.42 cm^3, whereas the volume of the endocranial cavity was 5,025 cm^3. If brain mass was calculated directly from endocranial volume using the specific gravity of brain tissue, which is 1.036 (Stephan et al., 1981), the Yuka mammoth specimen would be predicted to have a brain mass of approximately 5,205.9 g; however, the brain does not occupy the entire endocranial volume, and therefore this estimate is likely to be an overestimate of the brain mass of the Yuka mammoth brain. As a second approximation, we measured the volume of the space left unoccupied by the intact dura mater, providing a subdural volume of 4,092.6 cm^3, approximately 81.44% of the endocranial volume. Thus the brain mass calculated on subdural volume would be 4,239.93 g, markedly smaller (by 965.96 g) than that calculated with the total endocranial volume. Even though this calculation appears to be a more realistic calculation of the Yuka mammoth brain mass, a third calculation was undertaken. In this case, to create regression equations from which brain volume, and thus brain mass could be extrapolated for the Yuka mammoth specimen (Fig. 2), we used previously reported endocranial and brain volumes from a range of extant mammals (Rohrs and Ebinger, 2001), i.e., 17 species including European rabbit (*Oryctolagus cuniculus*), least weasel (*Mustela nivalis*), stoat (*Mustela erminea*), Beech marten (*Martes foina*), tayra (*Eira barbara*), Falkland Island's wolf (*Dusicyon australis*), Azara's fox (*Dusicyon gymnocercus*), crab-eating fox (*Cerdocyon thous*), culpeo (*Dusicyon culpaeus*), golden jackal (*Canis aureus*), coyote (*Canis latrans*), gray wolf (*Canis lupus*), guanaco (*Lama guanicoe*), domestic goat (*Capra hircus*), southern tamandua (*Tamandua tetradactyla*), giant anteater (*Myrmecophaga tridactyla*,) and wild horse (*Equus ferus*). In this instance, we estimated that the brain volume of the Yuka mammoth specimen should be approximately 4,183.84 cm^3, and the brain mass should be approximately 4334.23 g. The largest species used in creating this regression is the horse; data for larger animals are not available, and thus the scaling may not be precisely reflective of the situation in mammoths, but is likely to be a good approximation. The last two estimates are within 100 g of each other, so we feel confident in estimating the mass of the Yuka mammoth brain specimen as somewhere between 4,230 and 4,340 g (giving a maximal error in mass determination of 2.30–2.36%).

The Yuka mammoth estimated brain mass is smaller than the actual brain masses of the African elephant brain specimens, but the Yuka woolly mammoth was not older than 9 years, and thus its brain mass could be expected to be somewhat smaller than the expected

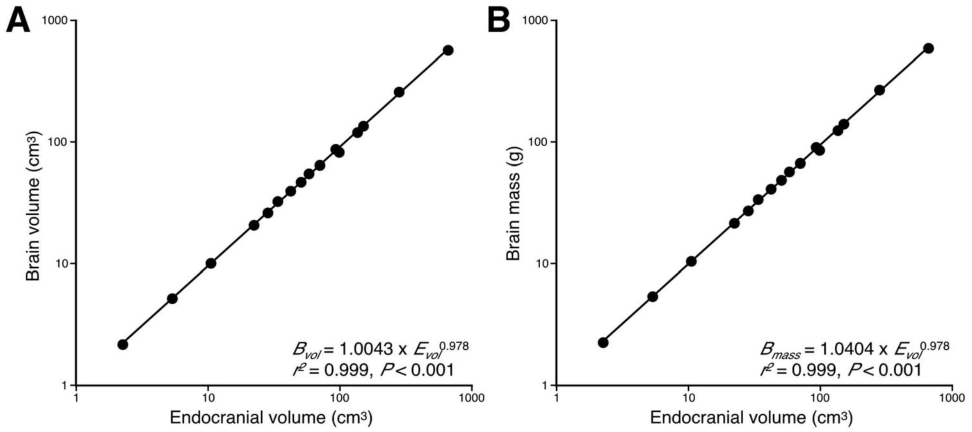

Figure 2. Plots of endocranial volume against brain volume (**A**) and brain mass (**B**) in a range of extant eutherian mammals. The data for creating these plots were taken from Rohrs and Ebinger (2001). The equations derived from these plots were used as one method to calculate the brain mass of the Yuka mammoth specimen. Note the slight negative allometry in the plots, indicating that as brains increase in size, the proportion of the endocranial cavity occupied by structures other than the brain (such as meninges and cerebrospinal fluid) increase in a predictable manner.

brain mass of the adult mammoths. Thus it appears that the woolly mammoths and extant elephants had similar overall brain masses. Encephalization quotients for the three African elephants used in the current study, with an estimated body mass of around 5,000 kg (they were all adult males aged between 20 and 30 years), and brain masses of 5,145 g, 5,250 g, and 4,835 g (Manger et al., 2009), were 1.25, 1.28, and 1.17, respectively, based on the equation provided in Manger (2006). For the Yuka mammoth, where estimates for body mass range from 350 to 700 kg (see Materials and Methods), the encephalization quotient could range from anywhere between 4.31 and 7.33 (based on the equation provided in Manger, 2006), although these estimates are likely to be unrealistically high, as the Yuka mammoth had not reached full body size. Futhermore, the Yuka mammoth specimen appeared to be a small specimen compared with the overall woolly mammoth population (Dr. E.M. Maschenko, personal communication), and the estimates of body mass appear to be markedly smaller than what an adult woolly mammoth would be expected to weigh. Thus, we do not place any strong value on the encephalization quotient estimates for the Yuka mammoth specimen, because an accurate prediction could not be made.

Features of the woolly mammoth telencephalon

The CT scans revealed that the Yuka mammoth specimen appeared to possess the typical major subdivisions of the telencephalon including the cerebral cortex, olfactory bulb and olfactory pallium (olfactory tubercle and piriform cortex), limbic pallium (cingulate cortex), hippocampal formation, amygdaloid complex, septal nuclear complex, and striatopallidal complex (caudate and putamen separated by a large internal capsule, globus pallidus, nucleus accumbens), as well as a distinctive corpus callosum. All these subdivisions of the telencephalon appeared to occupy the same position as seen in the African elephant. Unfortunately, the state of preservation of the tissue did not allow precise delineation of several of these structures, including the hippocampal formation, the septal nuclei, and the general borders of the striatopallidal complex. In addition, the olfactory tubercles, tracts, and bulbs appear to have degenerated, although the CT scans indicate the presence of these structures based on the morphology of the bony base of the endocranial cavity (Fig. 1). In addition, it was difficult to determine the exact pattern of the sulci and gyri from the surface view of the brain due to the smoothness of the cortical surface–even the sylvian sulcus (as defined by Shoshani et al., 2006; or pseudosylvian sulcus according to Nieuwenhuys et al., 1998) was difficult to define precisely (Fig. 1B). Even so, we were able to recognize the region of the piriform cortex, which, as in the African elephant, was clearly defined in CT scans by the presence of a large rhinal sulcus (Fig. 3).

