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A quantitative comparative analysis of the size of the frontoparietal sinuses and brain in vombatiform marsupials

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Abstract Sharp, A.C. 2016. A quantitative comparative analysis of the size of the frontoparietal sinuses and brain in vombatiform marsupials. *Memoirs of Museum Victoria* 74: 331–342.

Cranial sinuses result from the resorption and deposition of bone in response to biomechanical stress during a process known as pneumatisation. The morphology of a pneumatic bone represents an optimisation between strength and being light weight. The presence of very large sinuses has been described in a number of extinct marsupial megafauna, the size of which no longer exist in extant marsupials. With advances in digital visualisation, and the discovery of a number of exceptionally preserved fossil crania, a unique opportunity exists to investigate hypotheses regarding the structure and evolution of the atypically voluminous sinuses. Sinus function is difficult to test without first obtaining data on sinus variation within and between species. Therefore, the crania of seven species of extinct and extant vombatiform marsupials were studied using CT scans to provide a volumetric assessment of the endocast and cranial sinuses. Sinus volume strongly correlates with skull size and brain size. In the extinct, large bodied palorchestids and diprotodontids the sinuses expand around the dorsal and lateral parts of the braincase. Brain size scales negatively with skull size in vombatiform marsupials. In large species the brain typically fills less than one quarter of the total volume of the endocranial space, and in very large species, it can be less than 10%. Sinus expansion may have developed in order to increase the surface area for attachment of the temporalis muscle and to lighten the skull. The braincase itself would have provided insufficient surface area for the predicted muscle masses.

Keywords Diprotodontia; frontal sinus; marsupial; endocast; allometry; jaw musculature.

Introduction

Cranial sinuses are air-filled cavities resulting from the resorption and deposition of bone through pneumatisation in response to biomechanical stress, or bone remodelling during ontogeny (Edinger, 1950; Farke, 2008; Moss and Young, 1960; Preuschoft et al., 2002; Witmer, 1997). Areas of bone where no mechanical support is required will be pneumatised to form cavities in a process described by Wolff's Law (Wolff, 1870, 1892). When bone is subjected to a load, causing elastic deformation, its structure is modified by slowly remodelling over time. The shape of the sinuses therefore reflects the loads placed on the skull.

The structure and function of sinuses have been described and investigated in many taxa (Badlangana et al., 2011; Black et al., 2010; Black and Hand, 2010; Farke, 2008,2010a, b; Ferretti, 2007; Murray, 1992; Preuschoft et al., 2002; Siliceo et al., 2011; Tanner et al., 2008; Witmer, 1997) and several functional hypotheses have been put forward. One hypothesis explaining the presence of extensive endocranial sinuses proposes that the size of the sinus correlates with the relative growth rates of the inner and outer bony tables of the brain case and frontal bone in response to their respective soft tissue demands (Moss and Young, 1960). For example, if brain size scales negatively with skull size, sinuses may expand to fill the frontal bone to increase the surface area for attachment of masticatory muscles in large animals. Other hypotheses include decreasing the weight of the skull (Davis et al., 1996; Mitchell and Skinner, 2003; Shea, 1936), providing thermoregulation of the brain (Bremer, 1940; Dyce et al., 2002; Ganey et al., 1990; Mitchell and Skinner, 2003, 2004), shock absorption during head-butting or neck-sparring (Badlangana et al., 2011; Davis et al., 1996; Schaffer and Reed, 1972), serving as a resonance chamber for the production of low frequency sounds (Leakey and Walker, 1997; von Muggenthaler et al., 1999) and dissipation of stress over the skull during mastication, and particularly bone-cracking in carnivores (Buckland-Wright, 1971, 1978; Joeckel, 1998; Tanner et al., 2008). Nonetheless, hypotheses regarding sinus function are difficult to test without first obtaining data on sinus variation within and between species.

The presence of large cranial sinuses in certain marsupials was first described by Owen (1870, 1877) and later by Klaauw (1931, 946), Murray (1992) and Black et al. (2010). The extent of

Table 1. Details of the specimens used in this study. NMV, Museum Victoria; QVM, Queen Victoria Museum and Art Gallery.

Species	**Specimen Code**	**Slice thickness (mm)**	**Interslice spacing (mm)**	**No. of slices**	**Source**	**Additional information**
Diprotodon optatum	NMV P31299	0.6	0.3	978	NMV	Small form; Bacchus Marsh, VIC
Hairy-nosed wombat (*Lasiorhinus latifrons*)	NMV C33128	0.6	0.3	656	NMV	Adult male
Neohelos stirtoni	NMV P 187283	0.75	0.5	549	NMV	Bullock Creek, NT
Neohelos stirtoni	QVM2000 GFV57	0.75	0.5	281	QVM	Rostral fragment; Bullock Creek, NT
Zygomaturus trilobus	QVM1992 GFV73	0.75	0.5	2714 (total of 4 separate scans)	QVM	Scanned in four fragments; Mowbray Swamp, TAS
Palorchestidae *(Propalorchestes sp.)*	QVM2000 GFV459	0.75	0.5	629	QVM	Bullock Creek, NT
Koala (*Phascolarctos cinereus*)	TMM M-2946	0.238	0.238	599	Digimorph	
Common wombat (*Vombatus ursinus*)	TMM M-2953	0.45	0.45	399	Digimorph	
Common wombat (*Vombatus ursinus*)	NA	0.75	0.3	413	Zoos Victoria, under DSE collect permit #10005574	Road victim, wet specimen
Koala (*Phascolarctos cinereus*)	NA	0.75	0.3	317	Koala Conservation Centre, under DSE collect permit #10005574	Road victim, wet specimen

the endocranial sinuses in large marsupial crania is truly remarkable, resulting in crania composed of little more than air cells surrounded by thin cranial bone. The most impressive example can be found in the extinct *Diprotodon optatum*, the largest marsupial known (Sharp, 2014). The sinuses extend throughout the cranium from the frontals into the parietals, dorsally over the brain and into the occipitals. Large sinuses have also been noted in other large extinct marsupials (Black et al., 2010; Murray, 1992). Murray (1992) noted that the brain in large palorchestid, diprotodontid and thylacoleonid marsupials typically spans less than one third of the total width of the endocranial space when viewed in cross-section. In very large species, it can be less than a quarter. The remainder of the endocranial space consists of extensive sinuses. These "airheads" have no living marsupial analogue, and are all 2–10 times larger than any living marsupial (Murray, 1992).

