



Locomotor pattern fails to predict foramen magnum angle in rodents, strepsirrhine primates, and marsupials



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ABSTRACT

Foramen magnum position has traditionally been used as an indicator of bipedality because it has been thought to favor a more “balanced” skull position. Here, we analyzed foramen magnum angle (FMA) in relation to locomotion in three mammalian orders that include bipedal or orthograde species in addition to quadrupedal or pronograde species. In marsupials and strepsirrhine primates, we found that there is no relationship between locomotor pattern and FMA. In rodents, we found that there is a significant difference in FMA between bipedal and quadrupedal rodents. However, when these species are analyzed in the context of enlarged auditory bullae, this relationship is no longer significant. Additionally, we find a significant relationship between relative brain size and FMA in strepsirrhine primates. Taken together, these data indicate that several developmental modules of the cranium influence FMA, but that locomotion does not. We caution that basicranial evolution is a complex phenomenon that must be explored in the context of each taxon’s unique evolutionary and developmental history.

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1. Introduction

Anterior transposition of the foramen magnum (FM) remains a purported cardinal correlate of upright walking in hominids.¹ Indeed, a relatively anterior FM has been used to infer bipedality in fossil taxa from the type specimen of *Australopithecus africanus* (Dart, 1925) to *Sahelanthropus tchadensis* (Brunet et al., 2002). More than 50 years have now passed since Josef Biegert argued that FM position is, instead, a developmental correlate of relative size and structure of the face and neocortex (Biegert, 1957, 1963). Moreover, FM position has largely failed to generate any simple relationship with locomotor pattern in non-human primates.

1.1. Hypotheses of FM position

The hypothesis that anterior migration of the FM in humans is a direct response to upright posture dates back at least as far as

Broca (1872) and has since become one of the primary dogmas of physical anthropology. The most commonly cited hypothesis for this link is the “balancing” hypothesis, which holds that the FM has been relocated anteriorly in hominids to improve head balance atop the cervical column (e.g., Topinard, 1890; Bolk, 1909; Schultz, 1942, 1955; Ashton and Zuckerman, 1952, 1955; DuBrul, 1962; Dean and Wood, 1981, 1982; Russo and Kirk, 2013).

Biegert (1957, 1963) proposed that enlargement of the brain, and in particular the neocortex, induces flexion of the cranial base, while enlargement of the masticatory apparatus induces its extension. According to this hypothesis, specialization of either the brain or the masticatory apparatus is a primary inductor of basicranial morphology.

Ross and Ravosa (1993) confirmed that brain size relative to basicranial length is associated with an increase in basicranial flexion, so that shorter cranial bases relative to larger brains result in more flexed basicrania. Strait (1999) found that basicranial length scales isometrically with non-cortical components of the brain, such that a larger neocortex (relative to non-cortical brain components) shortens the basicranium and increases basicranial flexion. These data support the hypothesis that neocortex size influences basicranial flexion.

Bastir et al. (2010) directly tested Biegert’s hypothesis in non-human primates, humans, and hominids and found that cranial base flexion increased with larger brain size and decreased with

Abbreviations: FMA, foramen magnum angle; ER, encephalization ratio.

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¹ “Hominid” is used here to refer to humans and their ancestors after their separation from the ancestors of chimpanzees, as we recognize four hominoid families: Hominidae, Panidae, Gorillidae, and Pongidae.

larger masticatory apparatus size. Bastir et al. further concluded that this relationship holds true for Neandertals, which have greater midfacial prognathism and less flexed basicrania, but have comparable brain size to modern humans.

Relying on FM position in rodents, marsupials, and strepsirrhines, a recent study concluded that FM position lies relatively more anteriorly in bipedal/orthograde species than it does in quadrupedal/pronograde species (Russo and Kirk, 2013). We demonstrate here that the measurements used in that study do not accurately correspond to FM position, but instead with the relative position and size of the masticatory apparatus. We use an alternative angular measurement to represent both position and orientation of the FM in place of the metrics they used (for details and justification, see below). Using a measure of FM angulation, our first aim was to test whether differences existed between quadrupeds and bipeds within each taxon. Our second aim was to rule out potentially confounding factors in taxa in which differences exist. In rodents, we observed extremely expanded auditory bullae, and in strepsirrhines we examined the effect of brain size on FM position.

2. Methods

2.1. Sample

We collected cranial metrics from 61 extant species from mammalian orders Diprotodontia, Rodentia, and Primates (Tables 1–3) from the Mammals Section of the Carnegie Museum of Natural History (Pittsburgh, PA) the Division of Mammals at the Smithsonian Institution (Washington, D.C.), and the Field Museum of Natural History (Chicago, IL). Individuals with noticeable skeletal injury or postmortem damage were excluded from analysis, and we targeted species for which body weight and brain weight were known. For species in which notable sexual dimorphism exists, we analyzed only males. Our sample included 48 marsupials (22 species), 47 rodents (19 species), and 37 strepsirrhine primates (20 species).