As mentioned above, the brain of the Yuka mammoth specimen had undergone substantial shrinkage during preservation. This shrinkage was not uniform across the specimen, with the cerebral hemispheres having undergone substantially more shrinkage than the cerebellum. To make corrections to the measurements and

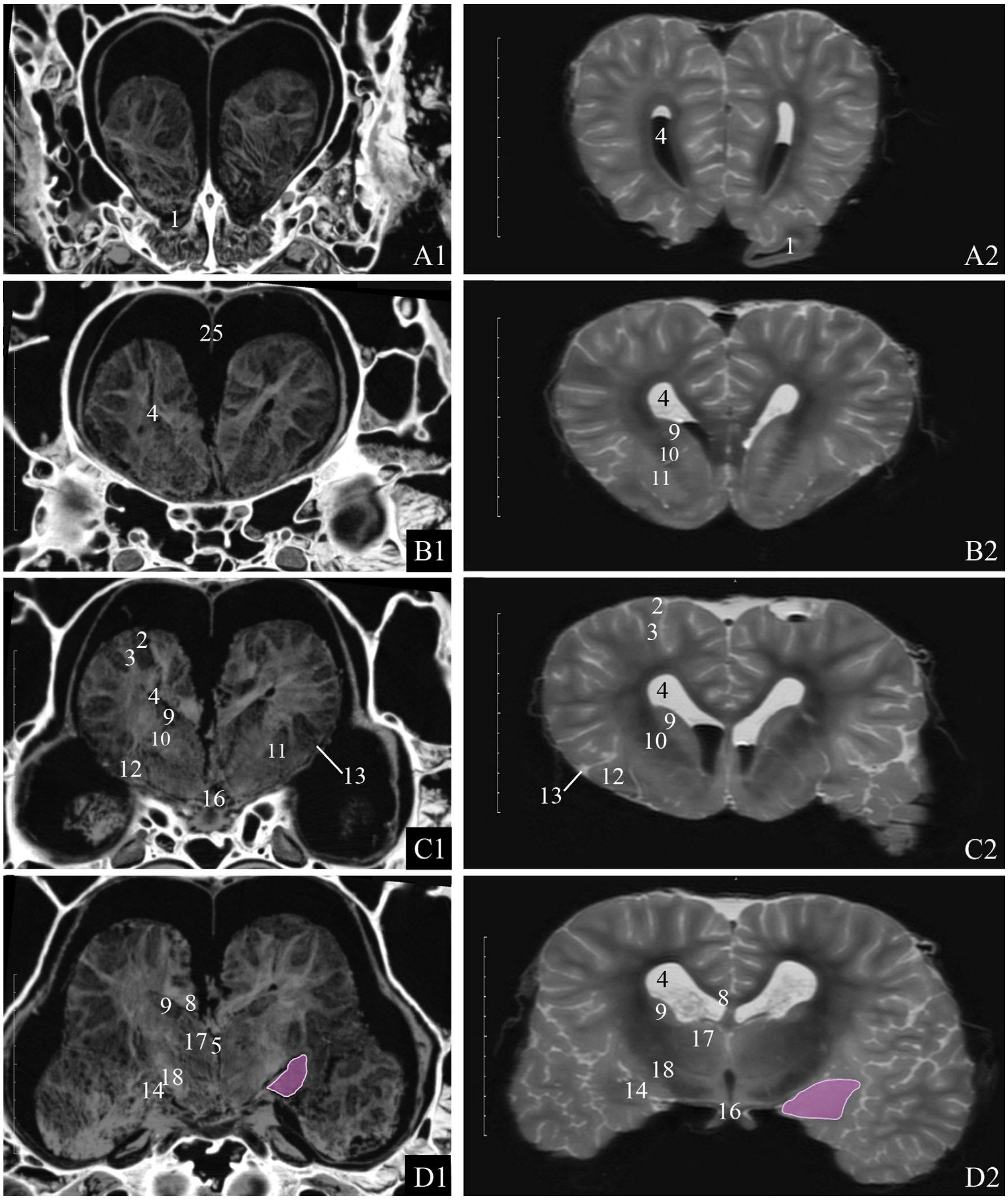

Figure 3. Coronal series of CT scans of the brain of the woolly mammoth (**A1**–**H1**) and corresponding MR images of the African elephant brain (specimen LA1) (**A2**–**H2**). Note that even despite the shrinkage occuring during the preservation of the Yuka mammoth specimen, the CT scans and MR images reveal very similar internal anatomical structures for both species. **D** and **H** are examples of the outlines used to determine the volume of the amygdala and vermis of the cerebellum, respectively. 1, olfactory bulb/olfactory bulb and tracts (these were damaged in the Yuka mammoth specimen), 2, cerebral cortex, gray matter; 3, white matter of the cerebral hemisphere; 4, lateral ventricle; 5, third ventricle; 6, cerebral aqueduct; 7, fourth ventricle; 8, corpus callosum; 9, caudate nucleus; 10, internal capsule; 11, putamen; 12, piriform cortex; 13, rhinal sulcus; 14, amygdala; 15, hippocampus; 16, optic chiasm; 17, dorsal thalamus; 18, cerebral peduncle; 19, lateral lemniscus; 20, superior and inferior colliculi; 21, cerebellar hemisphere; 22, cerebellar vermis; 23, middle cerebellar peduncle; 24, medulla oblongata (degraded in the Yuka mammoth specimen); 25, falx cerebri; 26, anterior lobe of cerebellum; 27, posterior lobe of cerebellum; 28, flocculonodular lobe; 29, nodule. (E1 was adapted from Kharlamova et al., 2014, with permission from Elsevier Science Publishers). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

