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.

Introduction

Anterior transposition of the foramen magnum (FM) remains a purported cardinal correlate of upright walking in hominids¹. 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.

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 noncortical 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 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.

Methods

Sample

We collected cranial metrics from 61 extant species from mammalian orders Diprotodontia, Rodentia, and Primates (Tables 1, 2, and 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).

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 (Figure 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 *Vombatus* (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 *Phascolarctos*, 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 planer position of the FM relative to another standard plane such as the Frankfurt 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) (Figure 2). A side-by side comparison of the species with the highest and lowest FMAs demonstrates that this measurement more accurately reflects both FM position and orientation in species in which the FM is positioned most posteriorly (Figure 1B). We conclude that FMA is a more appropriate measure of FM position because it does not depend on the position of masticatory structures, which differ with age, muscle size, and general masticatory adaptation both intraspecifically and interspecifically.

We also used the occlusal plane in rodents as we did not want to introduce variation related to bulla size to our measurement. The use of the occlusal plane serves as an arbitrary “baseline” to which we can compare FMA. It should be noted, however, that use of this plane means that rodent FMA cannot be compared with any of the other FMAs analyzed in this paper, but only with other rodents.

We measured bulla size by tracing the area of the bullae in norma basilaris. We then divided that area by the entire surface area of the cranium, also in norma basilaris, to obtain a relative bulla size. We took all measurements from scaled photographs in ImageJ ver. 1.46r.

We obtained measures of brain weight and body weight for each strepsirrhine species from Isler et al. (2008). Some of these measures were reported as endocranial volumes, and we converted these to brain mass by multiplying by 1.036 (Boddy et al., 2012). We calculated an encephalization ratio (ER) by dividing brain weight in grams by body weight in grams, and multiplying that number by 100. We calculated an ER instead of the more commonly used encephalization quotient because Biegert’s hypothesis states that brain size *relative to body size* (more specifically, relative to masticatory size) will impact FM position. Encephalization quotient (EQ) is calculated in an attempt to control for body size. However, we regard brain size in relation to body size as a more accurate measure with which to test the hypothesis.

We divided each group of mammals into bipedal vs. quadrupedal (marsupials and rodents) or orthograde vs. non-orthograde (strepsirrhines) following Russo and Kirk (2013). However, we

did change the classification of *Galago demidovii* from an orthograde primate to non-orthograde. While Gebo (1987 p.278) described *G. demidovii* as “predominantly a leaping species,” leaping is not a priori associated with vertical posture. Our observations of videos and cineradiographic sequences support the classification of *G. demidovii* as primarily pronograde, with bouts of verticality associated only with clinging, leaping, and vertical climbing- as in virtually all strepsirrhines (Charles-Dominique, 1977; Gebo, 1987; Daniel Gebo, personal communication).

Statistical analyses

We compared bipedal/orthograde species with quadrupedal non-orthograde species using independent sample t-tests. We conducted these tests separately for each taxon (i.e., marsupials, rodents, and strepsirrhines) in order to minimize the influence of phylogeny on our results. In rodents, we further explored our data by conducting a one-way Analysis of Covariance (ANCOVA) of the effect of locomotor category, size of the auditory bullae, and the interaction between the two on FMA. In strepsirrhines, we performed a standard linear regression of FMA onto ER. We set significance at $p < 0.05$ for all analyses and conducted them in SPSS Statistics v.22 (IBM).

Results

Marsupials

We found no difference in foramen magnum declination between bipedal and quadrupedal marsupials ($t = 1.53$, $p > 0.10$) (Table 4).

Rodents

Our initial t-test results showed that a difference in mean FM declination exists between bipedal rodents and quadrupedal rodents ($t = -2.79$, $p < 0.05$) (Table 4). However, as noted earlier we observed that many, if not most, of the bipedal species examined possessed grossly inflated auditory bullae, which lie in sufficiently close proximity to the FM to greatly impact the latter's position (Figure 3). We therefore conducted an ANCOVA to ascertain the relative contributions of bulla size and locomotor category to variance in FMA in rodents. This revealed that there is no difference in slope between bipedal and quadrupedal animals when bulla size is taken into consideration, and what appears to be a difference in FMA due to locomotor category is in fact variation due to bulla size (Table 5). Standard linear regression showed that bulla volume had an effect size of 50% and predicted FMA according to the expression $38.26 (x) + 106.64$ ($R^2 = 0.52$, $p < 0.005$) (Figure 4).

