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Scaling of bony canals for encephalic vessels in euarchontans: Implications for the role of the vertebral artery and brain metabolism

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ABSTRACT

Supplying the central nervous system with oxygen and glucose for metabolic activities is a critical function for all animals at physiologic, anatomical, and behavioral levels. A relatively proximate challenge to nourishing the brain is maintaining adequate blood flow. Euarchontans (primates, dermopterans and treeshrews) display a diversity of solutions to this challenge. Although the vertebral artery is a major encephalic vessel, previous research has questioned its importance for irrigating the cerebrum. This presents a puzzling scenario for certain strepsirrhine primates (non-cheirogaleid lemuriforms) that have reduced promontorial branches of the internal carotid artery and no apparent alternative encephalic vascular route except for the vertebral artery. Here, we present results of phylogenetic comparative analyses of data on the cross-sectional area of bony canals that transmit the vertebral artery (transverse foramina). These results show that, across primates (and within major primate subgroups), variation in the transverse foramina helps significantly to explain variation in forebrain mass even when variation in promontorial canal cross-sectional areas are also considered. Furthermore, non-cheirogaleid lemuriforms have larger transverse foramina for their endocranial volume than other euarchontans, suggesting that the vertebral arteries compensate for reduced promontorial artery size. We also find that, among internal carotid-reliant euarchontans, species that are more encephalized tend to have a promontorial canal that is larger relative to the transverse foramina. Tentatively, we consider the correlation between arterial canal diameters (as a proxy for blood flow) and brain metabolic demands. The results of this analysis imply that human investment in brain metabolism (~27% of basal metabolic rate) may not be exceptional among euarchontans.

1. Introduction

Some of the most intriguing and debated questions in evolutionary biology are those surrounding the evolution and scaling of brain size (Jerison, 1955, 1973; Martin, 1981; Armstrong, 1983, 1985; Dunbar, 1998; Pagel, 2002; Finarelli and Flynn, 2007; Isler et al., 2008; Grabowski, 2016; Grabowski et al., 2016). Relatedly, researchers have long sought to understand the cognitive benefits (Van Valen, 1974; Willerman et al., 1991; Dunbar, 1998; Deaner et al., 2007; Shettleworth, 2009; Hofman, 2014; Krupenye et al., 2016; MacLean, 2016) and energetic costs of a large brain (Pagel and Harvey, 1988; Aiello and Wheeler, 1995; Dunbar, 1998; Isler and Van Schaik, 2006; Weisbecker and Goswami, 2010; Karbowski, 2011; Navarrete et al., 2011; Isler, 2013; Seymour et al., 2015, 2016; Pontzer et al., 2016). In this study, we address the question of how, anatomically, brains maintain adequate blood perfusion. We do so using comparative data on cross sectional areas of bony canals for arteries capable of irrigating the brain, hereafter referred to as encephalic arteries.[1]

Among primates and their close euarchontan relatives, the encephalic arteries primarily include (1) the vertebral arteries, which originate from the subclavian arteries and ascend through the transverse foramina of the sixth through first cervical vertebrae, and (2) branches of the carotid arteries. In many taxa, encephalic branches of the carotid arteries anastomose with the basilar artery (formed by fusion of the vertebral arteries) in the circle of Willis (Fig. 1).

[1] Note that encephalic arteries are a type of cranial artery. Non-encephalic, cranial arteries include those associated with the cranium that do not necessarily supply brain tissue. The stapedial artery, which branches from the internal carotid artery in some taxa, and meningeal arteries can be considered non-encephalic, cranial arteries.

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Unlike the vertebral arteries, which ubiquitously contribute to encephalic circulation, euarchontans show several different configurations in their carotids. Scandentians (non-primate euarchontans, a.k.a. treeshrews), anthropoids, and tarsiers rely on an internal carotid vessel that travels to the brain via the promontorial canal (Bugge, 1974; Cartmill and MacPhee, 1980; MacPhee, 1981; MacPhee and Cartmill, 1986; Boyer et al., 2016). Certain other euarchontans involute (i.e., lose ontogenetically)