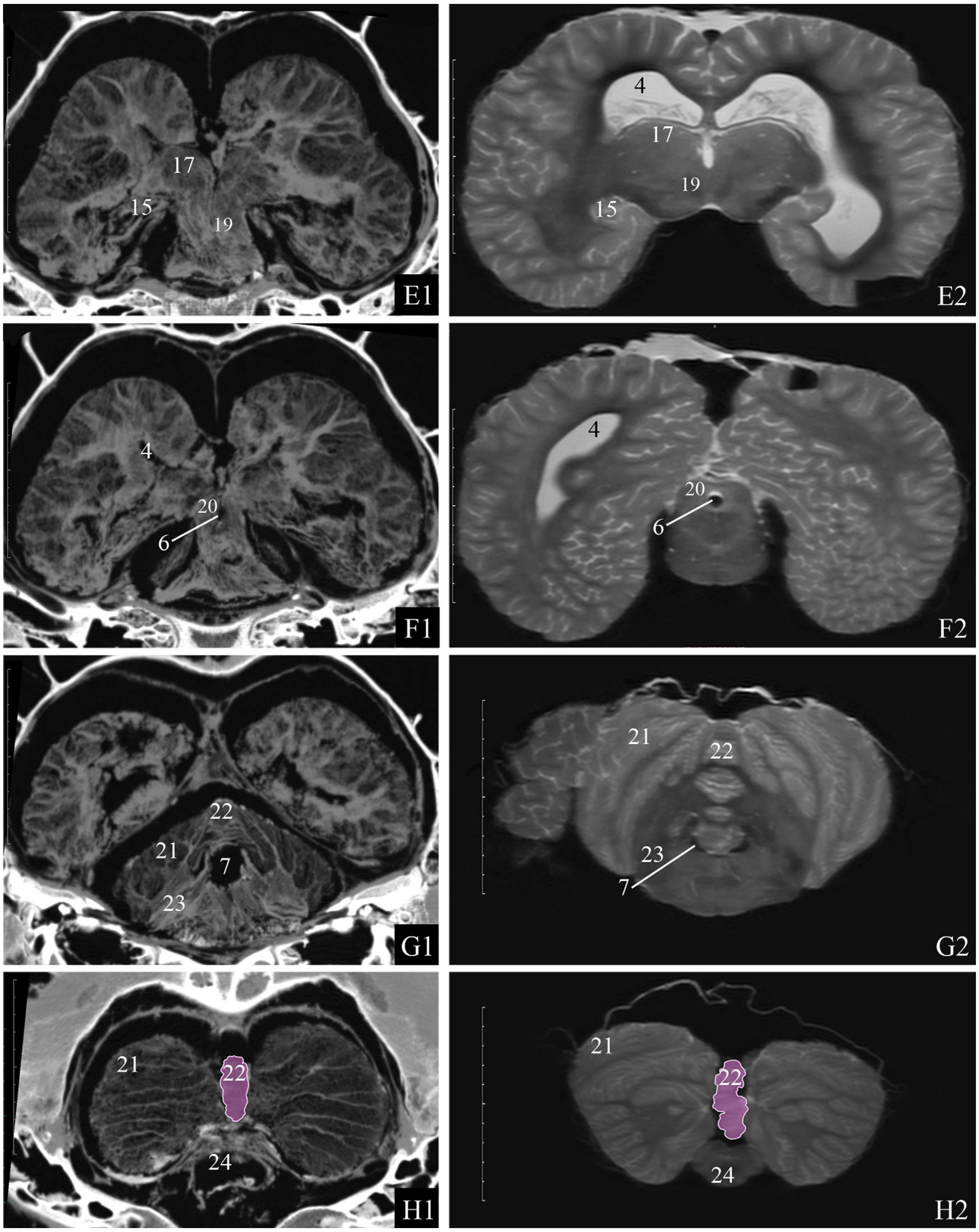

Figure 3. (Continued)

comparisons reported below, we calculated the actual volume of the cerebral hemispheres and the predicted volume of the cerebral hemispheres from the volume encased by the dura mater. In this case, the actual volume of the Yuka mammoth specimen right hemisphere was 1,009.64 cm^3 and the left hemisphere was 933.50 cm^3. The volume encased by the dura mater for the right hemisphere was 1,435.06 cm^3, and for the left hemisphere it was 1,643.95 cm^3. Thus we calculated that the right hemisphere had shrunk to approximately 70.36% of what the original size would have been, whereas the left hemisphere had shrunk to approximately 56.78% of what the original size would have been. Thus, below we report the actual values obtained from the specimen, along with the values obtained when this shrinkage was corrected for.

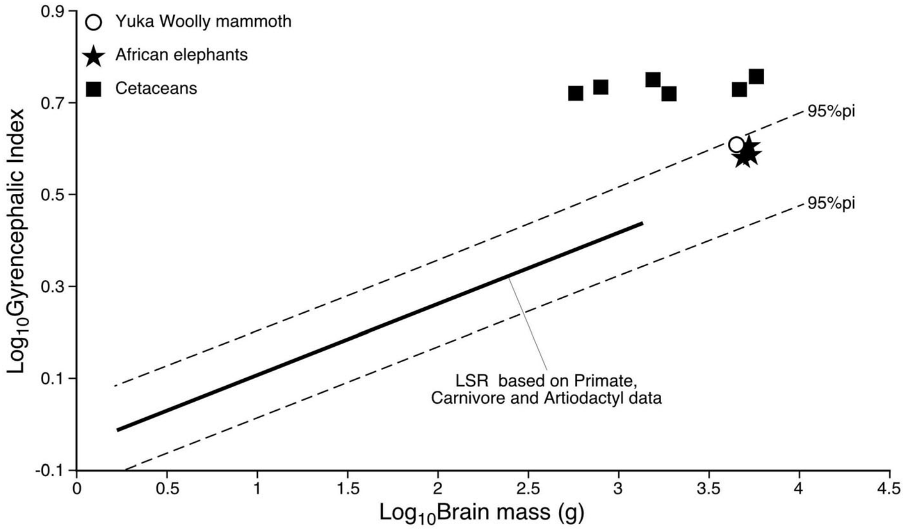

Figure 4. Graphic plot depicting the relationship between the gyrencephalic index (GI) and brain mass on log-transformed data of the primate, carnivore, and artiodactyl species investigated in Manger et al. (2012), from which the current image was redrawn. The least squares regression (LSR) with associated 95% prediction intervals (95%pi) were plotted on the graphs based on a combination of primate, carnivore, and artiodactyl data. Note that the gyrencephalic index of the Yuka mammoth specimen is very similar to that of the African elephants, although both fall within the prediction intervals based on data from other gyrencephalic mammals. This is unlike the cetaceans, which are significantly more gyrencephalic than all other mammals. In this sense, the mammoth and the elephants have a gyrencephalic index that one might predict based on their brain mass.

The CT scans of the Yuka mammoth specimen taken in the coronal plane revealed the distinctive pattern of the white–gray matter border of the cerebral cortex and the presence of many sulci and gyri. (However, these were difficult to name and relate to descriptions in the African elephant, except for the rhinal sulcus noted above.) The presence of relatively clear sulci and gyri in the CT scans (Fig. 3) allowed calculation of the gyrencephalic index, a measure of the extent of cortical folding (Zilles et al., 1989; Manger et al., 2012). The gyrencephalic index calculated for the Yuka mammoth specimen was 4.1, which is slightly higher than that calculated for the three African elephant specimens (4.01, 3.85, and 3.81; Manger et al., 2012), but still substantially lower than that observed for modern cetacean brains (5.23–5.70; Manger et al., 2012). Despite this high gyrencephalic index, the comparison with a broad range of mammals indicates that, unlike cetaceans, the degree of cortical folding in the Yuka mammoth specimen is within what could be predicted for a mammal with a brain mass of that determined for the woolly mammoth (Fig. 4). Unfortunately, it was difficult to correct for shrinkage in this case; thus the original value for the gyrencephalic index is used for comparison, but it is likely that if we could determine how to correct for shrinkage, the result would not change significantly.

The corpus callosum was readily visible in the medial sagittal CT scans in the Yuka mammoth specimen (Fig. 5C1), and although somewhat foreshortened in the rostrocaudal direction due to shrinkage of the brain, it evinced a shape similar to that seen in the African elephant. Although there appeared to be some damage to this specimen at the midline, we were able to obtain a direct measurement of the sagittal cross-sectional area from the right cerebral hemisphere, this value being 8.88 cm^2. This measurement of the actual specimen is comparable to those of three male African elephants (8.515, 10.192, and 9.191 cm^2) and a male Asian elephant (8.085 cm^2), but smaller than that obtained for a female African elephant (12.8 cm^2) and female Asian elephant (12.57 cm^2) (Manger et al., 2010). As this raw specimen measurement was made in the right hemisphere, we can apply a correction for shrinkage, which, for the Yuka mammoth specimen, would provide a midsagittal corpus callosum area of 11.49 cm^2. This corrected value is markedly larger than the values previously obtained for male African and Asian elephants, and is much closer to the values obtained previous for female African and Asian elephants. Given that the Yuka mammoth was a female, this corrected corpus callosum area appears to fit with previous data (Manger et al., 2010). In addition, the relative size of the Yuka mammoth corrected corpus callosum area is well within the range of what would be predicted for a mammal with a brain mass of that of the woolly mammoth (Fig. 6).