Strepsirrhines

We found no significant difference in FMA between orthograde and non-orthograde strepsirrhines ($t = -1.62$, $p = 0.12$) (Table 4). In order to test Biegert's (1957, 1963) hypothesis, we also performed a linear regression analysis for strepsirrhines between FMA and ER. We found that FMA is predicted by ER according to the expression $5.45 (x) + 139.99$ ($R^2 = 0.46$, $p < 0.05$) and has an effect size of 21.6 % (Figure 5).

Discussion

The results presented here essentially corroborate the large body of literature relating facial form and brain size to basicranial anatomy (Biegert, 1963; Ross and Ravosa, 1993; Ross and

Henneberg, 1995; Strait, 1999; Lieberman et al., 2000a; Bastir et al., 2006, 2010). The data we collected from rodents allow us to add auditory bulla size to an extensive suite of characters that may influence or are correlated with the development of the basicranium, including facial kyphosis and relative neocortex volume (Biegert, 1963; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Strait, 1999), midfacial prognathism (Bastir et al., 2010), relative brain size (Sporer, 1997), and pharyngeal anatomy (McCollum, 1999). Our data from strepsirrhines support the hypothesis that relative brain size influences FM position, though the moderate effect size indicates that it does so in association with some or all of the above-mentioned characters.

Additionally, our results corroborate previous studies that have failed to relate FM position to habitual posture or locomotion (Strait and Ross, 1999; Lieberman et al., 2000b; Kimbel and Rak, 2010). Neck position and orientation may be a more relevant variable for studies of FM position than trunk position, as the cervical vertebrae articulate directly with the basioccipital. However, the angle between head and neck does not correlate with locomotion in primates (Strait and Ross, 1999), nor does cervical spine orientation in other mammals (Vidal et al., 1986). This suggests that, instead of the FM changing orientation in order to adjust to the orientation of the trunk and spine, it is more likely that the cervical spine changes shape and position in order to unite the trunk and FM (Been et al., 2014).

Masticatory diversity and molar progression in diprotodontid marsupials

We did not find any association between FMA and locomotion or posture in marsupials.

However, our data do not permit an extensive test of Biegert's (1957, 1963) hypothesis. An important element of that hypothesis is that masticatory apparatus size scales positively with body size while neocortex volume scales negatively. Thus, large animals are expected to have relatively flat basicrania and posteriorly positioned foramina magna when compared with small animals. Diprotodontia exhibits extreme diversity in terms of masticatory size and morphology. It includes marmot-like wombats, insectivorous and nectarivorous opossums, and grazing kangaroos and wallabies. The diversity present within these marsupials closely approaches that present in several orders of placentals. It is therefore extremely difficult to test this and other hypotheses of FM position absent any control for masticatory apparatus size (including its soft tissues).

A further complication is the phenomenon of molar progression in many species of grazing and browsing macropodids (kangaroos and wallabies). The four molars in several species of these marsupials erupt over a period of as much as 11 years and migrate anteriorly throughout adulthood (Dawson, 1995). The most worn are progressively shed to accommodate this migration. The primary dentition degenerates before eruption except for a single P3, which, along with two permanent premolars, provides the initial chewing dentition (Vogelnest and Allan, 2015). These teeth migrate anteriorly as new alveolar bone is deposited posteriorly (Kirkpatrick, 1964; Lentle et al., 2003). Thus, anterior teeth are shed and replaced by migrating replacements, a process that continues throughout adulthood. Aged kangaroos may be left with as few as two molars (Kirkpatrick, 1964; Lentle et al., 2003; Vogelnest and Allan, 2015).

Molar progression results in anteroposterior elongation of the jaw with age as well as variable dental formulae in adults (Kirkpatrick, 1964; Lentle et al., 2003; Barber et al., 2008). This adaptation occurs only in the bipedal marsupials, though not all bipedal marsupials display this adaptation. For these reasons, marsupial basicranial and craniofacial data contain too many unknown sources of variation, which impact an examination of hypotheses related to FM position.