To date, no quantitative assessment of the volume of the sinuses in marsupial megafauna has been carried out. Limitations in technology and the quality of preservation of fossil crania have hindered such studies. However, with such techniques as computed tomography (CT) and digital reconstruction becoming more widely available and affordable for palaeontologists, there is no longer a need to rely on natural breaks exposing the sinuses in order to view the interior anatomy of fossil species.

This study presents results of the first quantitative comparative analysis of marsupial frontoparietal sinuses using CT scans and three-dimensional (3D) digital reconstructions. The relationship between the size of the brain endocast and sinuses in relation to the overall head size of a representative sample of diprotodontian marsupials, specifically those from the suborder Vombatiformes, was analysed. The suborder Vombatiformes includes the extinct, browsing herbivores from the families Palorchestidae and Diprotodontidae, and the extant families Phascolarctidae and Vombatidae, the latter two including modern koalas and wombats respectively. During the Cenozoic, palorchestid and diprotodontid marsupials show a gradual increase in body size from the most archaic palorchestid *Propalorchestes* to the cow-sized *Palorchestes* (Archer, 1984; Black, 1997a, b; Murray, 1986, 1990), and from the 500 kg diprotodontid *Euryzygoma dunense* to the largest marsupial *Diprotodon optatum* (approximately 2–3 tons; Wroe et al., 2004) (Price and Piper, 2009). It is hypothesised that with the increase in body size, the sinuses undergo positive allometric expansion, while the brain scales negatively, leading to relatively smaller brains and larger sinuses in larger-bodied marsupials.

Table 2. Cranial volume, brain volume and sinus volume (all in mm3) for each marsupial genus analysed, including the percentage of brain and sinus volume to cranial volume. A specimen specific body size estimate for each of the species is also included, calculated from the Diprotodontia regression equation in Wroe et al. 2003.

Genus	**Body mass (kg)**	**Cranial Volume**	**Brain Volume**		**Sinus Volume**	
Phascolarctos	7.4	115911	24972	22%	5596	5%
Lasiorhinus	31	253586	58817	23%	21000	8%
Vombatus	37	274468	64963	24%	17532	6%
Propalorchestes	38	528282	66690	13%	128680	24%
Neohelos	136	1166108	141515	12%	324322	28%
Zygomaturus	589	5808021	338538	6%	1416087	24%
Diprotodon	1048	10743554	476928	4%	2675163	25%

Materials and Methods

Specimens were from the collections of Museum Victoria (NMV, Melbourne, Australia), Queen Victoria Museum and Art Gallery (QVM, Launceston, Australia) and the Digital Morphology Library (Digimorph) at the University of Texas (www.digimorph.org). Permission to use Digimorph derived CT data was granted by Dr. Timothy Rowe, Project Director of Digimorph. The crania of seven representative vombatiform marsupial species, living and extinct, were scanned using computed tomography (CT) for comparative analysis (table 1). Crania of living genera include *Vombatus*, *Lasiorhinus* and *Phascolarctos*. Fossil material includes: Palorchestidae, *Propalorchestes* (QVM2000 GFV459); and, Diprotodontidae, *Neohelos* (NMV P 187283; QVM2000 GFV57), *Zygomaturus* (QVM1992 GFV73), and *Diprotodon* (NMV P31299). Two wet specimens, one koala and one wombat, were also collected under the Victorian Department of Sustainability and Environment Flora and Fauna permit number 10005574. Fossil specimens were restricted to those that are undistorted and near complete so that the best representation of the full volume of each structure could realistically be estimated. Where specimens were not complete, other fragments of the same species were also scanned to build a composite model.

Three-dimensional (3D) reconstructions of the crania, endocranial sinuses and brain cavities for each species were produced from the CT scans in Avizo (Visage Imaging, Inc.). Automatic and manual segmentation (the process of isolating and selecting structures based on their grey values, or density) was performed to isolate each structure and produce 3D surface reconstructions. An obvious advantage of using endocast volume as an estimate for brain size is that it can be applied to all species, including fossils. A disadvantage is that it might overestimate the brain volume depending on what proportion of the cranial cavity is occupied by the brain. The majority of Australian marsupials have brains almost completely occupying the endocranium (Ashwell, 2008; Taylor et al., 2006; Tyndale-Biscoe, 2005), so it was assumed that endocast volume is a reasonable proxy for brain size. To avoid as much error as possible, the volume of the endocast for each species was segmented so that the meninges, cranial nerves, blood vessels and the pituitary occupied similar proportions of the endocranial volume across the data set.