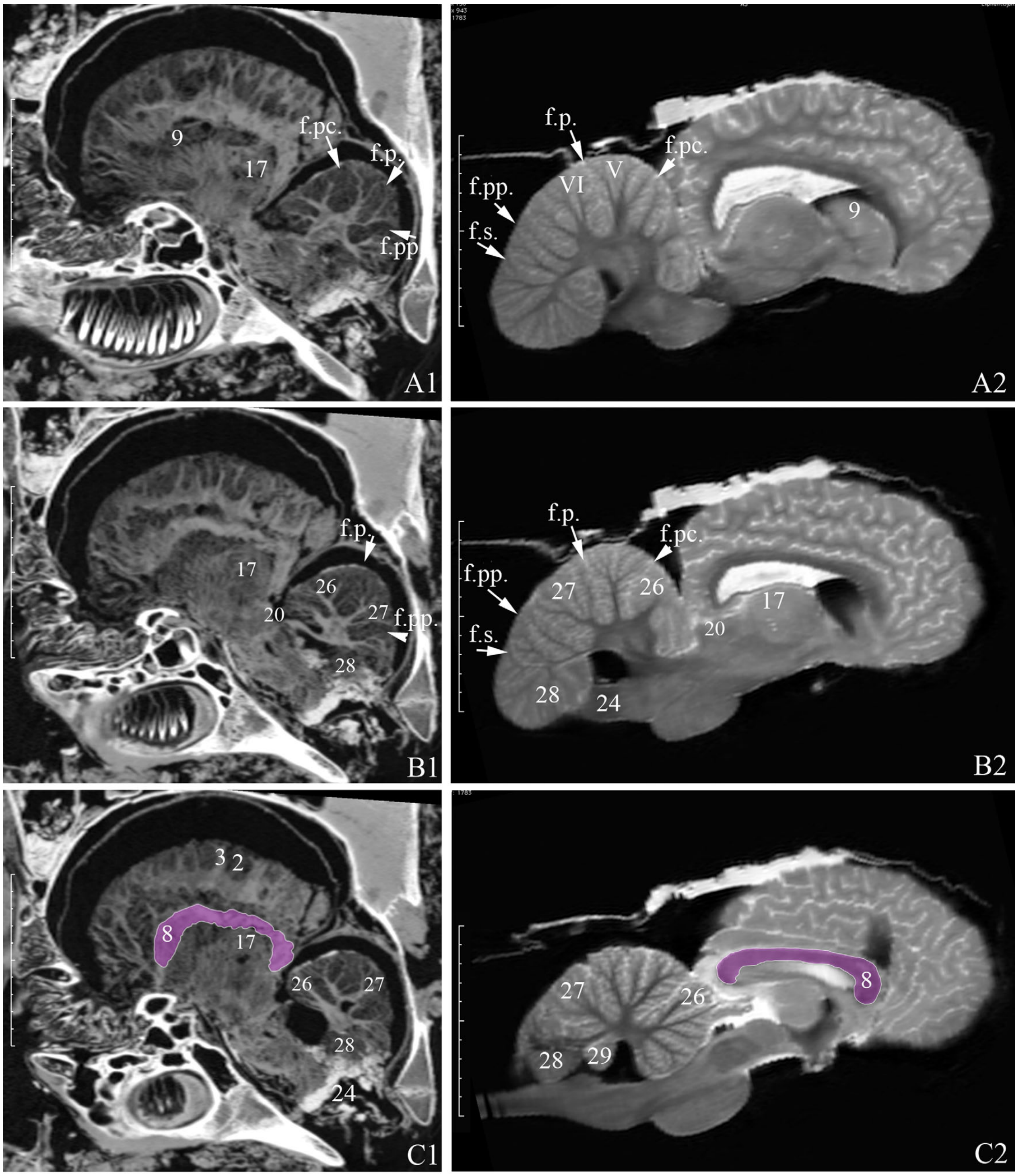

Figure 5. Sagittal series of CT scans of the brain of the woolly mammoth (**A1**–**C1**) and corresponding MR images of the African elephant brain (specimen LA1; **A2**–**C2**). In the C images, the outline of the measurement of the corpus callosum is shown. The boundaries of the cerebellar lobuli are marked by arrows that correspond to the likely position of the cerebellar fissures: primary fissure (p), secondary fissue (s), preculminate fissure (pc), prepyramidal fissure (pp); simplex lobule (VI), fifth lobulus of the anterior lobe (V). 1, olfactory bulb/olfactory bulb and tracts (these were damaged in the Yuka mammoth specimen); 2, cerebral cortex, gray matter; 3, white matter of the cerebral hemisphere; 4, lateral ventricle; 5, third ventricle; 6, cerebral aqueduct; 7, fourth ventricle; 8, corpus callosum; 9, caudate nucleus; 10, internal capsule; 11, putamen; 12, piriform cortex; 13, rhinal sulcus; 14, amygdala; 15, hippocampus; 16, optic chiasm; 17, dorsal thalamus; 18, cerebral peduncle; 19, lateral lemniscus; 20, superior and inferior colliculi; 21, cerebellar hemisphere; 22, cerebellar vermis; 23, middle cerebellar peduncle; 24, medulla oblongata (degraded in the Yuka mammoth specimen); 25, falx cerebri; 26, anterior lobe of cerebellum; 27, posterior lobe of cerebellum; 28, flocculonodular lobe; 29, nodule.

The last structure of the Yuka mammoth specimen telencephalon for which we could readily identify borders was the amygdaloid complex. Perhaps due to its nuclear nature, this structure appeared to remain relatively undamaged during the process of preservation. As with extant elephants, the amygdaloid complex was located on the medial ventral surface of the anterior temporal lobe, close to the level of the optic chiasm (Fig. 3D1). Our estimation

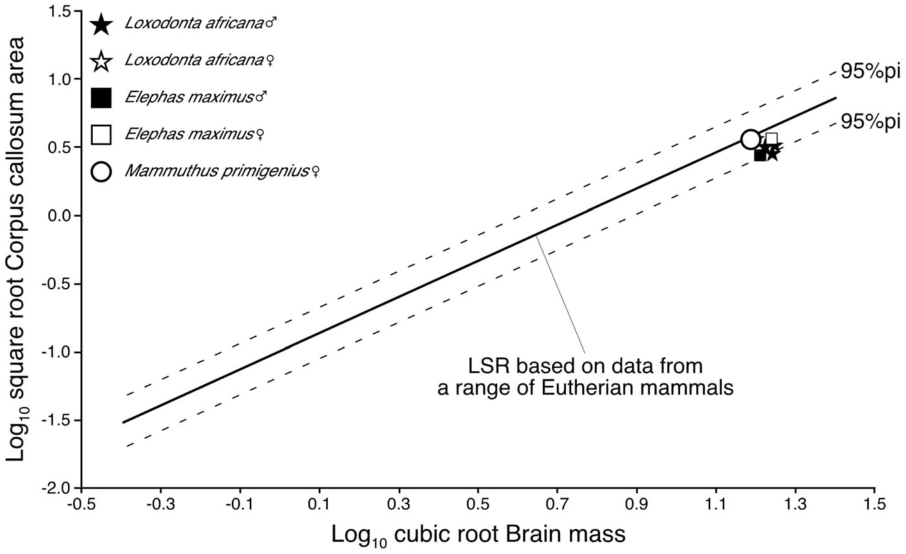

Figure 6. Plot depicting the relationship between the cubic root of brain mass and the square root of corpus callosum area. A least squares regression (LSR) based on data from several Eutherian mammals (excluding primates and cetaceans), with associated 95% prediction intervals (95%pi) from Manger et al. (2010), demonstrates that for its brain mass, the female Yuka mammoth specimen (*Mammuthus primigenius*) has a corpus callosum size one would expect to find. Note also, that as with the other female Elephantidae specimens, the midsagittal area of the corpus callosum is larger than in male specimens.