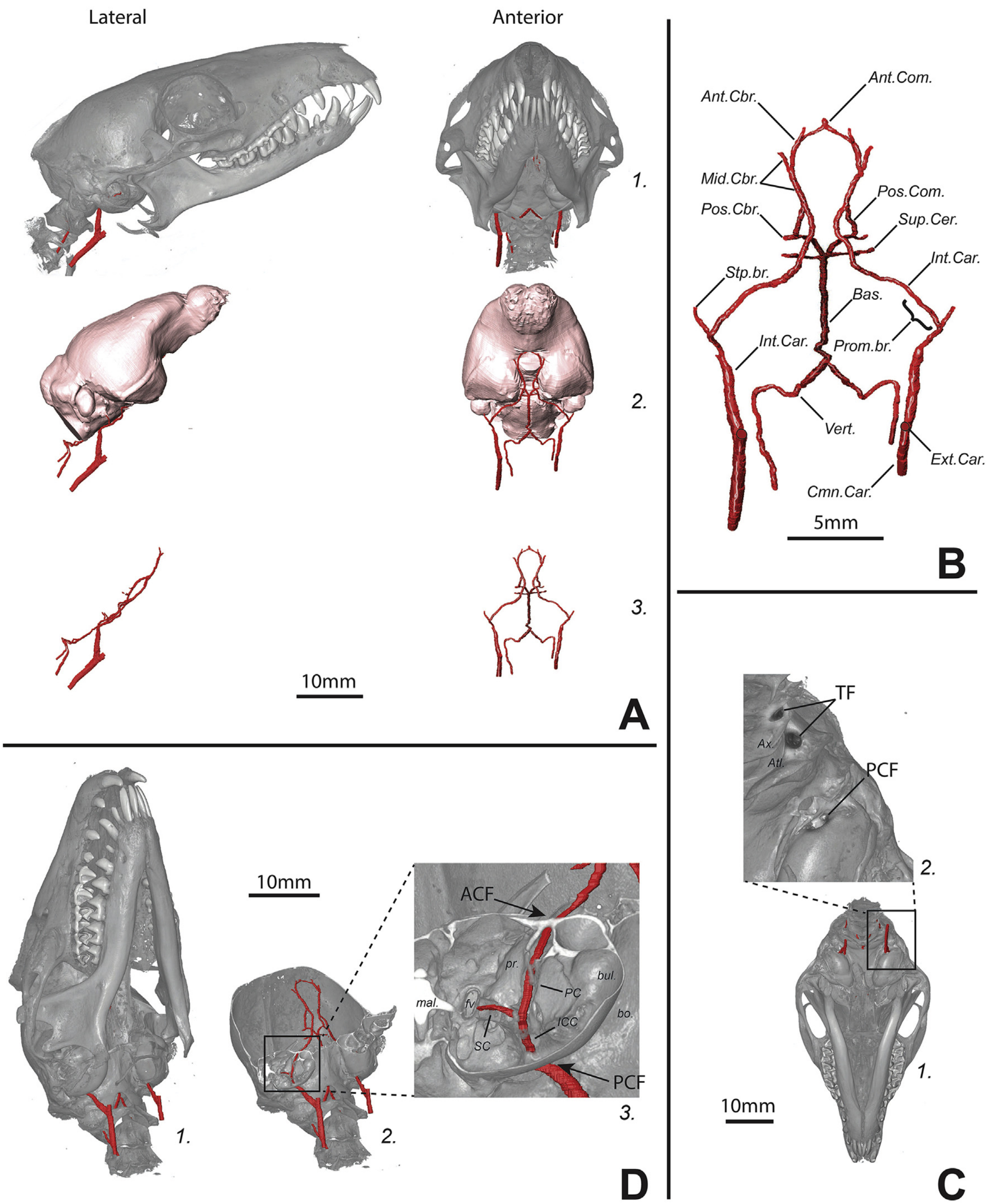

Figure 1. Diagram of encephalic blood supply. This study focuses on understanding the role of the vertebral artery in cerebral and encephalic blood supply and on predicting the metabolic energy consumption of the brain using estimates of the brain size and encephalic arterial canal diameter. **A**(*1*), microCT rendering of a *Tupaia* skull in lateral and anterior view. **A**(*2*), bone removed to show segmentation of the endocranial cast (which approximates brain volume, mass and morphology) and encephalic vasculature. **A**(*3*), endocranial cast removed to show arterial segmentation. This specimen retained alcohol-preserved soft tissue. The vascular system was perfused with latex and the dilated arterial lumen were traced using ImageJ and Avizo 8.1. **B**, detail of encephalic vasculature lumen casts showing the major components of the arterial circle of Willis. The pattern in haplorhine primates and humans is almost identical. Abbreviations: Ant, Anterior; Bas, Basilar; br, branch; Car, Carotid; Cbr, Cerebral; Cer, Cerebellar; Cmn, Common; Com, Communicating; Ext, External; Int, Internal; Mid, Middle; Pos, Posterior; Prom, Promontorial; Stp, Stapedial; Sup, Superior; Vert, Vertebral. **C**(*1*), microCT rendering of skull in ventral view. **C**(*2*), inset of microCT rendering of skull showing transverse foramen (TF) in atlas (Atl) and axis (Ax), as well as posterior carotid foramen (PCF) between petrosal and entotympanic. **D**(*1*), microCT rendering of skull in ventrolateral view. **D**(*2*), cut away to show tympanic cavity and endocranium. **D**(*3*), inset showing details of tympanic cavity. Abbreviations: ACF, anterior carotid foramen; bo, basioccipital; bul, bulla (entotympanic); fv, fenestra vestibule; ICC, internal carotid canal; mal, malleus; PC, promontorial canal (measured to represent promontorial artery); PCF, posterior carotid foramen; pr, promontorium of petrosal; SC, stapedial canal.