Moreover, marsupial dental specializations are almost inconsequential when compared to the vast differences in developmental progression and timing in marsupials and placentals. In the former, the facial skeleton and basicranium both begin and complete ossification before the neurocranium, and indeed even before the telencephalon evaginates (Clark and Smith, 1993; Smith, 1996). In *Macropus eugenii* (Tamar wallaby), the basioccipital forms a synchondrosis with the surrounding basisphenoid at three postnatal days (Clark and Smith, 1993), while the dermal bones of the calvarium do not form until 50 days postnatally (Clark and Smith, 1993). This general pattern holds in all marsupials, in which morphogenesis of the central nervous system (CNS) extends well into the period of cranial skeletal development, in contrast to the pattern in placental mammals, in which CNS development precedes differentiation of the cranial skeleton (Clark and Smith, 1993; Smith, 1996; 2001; Vaglia and Smith, 2003; Goswami, 2007). This developmental pattern allows marsupials to be born in an extremely altricial state - soon after the onset of organogenesis - and to remain in the marsupium as organogenesis proceeds. The extremely early formation and ossification of the marsupial basicranium likely influences its interaction with other structures. Further study on the developmental

consequences of this early cranial development in marsupials is needed in order to make conclusions about the relationship of the basicranium to other proximate structures.

Auditory adaptations in desert-dwelling rodents

We demonstrate here that the use of heteromyid and dipodid rodents in studies of FM position and locomotion is problematic because the entire skull is grossly distorted by highly inflated auditory bullae (Figure 3). Each bulla in *Dipodomys merriami* (Merriam's kangaroo rat) occupies 0.49 cm^3 , while brain volume is 1.11 cm^3 (Webster, 1962). Bulla volume is 0.88 cm^3 in *Dipodomys spectabilis* (Banner-tailed kangaroo rat) (Webster, 1961) with a brain volume of 2.08 cm^3 (Hafner and Hafner, 1984). Such large middle ear volume is thought to be an adaptation to predator detection by increasing sensitivity to resonance frequencies (Webster, 1962).

Increased middle ear volume is but one of a suite of convergent adaptations shared in several nocturnal, desert-dwelling rodents, including several mechanisms of water conservation and, perhaps most strikingly, a form of saltatory bipedal locomotion (Bartholomew and Caswell, 1951; Webster, 1961; 1962; Harris, 1984). There are no bipedal species that do not display moderate to tremendous bulla modification. The auditory bulla's proximity to the FM in these species (including those in genera *Dipodomys*, *Microdipodops*, and *Jaculus*) and its inclusion in this convergent suite of adaptations, including bipedality, confounds attempts to relate FM position to locomotor pattern in these rodents.

Our results should encourage caution in inferring bipedality in fossil hominids from FM position and/or orientation. Our data from all three taxa examined show that locomotion and

posture do not influence FM position or orientation, and we conclude that this is likely in hominids as well. Anterior migration of the foramen magnum in early, small-brained hominids likely reflects changes in the relative sizes of the brain's components (i.e., an expanded neocortex)(Holloway, 1966, Holloway et al., 2003), and as such is still a useful indicator of the behavior and biology of extinct species. Bipedality, however, should be inferred from the postcranium.

Summary

While Russo and Kirk (2013) reported that bipeds have more anteriorly positioned foramina magna, we conclude here that those results must be reinterpreted in light of the unique biology of each taxon. Instead of using landmarks that may be responsive to adaptations within other cranial modules, we measured the FMA relative to the Frankfort Horizontal or occlusal plane and regard this as a more accurate representation of FM location, including both position along the anterior-posterior axis of the cranium and its orientation relative to a reference plane (Figure 1).

When we explored the variation in marsupial FM location, we found no relationship to locomotion (Table 4). Within rodents, heteromyids and dipodids have independently evolved grossly enlarged auditory bullae, which distort the entire splanchnocranium. When the effects of these structures are accounted for, the impact of locomotion on FM position becomes statistically negligible (Table 5, Figure 4). We analyzed FMA and locomotor category in

strepsirrhines and found no significant difference between pronograde and orthograde species (Table 4), but did find a significant relationship between FMA and ER (Figure 5). Our results show that locomotion does not influence FM orientation in marsupials, rodents, or strepsirrhines, and 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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Notes: 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.

