



Locomotion and basicranial anatomy in primates and marsupials



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ABSTRACT

There is ongoing debate in paleoanthropology about whether and how the anatomy of the cranium, and especially the cranial base, is evolving in response to locomotor and postural changes. However, the majority of studies focus on two-dimensional data, which fails to capture the complexity of cranial anatomy. This study tests whether three-dimensional cranial base anatomy is linked to locomotion or to other factors in primates ($n = 473$) and marsupials ($n = 231$). Results indicate that although there is a small effect of locomotion on cranial base anatomy in primates, this is not the case in marsupials. Instead, facial anatomy likely drives variation in cranial base anatomy in both primates and marsupials, with additional roles for body size and brain size. Although some changes to foramen magnum position and orientation are phylogenetically useful among the hominoids, they do not necessarily reflect locomotion or positional behavior. The interplay between locomotion, posture, and facial anatomy in primates requires further investigation.

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1. Introduction

The basicranium is an important region of the skull, serving as a site of interaction between the many varied functions of the head and those of the postcranium. In hominins, the basicranium underwent a fairly drastic reorganization in its orientation and relationship to the face, with alterations to the morphology of the temporal and occipital bones (Kimbel et al., 2014). Among those features said to differ in hominins and hominoids is the position of the foramen magnum, which is often argued to indicate locomotor or positional behaviors. Specifically, the foramen magnum is argued to be more anterior (e.g., Şenyürek, 1938; Schultz, 1955; Dean and Wood, 1981; Schaefer, 1999; Russo and Kirk, 2013, 2017) and more inferiorly oriented (e.g., Moore et al., 1973) in bipeds than in quadrupeds. As a result, basicranial morphology, and foramen magnum position specifically, is often used to assess locomotor and positional behaviors, especially in fossil remains when postcranial elements are missing. Important examples include *Sahelanthropus* (Brunet et al., 2002; Zollikofer et al., 2005) and *Ardipithecus ramidus* (White et al., 1994), and notably in Dart's (1925) initial assessment of the Taung skull, the holotype of *Australopithecus africanus*.

An anterior position of the foramen magnum has long been linked to differences in head balance and neck musculature (reviewed in Schultz, 1942; Dean, 1985; Luboga and Wood, 1990) and is argued to confer a mechanical advantage to orthograde taxa (Şenyürek, 1938; Schultz, 1942, 1955). More anteriorly placed foramina magna may reduce the amount of nuchal musculature required to sustain the head in an upright posture by shifting the center of gravity of the skull (Şenyürek, 1938). Differences between humans and other hominoids in the size and position of muscles with origins on the basicranium have been attributed to shifts in foramen magnum position (Dean, 1985). The rectus capitis anterior muscle in humans, for example, is further from the midline and not anterior to the foramen magnum, while the longus capitis is shorter and oriented transversely, rather than anteroposteriorly as in other hominoids (Dean, 1985). Both these muscles are tied to flexing and supporting the head. The more inferior orientation of the foramen magnum found in hominins relative to the posterior orientation in other hominoids has also been attributed to the more vertical orientation of the cervical vertebral column in bipeds (Moore et al., 1973). Variation in the orientation of the foramen magnum has been tentatively tied to cervical lordosis in humans (Been et al., 2014), providing a direct link between cranial base morphology and posture. This relationship between the cranial base and posture remains, even though cervical lordosis itself is primarily a result of soft tissue structures (Been et al., 2014).

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However, the true relationship of foramen magnum position and orientation to posture and locomotion across taxa remains contested (Moore et al., 1973; Bolk, 1909; Lieberman et al., 2000; Kimbel and Rak, 2010; Russo and Kirk, 2013, 2017; Ruth et al., 2016). Strait and Ross (1999) found no clear evidence that head and neck postures are influencing basicranial morphology in primates. Further, many primates, including monkeys and apes, appear to have undergone a shift in foramen magnum anatomy relative to other mammals so that the foramen magnum is oriented more inferiorly rather than posteriorly, regardless of whether they remain primarily quadrupedal (Le Gros Clark, 1934). Such a shift, with a more centralized and inferiorly oriented foramen magnum, may have been present in the ancestor of all modern anthropoids (Le Gros Clark, 1934). Instead of reflecting aspects of locomotor behavior, foramen magnum position and orientation may instead be related to aspects of brain size, brain growth and restructuring (Le Gros Clark, 1934; Weidenreich, 1941; Biegert, 1963; Lieberman et al., 2000), cranial vault shape (Bolk, 1909), or anatomy and positioning of the face (Le Gros Clark, 1934; Ruth et al., 2016). Luboga and Wood (1990) also found an allometric influence on basicranial morphology—in humans, individuals with larger crania have more posteriorly located foramina magna.