The fossil specimens were all well preserved with little or no distortion and minimal missing or damaged regions. When damaged regions were present, they were reconstructed based on the morphology of the surrounding bone. Delicate internal struts, or trabeculae, within the sinuses that had noticeably been broken were reconstructed manually in Avizo from the CT slices. The *Zygomaturus* specimen was scanned in four pieces and processed separately in Avizo, then imported into Geomagic Studio (Geomagic, Inc.) to align and reconstruct the full cranium (fig. 1). Similarly, for *Neohelos* a rostral fragment was scanned and processed separately and attached to the cranium in Geomagic. Damaged and missing regions were reconstructed using a combination of techniques including the mirroring tool, defeature and smoothing in Geomagic, and the interpolate tool and manual selection using the paintbrush in Avizo. In all steps involving modification, careful consideration was taken when editing the geometry to maintain biological accuracy. Finally, when each model was fully reconstructed, volumetric data for the sinuses, endocast and bone were obtained using the Avizo "MaterialStatistics" module.

To compare both the relative and absolute size of the brain endocast and frontal sinuses, cranial volume (the combined volumes of the cranial bone, endocranial sinuses and endocast) was used as a proxy for head size rather than using body size or geometric measurements, because the relative body size and head size vary greatly between species, as well as skull length and skull width. The log-transformed values of cranial volume were then regressed against log-transformed frontal sinus volume and brain endocast volume using linear least squares regression in R statistical software (http://www.r-project.org/). Specimen specific body size was also estimated using the Diprotodontia equation for body mass estimation from Wroe et al. (2003) (table 2). Using this method, body mass is based on brain volume and it must be noted that the estimates shown for *Neohelos* and *Diprotodon* are under previous estimates for the species (300 kg and 2–3 tons respectively). This may be because the specimens used here are considered small for the species. This is most certainly the case for the *Diprotodon* specimen that is considered a 'small-form' *Diprotodon*, possibly female (Long and Mackness, 1994; Price, 2008).

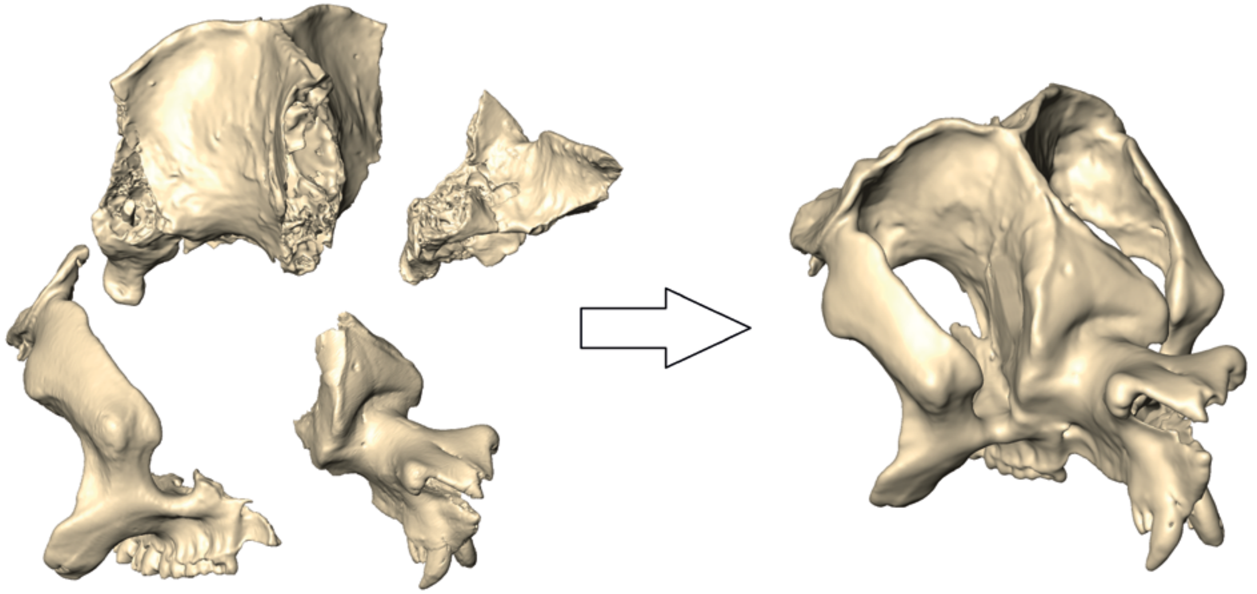

Figure 1. Three-dimensional digital reconstruction of *Zygomaturus trilobus* cranium, QVM1992 GFV73 from CT scans. Each fragment of the specimen was scanned separately and reconstructed to form the complete cranium on the right.

Results

Morphology of the Endocranial Sinuses

Endocranial sinuses among the marsupials in this study display considerable variation in relative size and morphology. In the large, extinct palorchestids and diprotodontids, the sinuses surround the inner brain capsule in all but the ventral region (fig. 2). Whereas, in the smaller, extant species, the sinuses are small and restricted to the frontal bone, just posterior to the ventral conchal sinus (fig. 3).

The sinuses of the extinct species studied here are located in the frontal bone and extend caudally into the parietals and interparietals, laterally into the squamosal section of the zygomatic arch, dorsally over the endocranial cavity and into the occipitals (Sharp, 2014). The braincase is surrounded by epitympanic sinuses, squamosal sinuses and parietal sinuses separating it from the external surface of the skull. In all species, the sinuses are divided by numerous strut-like trabeculae and a bony septum that extends from the nasals to the occipitals along the midsagittal plane.

The frontal sinuses in *Diprotodon* are bilaterally symmetrical and relatively simple, divided by two bony septa, one lying in the sagittal plane (dividing the area into left and right parts) and another in the frontal plane (dividing the area into anterior and posterior parts) (Sharp, 2014). These partitions align with the coronal suture between the frontal and parietal bones and the sutural contact between the frontals along the midsagittal plane. The posterior parietal and squamosal sinuses are also further subdivided and form a complex, interconnected network of chambers and passages surrounding the middle ear cavity and braincase. In *Zygomaturus*, the sinuses expand into the squamosal segment of the large, broad zygomatic arch more so than in the other species, which have relatively slender zygomatic arches compared to *Zygomaturus*.