of raw specimen volume for the right amygdala was 2.12 cm^3, and that for the left amygdala was 1.71 cm^3. When corrected for specific hemispheric shrinkage, the corrected amygdala volume for the right hemisphere was 3.013 cm^3, with that for the amygdala of the left hemisphere being also 3.012 cm^3, giving a combined amygdal volume of 6.025 cm^3 in the Yuka mammoth specimen. This value is significantly lower than that seen in the African elephants, which had amygdala volumes of 17.46, 15.95, and 15.36 cm3 (Patzke et al., 2015), but this may be due to the state of the tissue, as we could not identify the more rostral and caudal aspects of the amygdaloid complex with certainty. When this total amygdala volume for the Yuka mammoth specimen is compared with data from other mammals, the mammoth clearly falls on the lower side of the range regarding relative amygdala size (Fig. 7). It is likely that the difficulty with identifying the more rostral and caudal aspects of the amygdala causes this small relative amygdala volume in the woolly mammoth, although it should be noted that although the data obtained are only just smaller than the 95% confidence intervals derived from data in other mammals (Fig. 7), the relative amygdala volume is still larger than that seen in cetaceans (Patzke et al., 2015).

The meninges and ventricular system

In African elephants the three meninges typical of all mammals are present (Shoshani et al., 2006). In the Yuka mammoth specimen we could only clearly identify the dura mater of the three meningeal layers. The microscopic pia mater and the thicker arachnoid appear to have undergone some degradation and merged with the superficial layers of the brain parenchyma, leading to the relatively smooth surface of the brain (Fig. 1). In regard to the dura mater, this fibrous meningeal layer, including the calvarial and basal dura, had not been significantly degraded in the preservation process of the Yuka mammoth specimen and evinced the appearance typical of this meningeal layer in the extant elephants (Shoshani et al., 2006). Distinct osteal and visceral layers of the dura mater with folds forming venous sinuses were apparent in the CT scans of the Yuka mammoth specimen (Figs. 3 and 5). The falx cerebri, which usually fills the interhemispheric fissure, was readily apparent in the coronal CT scans, and the superior sagittal sinus was visible. In both the coronal and sagittal CT scans (Figs. 3 and 5) the tentorium cerebelli, separating the cerebral hemispheres from the cerebellum, was also evident. The confluence of the sinuses, the straight sinus and the transverse sinuses, was apparent in the Yuka mammoth specimen. At the region of the confluence of sinuses, the dura mater became very thick, greater than 1 cm, approaching in size that observed in the African elephant (Manger et al., 2009). In addition, the dura mater covering the brainstem could be seen entering the foramen magnum, although the medulla

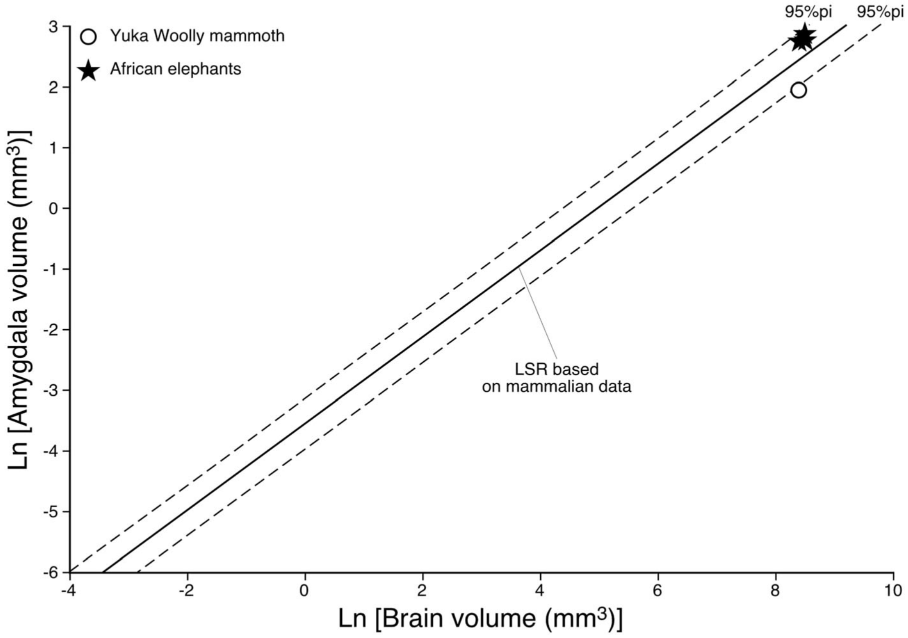

Figure 7. Plot depicting the relationship between brain volume and amygdala volume on log-transformed data of the mammalian species investigated in Patzke et al. (2015), from which the current image was redrawn. The least squares regression (LSR) with associated 95% prediction intervals (95%pi) were plotted on the graphs based on the mammalian data. Although the data for the Yuka mammoth specimen falls on the lower end of the predicted range for mammals, this low value for the mammoth amygdala volume may be due to the state of the tissue, making it difficult to identify the more rostral and caudal aspects of the amygdala with certainty.

oblongata had degraded and was absent (Figs. 3H1, 5C1). It would appear that the meninges of the Yuka mammoth specimen do not differ significantly from those observed in the extant elephants.

The paired lateral ventricles, the third ventricle, the fourth ventricle, and the cerebral aqueduct could all be readily observed on the series of CT images of the Yuka woolly mammoth brain (Fig. 3). Unfortunately, due to the preservation of the brain, the ventricles in total, especially the lateral ventricles, had undergone major shrinkage in comparison with the expected intact condition as observed in the African elephant brain (Fig. 3). Even so, the general appearance, shape, and size of the ventricles within the Yuka mammoth brain appear to correlate strongly to what is seen in the extant elephant brain, including the fourth ventricle dorsal recess into the ventral cerebellar white matter only observed in extant elephants to date (Shoshani et al., 2006; Maseko et al., 2011). The damage to the olfactory bulbs in the Yuka mammoth specimen did not allow identification of the olfactory ventricle, which is a prominent feature of the African elephant olfactory bulb (Ngwena et al., 2011; Maseko et al., 2011). Due to the shrinkage of the Yuka mammoth specimen, we could not estimate the volume of the ventricular system for quantitative comparison with other mammals, but we expect that the mammoth would have ventricular volumes close to that observed in the African elephant (Maseko et al., 2011).

