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Landi, Federica, Profico, Antonio orcid.org/0000-0003-2884-7118, Veneziano, Alessio et al. (2 more authors) (2020) Locomotion, posture, and the foramen magnum in primates:Reliability of indices and insights into hominin bipedalism. AMERICAN JOURNAL OF PRIMATOLOGY. e23170. ISSN 0275-2565

https://doi.org/10.1002/ajp.23170

Title:

Locomotion, posture and the foramen magnum in primates: reliability of indices and insights into hominin bipedalism

Short title:

Foramen magnum, locomotion and posture

Federica Landi* [1], Antonio Profico [2], Alessio Veneziano [3], Isabelle De Groote[4], Giorgio Manzi [5]

1 Centre for Anatomical and Human Sciences, Hull York Medical School, York, United Kingdom

2 PalaeoHub, Department of Archaeology, University of York, United Kingdom

3 Elettra-Sincrotrone Trieste S.C.p.A., Basovizza, Trieste, Italy

4 Department of Archaeology, Department of Archaeology, Section Prehistory of western Europe, Ghent University, Ghent, Belgium

5 Department of Environmental Biology, Faculty of Mathematics Physics and Natural Sciences, Sapienza University of Rome, Rome, Italy

Corresponding author's contacts:

Name: Federica Landi

Email: hyfl4@hyms.ac.uk

Address: 23 Bedford Park, PL4 8HN, Plymouth (UK)

ABSTRACT

The position (FMP) and orientation (FMO) of the foramen magnum have been used as proxies for locomotion and posture in extant and extinct primates. Several indices have been designed to quantify FMP and FMO but their application has led to conflicting results. Here we test six widely used indices and two approaches (univariate and multivariate) for their capability to discriminate between postural and locomotor types in extant primates and fossil hominins. We then look at the locomotion of australopithecines and *Homo* on the base of these new findings. The following measurements are used: the opisthocranion-prosthion (OP-PR) and the opisthocranion-glabella (OP-GL) indices, the basion-biporion (BA-BP) and basion-bicarotid (BA-BC) chords, the foramen magnum angle (FMA), and the basion-sphenoccipital ratio (BA-SF). After exploring the indices variability using Principal Component Analysis, pairwise comparisons are performed to test for the association between each index and the locomotor and postural habits. Cranial size and phylogeny are taken into account. Our analysis indicates that none of the indices or approaches provides complete discrimination across locomotor and postural categories, although some differences are highlighted. FMA and BA-BP distinguish respectively obligate and facultative bipeds from all other groups. For what concerns posture, orthogrades and pronogrades differ with respects to OP-PR, OP-GL and FMA. Although the multivariate approach seems to have some discrimination power, the results are most likely driven by facial and neurocranial variability embedded in some of the indices. These results demonstrate that indices relying on the anteroposterior positioning of the foramen may not be appropriate proxies for locomotion among primates. The assumptions about locomotor and postural habits in fossil hominins based on foramen magnum indices should be revised in the light of these new findings.

Keywords: primate adaptation, skeletal morphology, cranial base, human evolution

INTRODUCTION

Primates exhibit high variability in their locomotion. Different locomotor patterns have influenced primate morphological evolution and factors such as limb proportions, pelvis and long bone morphology are often used to make inference about locomotion (Demes and Jungers, 1993; Profico et al., 2017; Sarringhaus et al., 2016). Nevertheless, other skeletal structures such as the cranial base may have undergone important locomotor adaptations, likely because of its articulation with the axial skeleton (Kimbel and Rak, 2010; Lieberman et al., 2000). The foramen magnum, one of the key regions of the cranial base, allows the passage of the major circulatory and neural connections between the skull and the postcranial skeleton. Also, the foramen magnum is physically connected to the vertebral column, whose morphology has a remarkable influence on the locomotion of a species (Kimbel and Rak, 2010; Kimbel et al., 2014; Lieberman et al., 2000; Jones et al., 2018). Because of its role in linking the head with the axial skeleton, and its alleged role in balancing the head atop the vertebral column in humans (Lieberman, 2011), the morphology, position and orientation of foramen magnum have been linked to postural and locomotor differences in fossil hominins (Ahern, 2005; Brunet et al., 2002; Neaux et al., 2017; Russo and Kirk, 2013) and primates (Luboga & Wood, 1990; Simons, 1967).