Volume comparison

A statistically significant correlation exists between log-transformed frontal sinus volume and cranial volume in the species studied (Slope = 1.36, $R^2 = 0.9617$, $p < 0.0001$; fig. 4). However, there is a considerable amount of spread around the best-fit line (standard error = 0.22). A significant correlation also exists between log-transformed endocast volume and cranial volume (Slope = 0.61, $R^2 = 0.9763$, $p < 0.0001$; fig. 4), with little scatter around the best-fit line (standard error = 0.08). A slope of 0.61 is slightly under the slope for previously calculated regressions (0.656) based on brain weight and body weight (Weisbecker and Goswami, 2014).

These data show that the volume of the sinuses scales positively with cranial volume so that species with larger craniums have relatively larger sinuses compared with those with smaller craniums. In the largest species (*Diprotodon* and *Zygomaturus*) the sinuses fill approximately one quarter of the entire cranial volume, whereas in the smaller species (*Vombatus*, *Lasiorhinus* and *Phascolarctos*) the sinuses fill less than 10% of the total cranial volume (table 2). Endocast or brain volume scales negatively with cranial size, so that the species with larger craniums have relatively smaller brains than species with small craniums. Species with small craniums have brains that occupy over 25% of the cranial volume, and species with large cranium have relatively small brains that occupy only 5% of the total cranial volume (table 2). The volumes determined for extant taxa are within the range measured by Ashwell (2008) for wombats, and Taylor et al. (2006) for koalas, so it is assumed that the estimated volumes for the extinct taxa are also realistic.

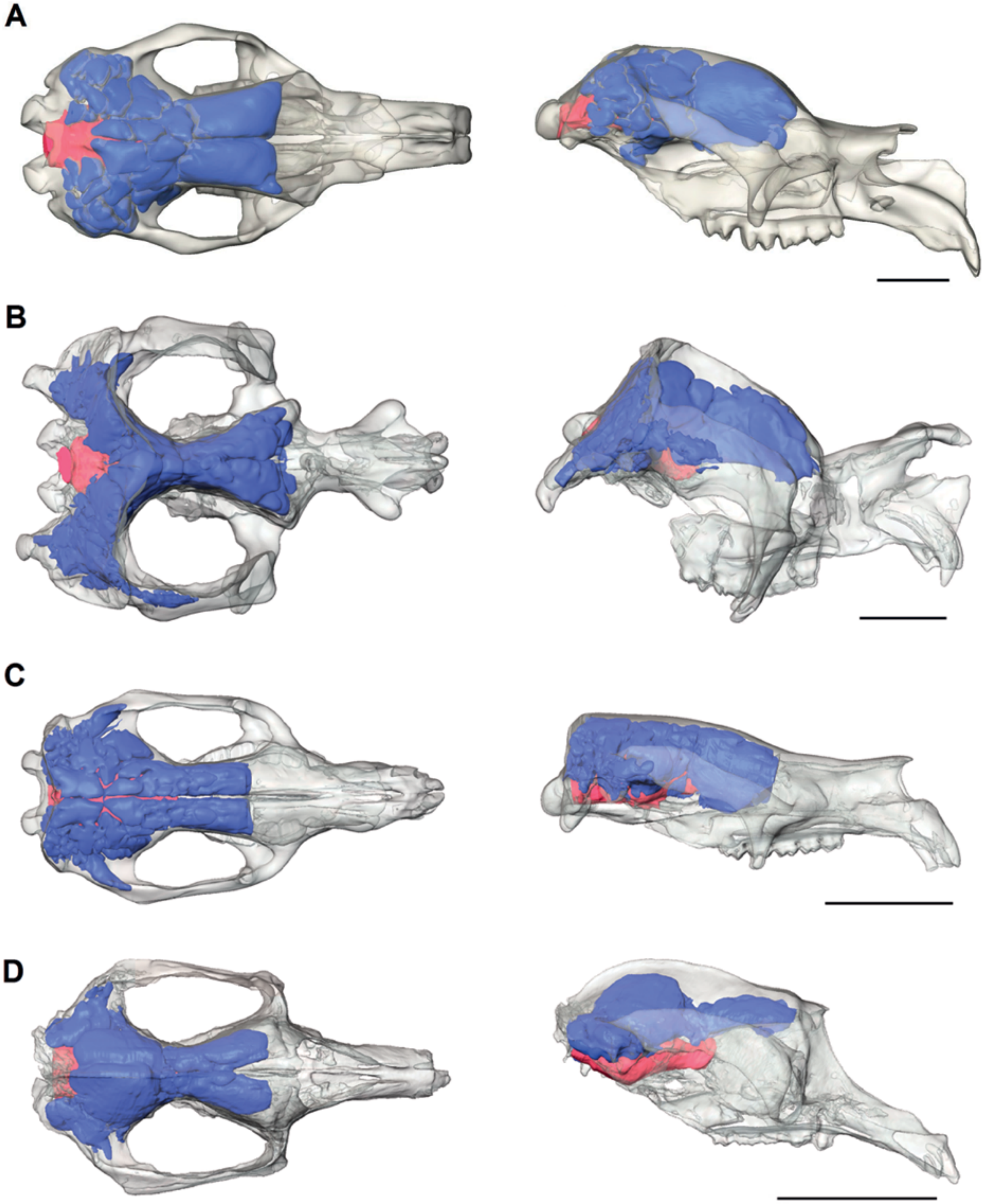

Figure 2. Three-dimensional reconstructions of *Diprotodon optatum* (A), *Zygomaturus trilobus* (B), *Neohelos stirtoni* (C) and *Propalorchestes sp*. (D) showing the extent of the auditory, squamosal, parietal and frontal sinuses in blue, and brain endocast in red. Skulls are shown in dorsal (left) and lateral (right) views. Scale bars represent 10 cm. Bone is 70% transparent.