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Figure 1 A) Basal view (left to right) of *Onychogalea lunata*, *Vombatus ursinus* and *Phascolarctos cinereus*. Each skull has been scaled such that the distance between prosthion and basion is identical. While *Onychogalea lunata* exhibits both the lowest temporal fossa ratio (TFR (0.39)) and the lowest palate ratio (PR (0.49)), it nevertheless clearly displays a moderately anterior FM. *Vombatus ursinus*, which has a molar ratio (MR) of 0.43, has the most posteriorly located FM of the three specimens. *Phascolarctos cinereus* (PR = 0.51, MR = 0.65, TFR = 0.79), exhibits a FM that lies clearly more anteriorly than does that of *Vombatus*. These three ratios clearly reflect the position of the masticatory apparatus and not that of the FM. In *Vombatus*, the molars are located more posteriorly relative to other cranial structures. This results in shorter distances between basion and anterior structures and thus smaller ratios. In grazing marsupials, the length of the diastema separating the incisors and premolars decreases the three ratios by demonstrably increasing the denominator (the geometric mean of skull length and width). The extremely high ratios in *Phascolarctos* likewise do not reflect a posterior FM, but instead a large temporalis muscle. **B)** A similarly scaled comparison of *Petrogale concinna* and *Wallabia bicolor*. The former exhibits the highest FMA (143.45), while the wallaby exhibits the lowest (106.31), demonstrating that the Foramen Magnum angle used in this paper more accurately reflects both FM position and orientation.

Figure 2. Measurement of FMA (FM plane against the occlusal plane) in

Dipodomys spectabilis (FMA = 127.50). A line is drawn through opisthion and basion. A second line extends from the occlusal plane. The angle between these two lines is the FMA, an indicator of its anteroinferior migration. A similar angle was measured in marsupials and strepsirrhine primates, except that the Frankfort Horizontal plane was used in place of the occlusal plane.

Figure 3. Skulls of (top, left to right) dipodid rodents *Napaeozapus insignus* and *Jaculus jaculus*, and (bottom, left to right) heteromyid rodents *Chaetodipus hispidus*, *Dipodomys spectabilis*, and *Microdipodops pallidus* in norma basalis (Not to scale; as previously, the distances between basion and prosthion have been made equal). Note the grossly inflated auditory bullae in the three bipeds (*J. jaculus*, *D. spectabilis*, and *M. pallidus*) vs. those in the two quadrupeds (*N. insignus* and *C. hispidus*). Taxa in both dipodid and heteromyid rodents share adaptations for desert living, including large auditory bullae and bipedal, saltatory locomotion. The immediate proximity of the bullae to the FM obviously influences both its position and orientation. Also note that the increased length and width of skulls with larger bullae has the same effect on the geometric mean of skull size as does the large diastema in macropodid marsupials: It increases the denominator (geometric mean), thus artificially decreasing the resulting ratios.

Figure 4. Regression of FMA with bulla size in rodents. Quadrupeds are represented by closed diamonds, while bipeds are represented by open circles. The expression $38.26(x) + 106.64$ predicts FMA in rodents ($R^2 = 0.52$, $p < 0.005$) and is shown on the graph. Moreover, its slope does not differ between quadrupeds and bipeds.

Figure 5. Regression of foramen magnum angle (FMA) with encephalization ratio (ER) in strepsirrhines. The expression $5.45 (x) + 139.96$ predicts FMA in strepsirrhines ($R^2 = 0.456$, $p < 0.05$).

Table 1. Values used in marsupial analysis. Locomotion category from Russo and Kirk (2013).

FMA= foramen magnum angle.

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	-	Q
	<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
Potoridae	<i>Bettongia penicillata</i>	3	134.00	1.02	B
	<i>Potorous tridactylus</i>	1	141.18	-	Q
Pseudocheiridae	<i>Petauroides volans</i>	3	130.39	3.91	Q
	<i>Pseudocheirops 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
Vombatidae	<i>Vombatus ursinus</i>	1	124.42	-	Q
	22 species	48			

Table 2. Values used in rodent analysis. FMA= foramen magnum angle. Locomotion category from Russo and Kirk (2013).

Family	Species	n	FMA (Mean)	FMA StD)	Locomotion	Relative Bulla Size (Mean)	Relative Bulla Size (StD)
Dipodidae	<i>Allactaga</i>	1	134.35	-	B	-	-
	<i>sibirica</i>						
	<i>Jaculus jaculus</i>	5	136.69	19.12	B	0.59	.02
	<i>Dipus sagitta</i>	1	129.67		B	0.60	-
	<i>Napaeozapus</i>	2	130.34	3.18	Q	0.19	.03
	<i>insignis</i>						
Heteromyidae	<i>Chaetodipus</i>	3	115.78	6.93	Q	0.41	.04
	<i>hispidus</i>						
	<i>Chaetodipus</i>	2	127.63	5.01	Q	0.49	.03
	<i>penicillatus</i>						
	<i>Dipodomys</i>	2	137.86	.97	B	0.72	.02
	<i>deserti</i>						
	<i>Dipodomys</i>	3	132.30	2.96	B	0.62	.03
	<i>merriami</i>						
	<i>Dipodomys ordii</i>	3	126.22	1.88	B	0.64	.02