Le Gros Clark (1934) argued that an increase in the size of the occipital lobes of the brain, linked to improved vision in primates, resulted in a posterior growth of the cranial vault and thus the repositioning of the foramen magnum on the basal aspect of the skull. This repositioning of the axis of the head in turn is linked to the repositioning of the face (Le Gros Clark, 1934). Ross and Ravosa (1993) and Lieberman et al. (2000) confirmed a link between brain size and cranial base angulation in primates, although these data do not generally match ontogenetic data, which shows that cerebral expansion does not account for changes to basicranial morphology (reviewed in Bastir et al., 2010).

Biegert (1963) argued based on ontogenetic data that a combination of a relatively larger face and smaller brain would result in a less flexed cranial base. Bastir et al. (2010) found support for this hypothesis in primates and in fossil hominins, in particular, those showing that larger faces and smaller brains are both linked to a more posteriorly rotated cranial base. Mice with relatively larger faces also tend to have longer cranial bases, and the size of the face accounts for a substantial portion of variation in cranial base angulation (Lieberman et al., 2008). More recent studies (e.g., Neaux, 2017) have also found links between the length, size, and orientation of the face and basicranial features.

This latter set of hypotheses, in which foramen magnum orientation is linked to brain size and facial anatomy, is supported by a variety of indirect data as well. For example, primate juveniles display more anterior, inferiorly oriented foramina magna than their adult counterparts despite no real differences in cervical orientation (Bolk, 1909; Moore et al., 1973), suggesting that there is no locomotor or positional component to foramen magnum orientation. Additionally, adult *Pongo* have a more vertical cervical column than other hominoids, but the position and orientation of their foramen magnum is indistinguishable from that of knuckle-walking hominoids (Moore et al., 1973), and the orientation of the foramen magnum among anthropoids is not associated with orientation of the orbit or measures of head and neck carriage (Strait and Ross, 1999; Lieberman et al., 2000). Adult *Alouatta*, however, display exceptionally posteriorly positioned and oriented foramina magna, which Bolk (1909) hypothesized are linked to their well-developed hyoid apparatus. Orthopedic data in humans also suggests a link between masticatory anatomy and cervical

posture (e.g., Özbek and Köklü, 1993; Tecco and Festa, 2007), further suggesting at least some interplay between the different regions of the skull and the orientation of the foramen magnum within taxa.

It is unclear how these relationships of brain size and facial size to basicranial anatomy are linked to the morphologies associated with locomotion and posture. Recent research into craniofacial growth, development, and modularity provide strong evidence that the skull is a highly integrated structure in which changes to one feature will affect many others (e.g., Bastir and Rosas, 2005, 2009; Lieberman et al., 2008; Martínez-Abadías et al., 2009; Bastir et al., 2010). Integration likely extends into the head and neck (Ross and Ravosa, 1993), suggesting a complex relationship between posture and skull shape.

I use three-dimensional data of the cranial base and face to investigate the relationship of foramen magnum position and orientation to locomotor behavior in primates and marsupials in order to consider morphological change in the foramen magnum in the context of the cranium as a whole. I test two primary hypotheses: 1) the foramen magnum is more anteriorly positioned in orthograde or bipedal taxa than in pronograde taxa, and 2) the foramen magnum is more inferiorly oriented in orthograde or bipedal taxa than in pronograde taxa. Marsupials serve as a comparative group in which to test and verify hypotheses about foramen magnum anatomy that have been constructed primarily for primates because, like primates, marsupial taxa engage in a variety of postures and locomotor behaviors, including orthograde and bipedalism. Bipedal rodents are excluded due to the unique morphology of their basicrania, which include greatly expanded auditory bullae (e.g., Ruth et al., 2016), and the difficulty of collecting microscribe data on such small animals.

I additionally test other factors potentially related to foramen magnum orientation (Weidenreich, 1941; Biegert, 1963; Luboga and Wood, 1990; Lieberman et al., 2000). These factors include overall body size, facial size and orientation, and brain size. Specifically, I test whether they are linked to the morphology of the cranial base and whether facial size is linked to locomotion and posture.

2. Materials and methods

The sample consists of 223 individuals from 11 strepsirrhine genera, 250 individuals from nine catarrhine genera (Table 1), and 231 individuals from eight marsupial genera (Table 2). All individuals are adult and maturity was assessed through both dental eruption and fusion of the sphenoccipital synchondrosis and other sutures, as necessary. Samples consist of approximately equal numbers of males and females generally. Species were chosen to represent different locomotor or postural behaviors and balance phylogenetic relationships. Phylogenetic trees for primates were downloaded from 10kTrees Version 3.0 (Arnold et al., 2010; see Supplementary Online Material [SOM] Figs. 1 and 2). The phylogenetic tree for macropods is based on the trees presented in Cardillo et al. (2004) and Meredith et al. (2008, 2009; SOM Fig. 3), and does not include branch lengths. The human sample consists of approximately equal numbers of native Ugandans and Zulus. Among primates, an attempt was made to use only one species for each genus or to keep different species separate in analyses, but in the case of *Eulemur*, *Nycticebus*, and *Propithecus* this proved impossible because a substantial portion of museum specimens were classified as species that have recently been split and renamed using soft tissue or geographical characteristics that were not available in

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