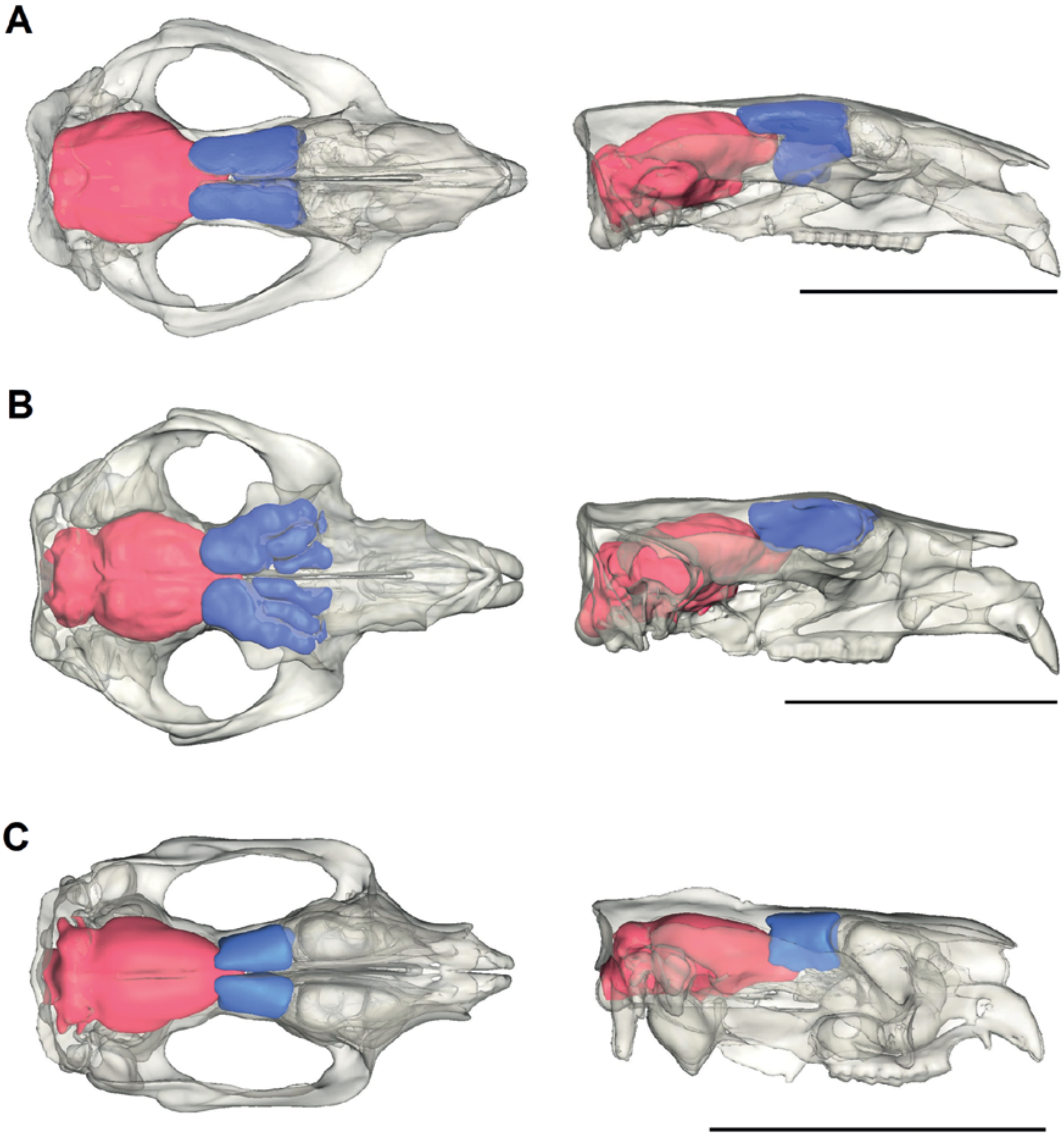

Figure 3. Three-dimensional reconstructions of *Vombatus ursinus* (A), *Lasiorhinus latifrons* (B) and *Phascolarctos cinereus* (C) showing the extent of the frontal sinuses in blue and brain endocast in red. Skulls are shown in dorsal (left) and lateral (right) views. Scale bars represent 10 cm. Bone is 70% transparent.

Discussion

Why have large sinuses?

Moss and Young (1960) outlined the principles of neurocranial growth, emphasising the response of different functional components (an outer table, a diploe, and an inner table) to the demands of soft tissue they support and protect. Essentially the external and internal tables respond to the demands of the masticatory musculature and brain respectively, and the intervening spongy bone layer, the diploe, expands to accommodate the separation. As the two layers separate during ontogeny, the bone first thickens through the formation of the diploe as seen in the skulls of adult wombat genera, *Vombatus* and *Lasiorhinus* (fig. 5). Air cavities start forming