Geomyidae	<i>Dipodomys</i>	3	127.50	4.66	B	0.65	.02
	<i>spectabilis</i>						
	<i>Heteromys</i>	3	122.05	2.54	Q	0.18	0
	<i>desmarestianus</i>						
	<i>Liomys salvini</i>	3	126.81	2.76	Q	0.46	.01
	<i>Microdipodops</i>	1	139.66	3.26	B	0.83	-
	<i>megacephalus</i>						
	<i>Microdipodops</i>	3	143.02	1.81	B	0.83	0.04
	<i>pallidus</i>						
	<i>Perognathus</i>	3	133.53	4.31	Q	0.54	0.03
	<i>parvus</i>						
	<i>Geomys</i>	2	115.69	1.95	Q	0.27	0.04
	<i>bursarius</i>						
	<i>Orthogeomys</i>	2	103.66	3.26	Q	0.29	0.03
	<i>hispidus</i>						
	<i>Zygogeomys</i>	1	103.64		Q	0.30	-
	<i>trichopus</i>						
	<i>Thomomys</i>		119.46		Q	0.36	0.01

	<i>talpoides</i>						
Muridae	<i>Gerbillus</i>	2	129.68	1.66	Q	0.46	.02
	<i>gerbillus</i>						
	<i>Tatera brantsi</i>	3	127.35	3.37	Q	0.58	.03
	21 species	47					

Table 3. Values used in strepsirrhine analysis.

FMA= foramen magnum angle. ER= encephalization ratio. ER calculated from brain weight and body weight from Isler (2008). Posture categories from Russo and Kirk (2013), except for *Galago demidovii* (Daniel Gebo, personal communication.)

Family	Species	n	FMA (Mean)	FMA (Std Dev)	ER	Posture
Cheirogalidae	<i>Cheirogaleus major</i>	2	139.52	5.33	1.5	NO
	<i>Cheirogaleus medius</i>	1	135.14	-	1.92	NO
	<i>Microcebus rufus</i>	1	152.15	-	4.14	NO
Daubentoniidae	<i>Daubentonia madagascariensis</i>	1	143.77	-	1.82	NO
Galagidae	<i>Galago demidovii</i>	2	162.45	0.21	3.67	NO
	<i>Galago senegalensis</i>	3	163.27	2.72	2.11	O
	<i>Otolemur crassicaudatus</i>	2	152.70	0.43	1.07	NO
Indriidae	<i>Avahi laniger</i>	1	151.01	-	0.85	O
	<i>Propithecus verreauxi</i>	3	153.93	1.90	0.92	O

Lemuridae	<i>Indri indri</i>	3	141.55	0.38	0.57	O
	<i>Lemur catta</i>	2	142.50	3.95	1.07	NO
	<i>Hapalemur griseus</i>	1	144.51	-	2.06	O
	<i>Lepilemur mustelinus</i>	1	146.47	-	1.27	O
	<i>Varecia variegata</i>	3	138.37	0.76	0.93	NO
Lorisidae	<i>Arctocebus calabarensis</i>	1	161.75	-	2.32	NO
	<i>Perodicticus potto</i>	3	128.36		1.54	NO
	<i>Loris tardigradus</i>	2	165.56	3.13	3.15	NO
	<i>Nycticebus coucang</i>	3	145.60	2.69	1.65	NO
	18 species	37				

Table 4. Results of t-tests comparing FMA in bipedal/orthograde and quadrupedal/non-orthograde animals. In marsupials, no significant relationship was found between locomotion and FMA. Rodents did show a significant difference in FMA between quadrupeds and bipeds. See text for further discussion. Strepsirrhines showed no significant difference between “orthograde” and “non-orthograde” species.

Taxon	t	Significance
Marsupials	-1.53	0.14
Rodents	-2.79	0.01
Strepsirrhines	-1.62	0.12

Table 5. Results of three ANCOVA in marsupials. Model one includes bulla size, locomotor category, and an interaction term. Results are not significant. Model 2 includes bulla size and locomotor category, and results are again not significant. Model 3 includes bulla size only, and is significant at the 0.001 level.

Variable	t	Significance
Model 1		
Bulla Size	2.23	0.04
Locomotor Category	-1.01	0.33
Interaction Term	0.97	0.35
Model 2		
Bulla Size	2.97	0.004
Locomotor Category	-0.28	0.78
Model 3		
Bulla Size	4.37	<.001

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5