Features of the woolly mammoth diencephalon

The diencephalon of the Yuka mammoth specimen was somewhat of a featureless mass as revealed by CT scans, although we could identify the regions of the dorsal thalamus, hypothalamus, and pituitary gland (Fig. 3C1,D1,E1), as can also be seen in the MR images of the African elephant brain (Fig. 3D2,E2) (although the pituitary gland was removed separately when preparing the African elephant brains due to the presence of the diaphragma sellae between the diencephalon and the pituitary gland; Manger et al., 2009). The epithalamus and subthalamus were not evident in the CT scans of the Yuka mammoth specimen, but they are also not evident in the MR images of the African elephant. The anterior border of the diencephalon was coincident with the level of the optic chiasm and continued through to the level of the midbrain, in a fashion similar to that seen in the African elephant, although we could not distinguish more detailed features of these nuclear masses. The general shape of the diencephalon in the Yuka mammoth specimen was similar to that of the African elephant, although the dorsal thalamus did not appear to be as expanded in the lateral aspects as that of the African elephant. Fiber pathways in this region of the brain, such as the cerebral peduncles and the medial lemnisci, could be readily observed in the MR images of the African elephants, and also could be identified on the CT scans of the Yuka mammoth specimen (Fig. 3D1,E1). In the CT scans of the Yuka mammoth specimen, remnants of the pituitary gland, or neurohypophysis, were visible (Fig. 2C1). The actual volume of the remnants of this gland was 0.91 cm^3, although the volume under the diaphragma sellae was 2.04 cm^3. The size and shape of the pituitary gland in the Yuka mammoth specimen are similar to that seen in the elephant, although the gland does appear to be somewhat smaller than the size reported by Shoshani et al. (2006).

Brainstem: midbrain, pons, and medulla oblongata of the woolly mammoth

The midbrain of the Yuka mammoth specimen could be identified by the position of the superior and inferior colliculi on the sagittal CT scans (Fig. 5). On the frontal CT scans the cerebral aqueduct and the adjacent mesencephalic tegmentum could be identified (Fig. 3F1), but defining the precise border between the tectum and tegmentum was difficult (although this border is clear in the African elephant; Fig. 3F2). The ventral aspects of the midbrain were also apparent in the Yuka mammoth specimen, although they appear to have undergone significant degradation. Portions of the pons, ventral to the cerebellum, were apparent, but this was a featureless mass and we could not identify any specific nuclei or fiber pathways within the pons. The medulla oblongata had completely degenerated in the Yuka mammoth specimen.

Features of the Woolly mammoth cerebellum

Perhaps due to the structural nature of the cerebellum, being invested with several large white matter pathways, a thin cerebellar cortex and deep nuclei invested in large white matter pathways, the cerebellum of the Yuka mammoth specimen was the most well-preserved portion of the brain and had undergone less shrinkage than the cerebral hemispheres (Fig. 1). We could readily recognize the cerebellar hemispheres, vermis, and middle and superior cerebellar peduncle in the Yuka mammoth specimen, and these were very similar to those seen in the African elephants. The fourth ventricle of the Yuka mammoth specimen appeared comparatively large in comparison with the African elephants, but this appears to be due to the shrinkage and degradation of the portion of the vermis lying just above the dorsal recess of this ventricle.

We could readily visualize the white matter arbor vitae of the Yuka mammoth cerebellum in the CT scans, and it evinced 10 main branches, allowing the definition of the cerebellar lobuli (Fig. 5). This appearance is very similar to that of the African elephant. Anterior, posterior, and caudal lobes, which are defined by the positions of the primary and secondary fissures, could be identified in the sagittal CT scans and MR images of both species (Fig. 5). The preculminate and prepyramidal fissures, as well as the nodular lobe, were also evident (Fig. 5). The caudal lobula of the anterior lobe and the lobus simplex (lobuli V and VI according to Larsell, 1947) are large in both species. The vermis was partly damaged (Figs. 3 and 5), but its borders were readily identified.

The raw volume of the actual cerebellum in the Yuka mammoth specimen was 812.28 cm^3 (767.11 cm^3 being cerebellar hemispheres, with 45.17 cm^3 being vermis). The potential volume of the entire cerebellum, as measured by the volume of the area beneath the tentorium cerebelli and the pons, was 1,013.59 cm3. This means that the cerebellum appears to have shrunk to approximately 80.14% of what could be considered its living size. Thus, the size of the woolly mammoth cerebellum, as corrected for shrinkage, would be 1,013.59 cm3, with hemispheric and vermal portions measuring 957.23 cm^3 and 56.36 cm^3, respectively. These values are very close to those measured in the adult male African elephants previously (Fig. 8A) (Maseko et al., 2012). Using the equation provided in Maseko et al. (2012), the cerebellar quotient of the Yuka mammoth specimen is 1.96, which falls into the range of extant elephants and above that seen in other mammals with enlarged cerebellums such as odontocete cetaceans and microchiropterans and significantly larger than the remaining mammals for which data is available (Maseko et al., 2012). In addition, as with previous findings in the African elephants (Maseko et al., 2012), in comparison with other mammals, the hemispheric portion of the Yuka mammoth specimen is significantly larger than that observed in other mammals (Fig. 8B). The vermal portion of the Yuka mammoth specimen is larger than one would expect compared with other mammals (Fig. 8C), but not significantly larger as seen for African elephants. This nonsignificant result may be due to the portion of the vermis that was damaged during preservation of the tissue, as mentioned above. It would appear safe to assume that, as with African elephants, the relative size of the cerebellum in the Yuka mammoth is significantly larger than is seen in other mammals, and that as with the African