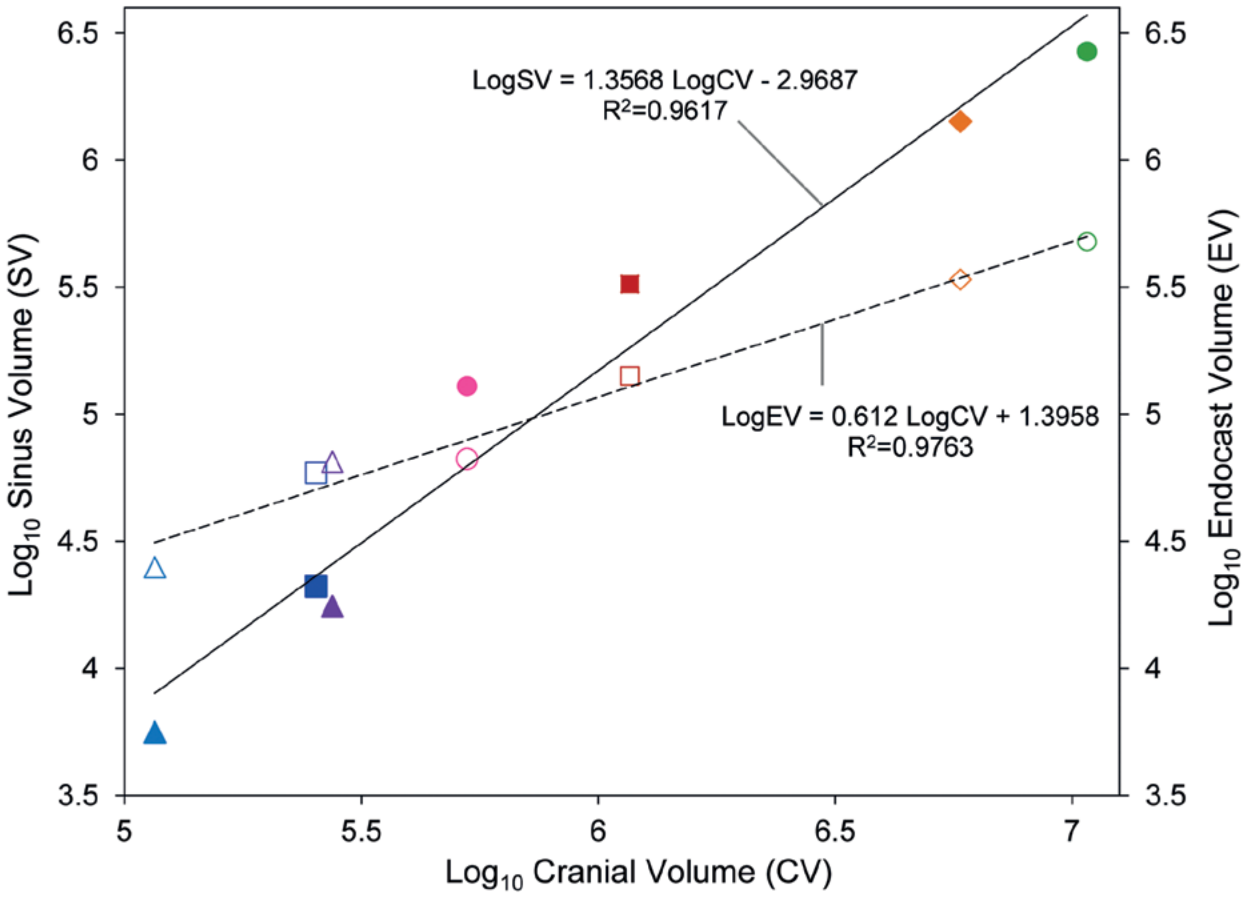

Figure 4. Endocast volume (dashed line, open symbols; EV) and sinus volume (solid line, solid symbols; SV) plotted against total cranial volume (CV) with regression equations. Symbols for each species are: *Phascolarctos* (▲);*Lasiorhinus* (■);*Vombatus* (▲);*Propalorchestes* (●); *Neohelos* (●); *Zygomaturus* (◆); *Diprotodon* (■).

in the diploic layer, increasing in size as the separation continues until the region is fully pneumaticised. Murray (1992) suggested endocranial sinuses develop in response to positive allometric growth of the outer bony table that forms the cranium, relative to the inner table that forms the braincase. This trend is observed in the present study. Effectively, the expansion of the diploe to form sinuses increases the surface area of the skull for muscle attachment, without increasing the size of the brain or mass of the skull. Evidence gathered from this study supports the hypothesis that the area available for temporalis muscle attachment may be a large contributor to sinus expansion. This is well represented in the vombatiform families, Palorchestidae and Diprotodontidae, reflected by the relatively small brain endocast compared to their large head sizes. Species with larger craniums than modern wombats have expanded sinuses, allowing for an increase in the area available for attachment of the masticatory muscles, compensating for the limited external surface area of the braincase resulting from a small brain.

The stage at which sinuses begin to form in the crania of marsupial taxa can be informed by examining the ontogenetic series of *Kolopsis torus* (Murray, 1992) and *Nimbadon lavarackorum* (Black et al., 2010). In *K. torus*, a diprotodontoid from the late Miocene (body size approximately 125–250 kg; Murray, 1997), pneumatisation becomes apparent when the M4 has begun to emerge. In *N. lavarackorum* (body size approximately 70 kg; Black et al., 2012), sinuses develop early, becoming larger and more expansive as the animal matures to accommodate the progressive separation of the outer and inner bony tables (Black et al., 2010). Black et al. (2010) found that in *N. lavarackorum*, a thick diploe layer was present in suckling pouch young (Stage II), and by the time the animal was fully weaned (Stage IV), sinuses had begun developing in the squamosal and were already well developed in the frontals. Parietal sinuses did not develop until Stage VI, when the animal was a young adult (Black et al., 2010).