2.2. Metric selection and data collection

Russo and Kirk (2013) relied on cranial base dimensions involving basion and other anterior landmarks such as the last

molar, temporal fossa, and palate. Such dimensions are likely influenced by the size of the masticatory apparatus and/or the length of the basicranium and not necessarily by FM position. As an illustration of this principal, we chose the species with the highest and lowest values of each measurement from Russo and Kirk (2013) and scaled them such that the distance between prosthion and basion was identical in each specimen (Fig. 1A). The animals with the lowest ratios are reported to have the most anteriorly positioned FM. While the species with the lowest temporal fossa ratio (TFR) and palate ratio (PR) (*Onychogalea lunata*, 0.39 and 0.49, respectively) clearly displays a moderately anterior FM, the species with the lowest molar ratio (MR) has an FM so posteriorly positioned that basion and opisthocranium are essentially in the same plane (*Vombatus ursinus*, MR = 0.43). On the other hand, the species with the highest of all three measurements, *Phascolarctos cinereus*, displays a FM that is clearly more anterior than in *V. ursinus* (PR = 0.51, MR = 0.65, TFR = 0.79). Instead of reflecting FM position, these three ratios obviously reflect the positioning of the masticatory apparatus. In *Vombatus* the molars are located more posteriorly relative to other structures of the cranium, resulting in shorter distances between basion and anterior structures and smaller ratios. In grazing marsupials with diastemata between incisors and premolars (which includes almost all bipedal marsupials) any increase in the length of this space will reduce the ratio. Finally, in *P. cinereus*, the temporal fossa is extremely long anteroposteriorly, reflecting the size of its large temporalis muscle. Thus, the extremely high ratios in this species do not reflect a posterior FM, but instead the substantial length between basion and anterior landmarks caused by the unusually large temporalis muscle.

According to Biegert's (1957, 1963) hypothesis, both masticatory size and brain mass affect the degree of basicranial flexion. Such flexion should be reflected in the position of the FM relative to another standard plane such as the Frankfort Horizontal. Therefore, in place of using the above metrics, we measured FM declination by placing a rigid wire between basion and opisthion and photographed the skull in norma lateralis. We measured the angle that this wire (acting as a plane) defined with the Frankfort Horizontal in marsupials and strepsirrhines and with the occlusal plane in rodents. We defined this as foramen magnum angle (FMA) (Fig. 2). A side-by-side comparison of the species with the highest and

Table 1
Values used in marsupial analysis.

Family	Species	N	FMA (mean)	FMA (SD)	Locomotion
Macropodidae	<i>Dendrolagus lumholtzi</i>	1	130.31	—	Q
	<i>Macropus eugenii</i>	5	134.03	1.85	B
	<i>Macropus giganteus</i>	6	131.01	1.85	B
	<i>Macropus robustus</i>	2	126.48	3.58	B
	<i>Macropus rufogriseus</i>	1	109.27	—	B
	<i>Macropus rufus</i>	1	134.00	—	B
	<i>Thylogale stigmatica</i>	1	129.29	—	B
	<i>Wallabia bicolor</i>	1	106.31	2.23	B
	<i>Petrogale penicillata</i>	4	136.12	7.06	B
	<i>Petrogale concinna</i>	1	143.45	—	B
	<i>Dorcopsis hageni</i>	3	135.76	6.81	B
	Phalangeridae	<i>Trichosurus vulpecula</i>	1	131.94	—
<i>Phalanger orientalis</i>		1	138.28	—	Q
<i>Spilocuscus maculatus</i>		3	124.30	6.62	Q
Phascolarctidae	<i>Phascolarctos cinereus</i>	1	125.87	—	Q
	<i>Bettongia penicillata</i>	3	134.00	1.02	B
Potoridae	<i>Potorous tridactylus</i>	1	141.18	—	Q
	<i>Petauroides volans</i>	3	130.39	3.91	Q
Pseudocheiridae	<i>Pseudocheirus cupreus</i>	1	117.33	—	Q
	<i>Pseudocheirus peregrinus</i>	3	125.39	3.31	Q
	<i>Hemibelideus lemuroides</i>	4	132.91	3.40	Q
	<i>Vombatus ursinus</i>	1	124.42	—	Q
Vombatidae	22 species	48			

FMA = foramen magnum angle. Locomotion category from Russo and Kirk (2013). B = Bipedal. Q = Quadrupedal.

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