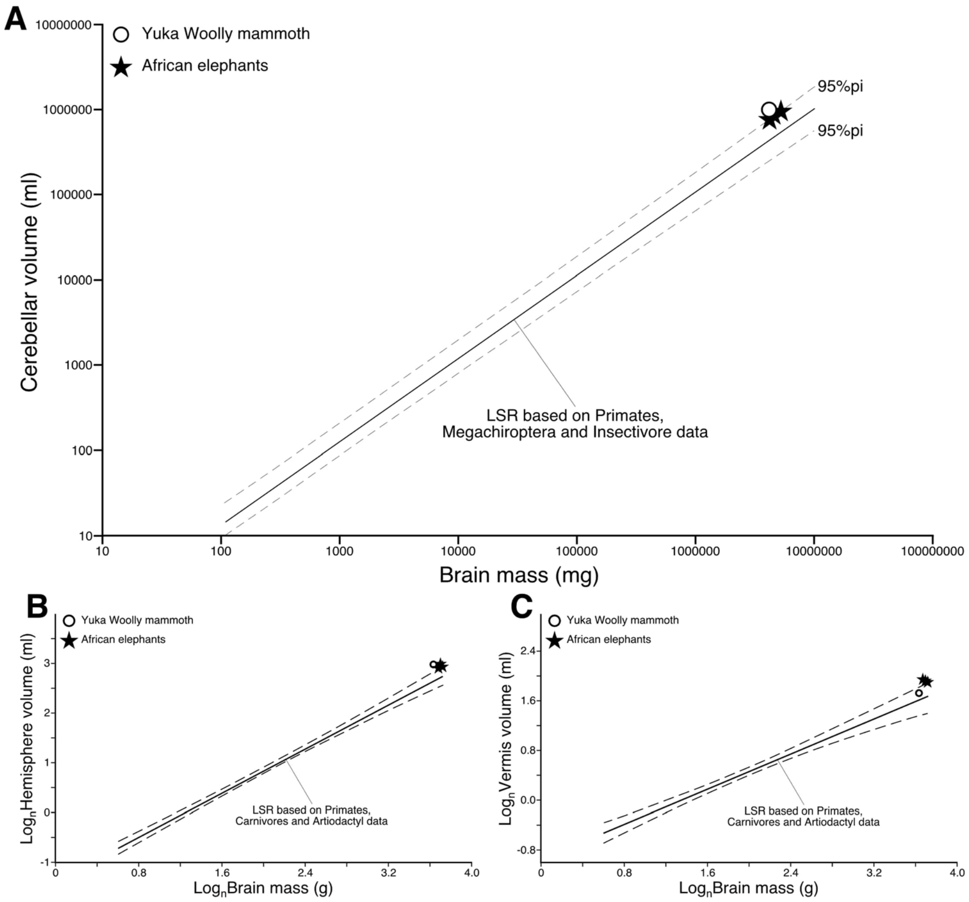

Figure 8. **A:** Plot depicting the relationship between brain mass and total cerebellar volume for the Yuka mammoth specimen and African elephants provided in relation to the least squares regression (LSR) and 95% prediction intervals (95%pi) based on data from other mammals (redrawn from Maseko et al., 2012). Note that, like the African elephants, the Yuka mammoth specimen has a significantly larger cerebellar volume than other mammals. Plots of the relationships between brain mass and cerebellar hemispheric (**B**) and vermal (**C**) volumes (both redrawn from Maseko et al., 2012). Note that like the African elephants, the hemispheric volume of the Yuka mammoth specimen is significantly larger than other mammals, but the vermal volume falls within the range seen by other mammals. This latter observation appears to be due to some degradation of the vermal tissue during the preservation process in the Yuka mammoth specimen.

elephants, the hemispheric and vermal portions are also markedly larger than one would expect based on data from other mammals.

DISCUSSION

The images and data presented in the current study provide the first comparative investigation of the structure of the extinct woolly mammoth brain with the extant elephants. Our findings, ranging from gross morphological features to comparative volumetrics, indicate that the structure of the woolly mammoth brain is not markedly different from that of extant elephants. Unfortunately, we were unable to make as many comparisons as we would have liked to do, especially at the histological level, as the preservation of the tissue in the permafrost, having undergone repeated freezing and thawing events, meant that the tissue was significantly degraded and no readily identifiable neural structures could be observed histologically (Kharlamova et al., 2014). The freezing and thawing events, without any specific protection for the tissue (such as being dehydrated and stored in an antifreeze solution), likely led to the formation of water crystals within the neurons and other cells of the brain, causing tearing of the tissue, and, on a larger scale, degradation of large portions of the brain parenchyma. Even so, we were able, with reasonable caution, to identify many structures, and quantify others, of the Yuka mammoth brain specimen using gross anatomical observation and imaging techniques, which provided a unique view into the structure of the woolly mammoth brain, supporting the notion that the woolly mammoth has a brain that appears very typical in structure for a member of the Elephantidae family.

Brain mass and encephalization quotient of the Yuka mammoth specimen

Our estimation of the mass of the brain of the Yuka mammoth specimen was based on three techniques: endocranial volume, subdural volume, and regression analysis based on other mammals. The brain mass derived from the endocranial volume, at 5,205.9 g appears to be far larger than one would expect, especially given that a significant porportion of the endocranial volume is occupied by meninges and cerebrospinal fluid. In contrast, the estimated brain mass from the subdural volume and the regression technique provided masses that were within 100 g of each other, 4,239.93 g and 4,334.23 g, respectively, allowing us to feel confident in estimating the mass of the Yuka mammoth brain specimen as somewhere between 4,230 and 4,340 g. This estimation of brain mass places the Yuka mammoth specimen well within the range of brain masses measured in extant African and Asian elephants (Shoshani et al., 2006; Manger et al., 2009). In fact, the average brain mass for female elephants has been reported as 4,677 g (Shoshani et al., 2006), which is only 300–400 grams heavier than the estimated brain mass of the Yuka mammoth specimen. Given that: 1) Shoshani et al. (2006) note that many of their measurements of brain mass were made with parts of the dura mater attached and variable lengths of the medulla oblongata in place; 2) the Yuka mammoth specimen is not a fully mature adult female, being between 6 and 9 years of age; and 3) the medulla of the Yuka specimen, as well as some other regions of the brain, had undergone major degradation, the estimated brain mass provided here for the Yuka mammoth specimen appears to be very close to what one would expect for an adolescent female woolly mammoth.

The potential range of the encephalization quotient calculated for the Yuka mammoth specimen, from 4.31 to 7.33, is very high in relation to other mammals, and in relation to other elephants (which have encephalization quotients of around 1.23). This great variation is due to the range in estimates of body mass of the Yuka specimen, from 350 to 700 kg, plus the apparently small size of the Yuka specimen due to its being an adolescent female. Whereas the brain mass is close to what we would reasonably expect for an adult female woolly mammoth, the body mass is far lower. Thus the encephalization quotient calculated here is likely to be erroneous as a representative of the woolly mammoths in general and should be interpreted with extreme caution.

Woolly mammoth and extant elephant similarities in brain structure

In the current study we could identify a vast range of similarities in the structure of the woolly mammoth brain with, in particular, the African elephant brain. Based on our gross morphological examination and the imaging data, we could, with certainty, identify almost 40 specific structures that were the same in the woolly mammoth and African elephant brain. Although these structures may also be found across a range of mammals, the distinct “elephantine” similarity of these structures was striking. For example, in both woolly mammoths and African elephants, the frontal lobe tapers gently toward the rostral pole, the expanded temporal lobe shows a similar angle of the main axis when measured against the interhemispheric fissure, and the cerebellum provides an overall gross similarity in the location of the vermis and the manner in which the cerebellar hemispheres have undergone lateral expansion. The side-by-side comparison of the CT scans and MR images furthers the range of similarities, with features such as the location and shape of the meninges, ventricles, amygdala, corpus callosum, midbrain tectum, large fiber pathways, and even specific lobules of the cerebellum being readily identified as very similar in both species. Thus, from a purely qualitative standpoint, and if the specimens were in a similar state of preservation, it would not be a particularly easy task to identify which specimen was a woolly mammoth and which was an extant elephant. In addition to this qualitative impression of the extensive similarities, the quantitative analysis extended these observations (see below).

What the current study revealed is that we can readily describe the Elephantidae type of brain and this likely extends to all members of the Elephantidae, extinct and extant. The divergence of the lineage of the three genuses of the Elephantidae family is dated to the early Pliocene, near 5.3–3,4 million years ago (5,5–3,5 according to Maglio, 1973). In the mammoth lineage, successive species of the genus *Mammuthus* (Brookes, 1828) (Lister, 1996; Lister and Sher, 2001) or the genus *Archidiskodon* (Pohlig, 1885) were derived from the genus *Mammuthus* from the early to middle Pleistocene (Garutt et. al., 1990; Garutt and Tikhonov, 2001; Maschenko, 2002, 2010). The fossil record of *Mammuthus primigenius* (Blumenbach, 1799) stretches as far back as 180,000–200,000 years ago in Europe (Lister, 1996) and more than 300,000 years ago in northeast Asia (Lister and Sher, 2001). It would be unusual to find any remarkable morphological changes in such an evolutionarily conservative structure as the brain during this period. According to Shoshani et al. (2006), the most notable change in Proboscidean brain structure occurred with the divergence of the Mammutidae and Elephantidae families, which was described as an increase in size of the cerebral hemispheres such that the frontal lobes obscure the olfactory bulbs in the dorsal view. The current study of the Yuka mammoth specimen confirms this observation, at least for the Elephantidae lineage.