The relationship between sinus volume and cranial volume identified in this study indicates that species larger than the

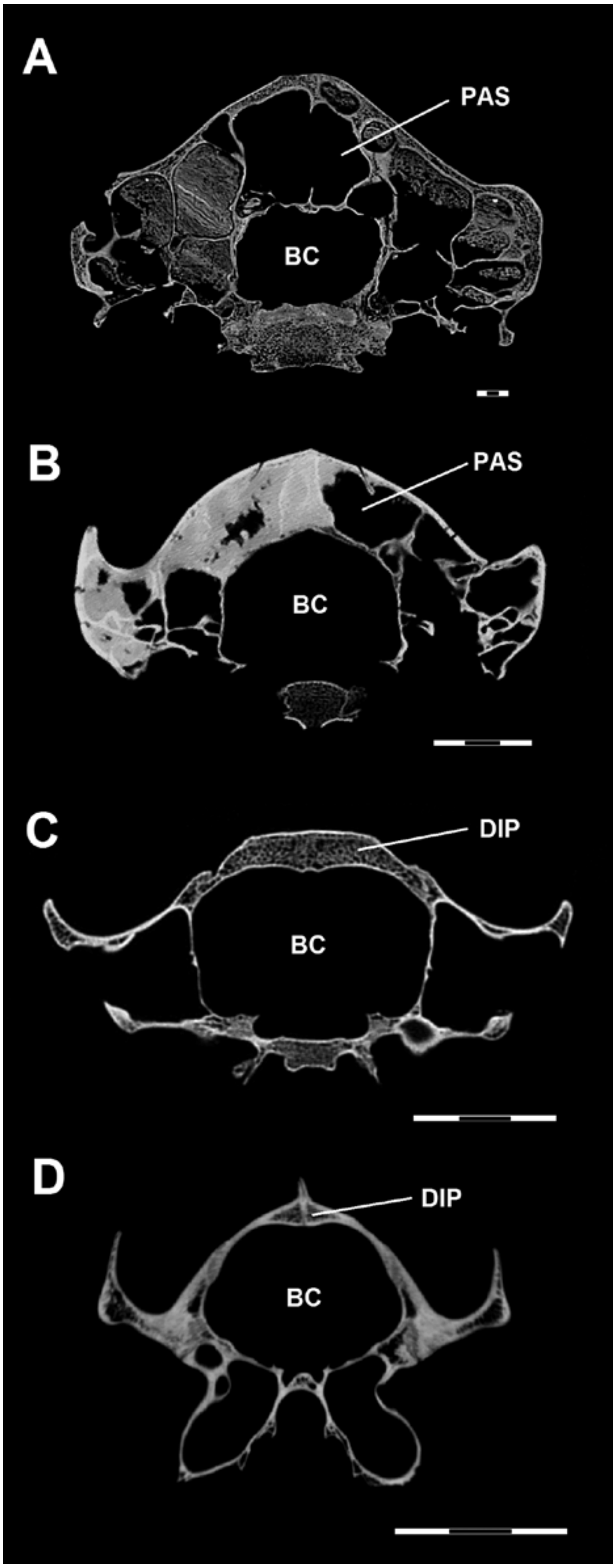

Figure 5. Frontal CT slices showing the braincase (BC), diploe (DIP) and parietal sinuses (PAS) in *Diprotodon* (A), *Neohelos* (B), *Lasiorhinus* (C) and *Phascolarctos* (D). Scale bars are 3 cm.

extant vombatids begin developing pneumatisation of the auditory, squamosal and parietal sinuses in addition to the frontal sinuses (fig. 4). Adult *Vombatus* and *Lasiorhinus* crania have a similar thickened diploe to that of immature *K. torus* and *N. lavarackorum* (fig. 5), representing the pre-pneumatised state. When vombatiform marsupials obtain a cranial volume greater than those of *Vombatus* and *Lasiorhinus*, the brain remains relatively small while the sinuses expand to provide adequate surface area for the attachment of the temporalis muscles.

The size of the masticatory muscles and the area needed for their attachment may account for some of the extensive sinus formation in large vombatiform herbivores. The braincase itself offers inadequate surface area for the attachment of the enlarged temporalis muscle in species larger than *Vombatus* and *Lasiorhinus*. In the largest marsupials (*Diprotodon* and *Zygomaturus*), the brain fills less than 10% of the total cranial volume, and less than 5% in *Diprotodon*. Qualitative analysis of the internal volume of the braincase in juvenile *Nimbadon lavarackorum*, suggests negative allometric growth of the inner table compared to skull length (Black et al., 2010). Measurements of *K. torus* indicate that the braincase ceases to expand by the time it reaches approximately half its mature cranial dimensions (Murray, 1992). Sinuses become larger and more expansive as the animal matures resulting in the progressive separation of the outer and inner bony table during cranial growth. This separation must continue to reach adult head size and allow for adequate attachment area for the temporalis muscle.

Why have small brains?

Brain size has been linked to both maternal life history investment traits, such as length of gestation and lactation, litter size, and basal metabolic rate (BMR) (Barton and Capellini, 2011; Isler, 2011; Isler and van Schaik, 2009a; Jerison, 1973; Martin, 1981; McNab and Eisenberg, 1989; Striedter, 2005). In general, as marsupials get larger, brain size progressively gets relatively smaller compared to placental mammals of equivalent body size (Black et al., 2010; Jerison, 1973; Murray, 1992). This trend does not however, occur in smaller marsupials (<13 g), which have relatively large brains compared to those of placental mammals of comparable body size (Weisbecker and Goswami, 2014).

Small brains in large marsupials may be due to a combination of factors, including the brain being a metabolically expensive organ, the short gestation length in marsupials, and environmental conditions, such as seasonality (Isler and van Schaik, 2009a; Martin, 1996). BMR is a standard measure of energy expenditure in endotherms. In marsupials, body mass accounts for 98.8% of the variation in total BMR (McNab, 1988). However, previous studies have provided no evidence of a positive correlation between brain size and BMR in marsupials (McNab, 1986, 2005; Weisbecker and Goswami, 2010), especially in marsupials less than 43 g, which have relatively large brains and low BMR compared to similar sized placental mammals. Large mammals, however, typically have a lower BMR and larger gut capacity (Owen-Smith, 1988), also a metabolically expensive organ (Aiello and

Wheeler, 1995), compared with those in smaller mammals. Therefore, a smaller brain may be necessary to meet total energy demands. The Expensive Brain Hypothesis claims that having a large brain must involve trade-offs by reducing the energy allocation to other expensive functions or organs, such as digestion or production (growth and development), or the cost of having a large brain must be met by increasing the total energy turnover (Isler and van Schaik, 2009a).

Brain size may be more strongly linked to maternal metabolic rate. The Maternal Energy Hypothesis predicts that relative brain size should correlate with the amount of energy that a mother is able to provide to her offspring (Martin, 1981; 1996). Marsupials are born at a very immature state (altricial) compared to placental mammals, and have a much shorter gestation period, followed by a longer lactation period (Lee and Cockburn, 1985). Barton and Capellini (2011) found that mammals that gave birth to more mature neonates (precocial) have larger-brained offspring, even after taking into account body size and gestation length. Most of the brain growth in marsupials occurs after birth (Darlington et al., 1999; Smith, 1997). Therefore, it would be expected that the longer and more energetically demanding lactation period would be correlated with brain size, and maternal metabolic rates would have a positive effect on brain size during this time. Weisbecker and Goswami (2010) found that this, indeed, was the case and that brain size most strongly correlated with the length of the lactation period, supporting the Maternal Energy Hypothesis. Thus, larger brains take longer to grow, resulting in prolonged maternal energy investment. For very large marsupials, such as *Diprotodon* and other extinct megafauna, maternal investment could have been very long. In an estimate of developmental times in *Diprotodon*, based on trends for macropodid marsupials (Russell, 1982), Tyndale-Biscoe (2001) predicted that a single young would be born after 6–8 weeks, leave the pouch permanently at 860 days, and be fully weaned after four to five years, at which point it would have weighed 270 kg. Therefore, the critical phase of lactation may have lasted for up to four years. This is a huge investment for the mother, and in the unpredictable and seasonal environment at the time of the Pleistocene, lactation time may have been less than these estimated values, thus reducing adult brain size. Therefore, there may be an upper limit to the size that the marsupial brain can reach, depending on lactation duration, maternal energy investment, BMR and seasonality (Isler, 2011; Isler and van Schaik, 2009b).

Behavioural functions for sinuses

Although the presence of sinuses may be due to the opportunistic growth and expansion of the outer table from the inner table driven by demands from soft tissue including the jaw muscles and brain, there may also be novel or secondary functions. Similarly voluminous sinuses to those of marsupial megafauna are also present in modern giraffes (Badlangana et al., 2011). Suggested functions include protection from impacts during neck-sparring, clubbing and other behaviours used in competition for mates and the establishment of hierarchies among individuals in herds (Badlangana et al., 2011; Simmons and Scheepers, 1996). There is also some degree of sexual dimorphism, where males have relatively larger sinuses than females. This could support the hypothesis that sinuses help protect the brain from male-male competition during neck-sparring. The outer wall of the skull, or the struts within the sinuses, could deform during impact, in place of deformation of the endocranium, because thin walls are more deformable than solid bone (Farke, 2008). However, this has not been tested in the giraffe, and there is little evidence to support this hypothesis for other species, including head-butting goats (Farke, 2008).

It has been suggested that *Diprotodon* moved in small herds over large areas (Price, 2008). The extensive sinuses may have functioned as sound resonance chambers for production and amplification of low frequency vocalisations. Low frequency sound has a much greater range, a fact exploited by many mammals including elephants and koalas, and even some birds, including emus and cassowaries. Modern koalas (*Phascolarctos cinereus*) produce low frequency vocalisations to communicate over long distances and display to females (Ellis et al., 2011; Martin and Handasyde, 1999; Mitchell, 1990; Smith, 1980). To help hear these vocalisations, koalas have large auditory bullae (Louys et al., 2009). Cassowaries have a highly pneumatised casque that may be used as an acoustic organ for social and sexual display (Naish and Perron, 2014). The large sinuses found in extinct marsupial megafauna such as *Diprotodon*, may have functioned to produce, amplify and receive low frequency vocalisations. Further behavioural work on giraffes and other living megafauna with extensive endocranial sinuses is needed to develop this hypothesis for extinct marsupial megafauna.

Conclusions

Larger-bodied vombatiform marsupials have larger sinuses and smaller brains relative to those in smaller marsupials. Larger body size is also associated with lower metabolic rate, slower growth, delayed sexual maturity and lower fecundity (Fisher et al., 2001). The volume of the sinuses in large marsupials has increased allowing for an increase in the area available for attachment of the masticatory muscles, compensating for the limited external surface area of the braincase resulting from a small brain, which may be a consequence of a lower maternal metabolic rate, linked to body size (Fisher et al., 2001; Stearns, 1992). Secondary functions of the sinuses may include stress distribution during mastication, or low frequency sound production and amplification for social and sexual communication between individuals.

Future work should investigate variation between individuals of the same species, including sexual differences and age differences; comparisons with other marsupial taxa such as macropods; and variation between marsupial and placental mammals. Sex and age of the specimens used in this study could have influenced the results. Sexual dimorphism in sinus volume has been shown in giraffe (Badlangana et al., 2011), and age influences relative brain and sinus volume as shown in the ontogenetic series of *K. torus* and *N. lavarackorum* (Black et al., 2010; Murray, 1992). Furthermore, the mechanisms that might control sinus morphology, including strut formation, could also be investigated through ontogenetic studies. It would be of considerable interest to determine whether sinus morphology and the pattern of trabeculae are based on phylogeny, behavioural functions, biomechanical stress distribution, ontogenetic development or through a combination of these.

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