Differential shrinkage of various regions of the Yuka mammoth brain

As outlined in the description of the calculations of the various components of the brain quantified for comparison with extant elephants and other mammals, the cerebral hemispheres and the cerebellum appear to have undergone differential shrinkage during the preservation process. Our calculations indicate that the right cerebral hemisphere appears to have shrunk to around 70% of its original size, the left cerebral hemisphere to around 57% of its original size, and the cerebellum to around 80% of its original size. In all cases of quantification of specific brain regions analyzed volumetrically within the current study, we have provided both the raw values and the shrinkage corrected values, to demonstrate this variability and the need to account for it in the process of tissue analysis (Stephan, 1960; Quester and Schroder, 1997). It is of interest that the cerebellum underwent the least amount of shrinkage of the three major regions of the roof of the brain. It would appear that during the mummification process of the Yuka mammoth brain specimen, the fatty tissue, especially the myelin, changed into adipocere. Thus the white matter pathways, of both the cerebral hemispheres and the cerebellum, became clearly visible on the CT scans (Previgliano et al., 2003). As the cerebellum contains large white matter pathways deep to a thin cortex, it appears logical that the amount of shrinkage was lower in this structure compared with the cerebral hemispheres.

Quantitative similarities in woolly mammoth and extant elephant brain structure

The quantitative analyses provided here reveal a similar story to that of the qualitative description, this being that the woolly mammoth brain has a morphology that is very similar to the extant elephants. The extent of the fissuring and folding of the cerebral cortex of the woolly mammoth is very similar to that of the African elephant, with both being significantly lower than the cetaceans, but in line with mammals with brains weighing 4–5 kg (Manger et al., 2012). The cross-sectional area of the corpus callosum is also very similar in the woolly mammoth specimen and the extant elephants. In fact, the woolly mammoth specimen studied here was an adolescent female, and when corrected for shrinkage, the size of the corpus callosum of this woolly mammoth is very similar to that seen in female African and Asian elephants and larger than that seen in male African and Asian elephants (Manger et al., 2010). Thus, the woolly mammoth extends the sexually dimorphic nature of the corpus callosum which was observed in all members of the family Elephantidae studied to date. This is an interesting finding, as to date primates are the only other mammalian group that show sexual dimorphism in the size of the corpus callosum. The size of the amygdala in the woolly mammoth appears to be quite similar to that of the African elephant (Patzke et al., 2015), although damage to the tissue provides a likely underestimate of the woolly mammoth amygdala size in the current study. Even so, it would appear that the proportions, and possibly the organization, of the limbic system in the woolly mammoth is likely to be similar to that in the extant elephants. Lastly, the size of the cerebellum and the size of the hemispheric and vermal portions of the cerebellum of the woolly mammoth are very similar to those of the African elephant (Maseko et al., 2012). In all cases, the sizes of these structures are much larger than the homologous structures in other mammals. Thus, the Elephantidae, rather than extant elephants, have the relatively largest cerebellums of mammals. This large cerebellum size in the Elephantidae, along with the huge numbers of neurons found in the African elephant cerebellum (Herculano-Houzel et al., 2014) and the complexity of the cerebellar neurons (Maseko et al., 2013a), all indicate that the need for cerebellar sensorimotor integration and learning and integration of movements of the trunk is an Elephantidae feature. What is clear from the quantitative analyses is that it is reasonable to speculate that the sizes of the various identifiable parts of the woolly mammoth brain are very close to that of the extant elephants, underscoring our qualitative impression of an Elephantidae type brain.

What do these findings mean for our understanding of woolly mammoth behavior?

Without doubt, the brain is the region of the body that controls overt activity and inactivity and body homeostasis, making comparative neuroanatomical studies a very useful tool for understanding behavior across species. For the woolly mammoth, the findings presented here showing the extensive similarities between the woolly mammoth and extant elephant brains means that it is likely that the morphophysiological characteristics of the extant elephant brains that control or augment specific behaviors are likely to apply to the woolly mammoth. Extant elephants are thought to exhibit a variety of potentially cognitively based behaviors (those behaviors that require conscious thought processes to enact) including tool use and manufacture, insight behaviors, discrimination learning, spatial–temporal and social memory, self-awareness and recognition of others, and the reactions of elephants to disabled and dead conspecifics (Hart et al., 2008). Although no specific neural structures have been directly associated with these types of behaviors in elephants (or indeed in many mammalian species), the overall similarity of the elephant and mammoth brain suggests that whatever an elephant can achieve in the cognitive realm should also be achievable by the woolly mammoth. Unfortunately, these types of behaviors tell us little about the life history and potential standard behavioral repertoire of the woolly mammoth.

Perhaps of more relevance to the understanding of the life history and behavior of the woolly mammoths are those histological features associated with specific behaviors being revealed in the extant elephant brains (see introductory section for a summary of these features). Given that all the qualitative and quantitative analyses we have performed suggest that the brains are very similar, it is not unreasonable to assume that even at a nuclear and microscopic level the organizations of the extant elephants and woolly mammoth brains are very similar (Manger, 2005). For example, specific neuronal types, laminar organization, and numbers of neurons within the elephant cerebral cortex (Hakeem et al., 2005; Jacobs et al., 2011; Herculano-Houzel et al., 2014) may be more informative about the range of behaviors, both cognitive and noncognitive, that could potentially be exhibited by woolly mammoths. This can be extended to other regions of the brain where specialized nuclei involved in the intertwined appetitive drive and arousal systems (Maseko et al., 2013b), along with a specialized olfactory bulb (Ngwena et al., 2011), are found in African elephants. The production and reception of infrasonic vocalizations is likely to have been part of the life history of the woolly mammoth. In extant elephants a suite of auditory, tactile, and motor specializations associated with the reception and production of infrasonic vocalizations in the elephants has been identified (Maseko et al., 2013b; Stoeger and Manger, 2014). It is likely that these specializations are also present in the woolly mammoth brain and would have allowed the woolly mammoth to produce such behaviors as infrasonic communication and vocal learning (Stoeger and Manger, 2014). Lastly, the one really outstanding feature in common between elephants and the woolly mammoth is the size of the cerebellum. Control of the woolly mammoth trunk likely relied on the same combination of size, neuronal number, and neuronal complexity observed in the cerebellum of African elephants (Maseko et al., 2012, 2013a; Herculano-Houzel et al., 2014).

Although we strongly state the case for the understanding of woolly mammoth behavior through the neuroethological study of extant elephants, we must do this with caution. There is no doubt that the woolly mammoth brain, to the extent we could examine the current specimen, is very similar to the extant elephant brain in most ways; however, the preservation state of the tissue prevented us from examining the specimen in more detail. Therefore, the case for the transference of neuroethological findings in extant elephants to woolly mammoths must be done with care—it is highly unlikely that woolly mammoths were just hairy elephants, and even extant animals with very similarly organized brains, such as lions and tigers, show substantial differences in such characteristics as social behaviors. Even so, the neuroethological study of extant elephants is likely to provide the most reliable predictions of woolly mammoth behavior. Nevertheless, in the face of these problems and cautionary notes, the current study has provided a unique and revealing glimpse into a woolly mammoth brain that was preserved for around 38,000 years, as well as a potential path for increasing our understanding of the life history and behavior of this and other unique members of the *Elephantidae* family.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ROLE OF AUTHORS

All authors had full access to all the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. ASK and PRM conceptualized the study. SVS, AP, BCM, and AB provided valuable assistance throughout the study in relation to the measurements undertaken and analysis of the data. ASK and PRM wrote the manuscript, and the remaining authors contributed to the editing and improvement of the early drafts of the manuscript.

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