Several methods have been used to describe and estimate foramen magnum position (FMP) and orientation (FMO) on the cranial base (Brunet et al., 2002; Dean and Wood, 1981; Kimbel et al., 1984; Luboga and Wood, 1990; Neaux et al., 2017; Russo and Kirk, 2013, 2017; Ruth et al., 2016; Simons, 1967; White et al., 1994). The early work of Topinard (1878) stressed the importance of a comparative approach to study the forward migration of the foramen magnum in modern humans compared to fossil hominins. In 1925, Dart assumed the bipedal posture of the Taung child (*Australopithecus africanus*) based on the “head balancing index", a measure of FMP relating the basion (the anterior border of the foramen magnum) with the prosthion-inion line (the line between the most anterior point on the maxilla and the occipital protuberance) (Dart, 1925). Dean and Wood (1981) and Luboga and Wood (1990) used a series of indices to describe differences in FMP and cranial base shape between *Homo* and the great apes, and between robust and gracile australopithecines. Other authors relied on the use of similar indices to describe cranial base affinities between the australopithecines and *Homo* (Kimbel et al., 1984). More recently, a series of linear indices based on FMP has been used to infer bipedalism, thus the hominin status, of fossil taxa such as *Sahelanthropus* (Brunet et al., 2002; Zollikofer et al., 2005) and *Ardipithecus* (Suwa et al., 2009; White et al., 1994). Also, some authors have focused on the use of foramen magnum indices for discriminating posture in mammals and fossil hominins (Neaux et al., 2017; Russo & Kirk, 2013, 2017).

Although foramen magnum indices have been widely adopted in locomotion and postural studies, their interpretation is still debated due to contrasting results (Ahern, 2005; Neaux et al., 2017; Russo and Kirk, 2013, 2017; Ruth et al., 2016). Some limitations may be the reason for such controversies. For example, some indices are based on cranial regions other than the cranial base and may reflect variations not related to the basicranial morphology (Neaux et al., 2017; Ruth et al., 2016). Therefore, these indices may only partially account for locomotion and posture and instead include information on other aspects of cranial morphology such as mandibular and cranial vault shape modifications due to changes in diet, mastication and encephalization across primates and the hominin lineage (Bastir & Rosas, 2009; Raia et al., 2018). Indeed, the morphology of the cranial base and the orientation and position of the foramen magnum have been observed to be affected by the growth and development of the neurocranium and facial complex as well as the orientation of the latter (Anton, 1989; Cheverud & Midkiff, 1992; Cheverud et al., 1992; Bastir & Rosas, 2006; Lieberman et al., 2008; Gkantidis & Halazonetis, 2011).

In addition, conclusions are often drawn based on untested indices, whose relation to posture and locomotion is therefore not supported by statistical evidence (Russo and Kirk, 2017). Testing should be performed by taking into account extant species and possible sources of error, such as size and phylogenetic relatedness among taxa. A broad comparative sample of extant and extinct species is essential to make assumptions on the status of fossil hominins. Partially because of these limitations and the conflicting results, the functional interpretation of the position and orientation of the foramen magnum as locomotor adaptations have been doubted (White et al., 2015). A comprehensive assessment of FMP and FMO indices is necessary to make order in the controversial results left behind by more than a century of studies. Such assessment is even more important as the debate around posture, locomotion and the foramen magnum is still ongoing, in particular for hominins. Bipedalism in fossil species is considered diagnostic of the hominin status. The passage from facultative to obligate bipedalism is believed to mark an important transition to a more modern lifestyle and skeletal anatomy. Nevertheless, unravelling the meaning of the skeletal variation within hominins has proven difficult, also due to the fragmentary nature of the fossil record. There is still disagreement about the significance of the anatomical changes occurred at the transition between australopithecines and *Homo*, and the locomotor behaviour of the early hominins, particularly *Homo habilis*, is still poorly understood and highly debated (Harcourt-Smith & Aiello, 2004; Ruff, 2009; Harcourt-Smith, 2015). A better understanding of FMP and FMO indices would help timing the evolutionary shift that led to hominins exhibiting a modern locomotor style.

The goal of this study is to clarify the limitations of FMP and FMO indices and to identify the best approach, if any, that could be reliably used for assessing locomotion and posture in extant primates and fossil hominins. We compare indices of FMP and FMO recorded on a large sample of 3D models of primate and hominin crania to test the following hypotheses:

(I) FMP and FMO indices differ significantly across locomotor and postural groups in extant primates and fossil hominins.

(II) The multivariate combination of the FMP and FMO indices is a suitable method for discriminating locomotion and posture of extant primates and fossil hominins.

The species in the sample are divided into unambiguous locomotor and postural categories, which are the target of the analysis. The discriminatory power of the indices is tested using univariate and multivariate approaches and by controlling for the phylogenetic relatedness among taxa and cranial absolute size.

METHODS

Ethical statement

The sample used for this study includes skeletal and fossil digital material. This material consists of CT-scans and digital mesh surfaces of primate skulls and fossil hominin skulls from different institutions. For this reason, the protocols did not require approval from any institutional animal care and use committees (IACUC). The research adheres to the legal requirements of the United Kingdom, where the study was conducted, and to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. Furthermore, the authors declare no conflict of interest.

Sample

The extant primate sample includes the following groups: Prosimians (13 species), New World Monkeys (12 species), Old World monkeys (38 species), and Apes (10 species), for a total of 73 species and 288 individuals of known sex (see Supplementary S. Table 1 and 2 for further details). Only adult specimens are included, their age-class being recognized by the eruption of the third molar. The sample consists of 3D virtual models of skulls obtained by surface scan or computed tomography (CT-scan). The models are kindly provided by the online databases of the Smithsonian Institution (NMNH), the Kyoto University Primate Research Institute (KUPRI, Digital Morphology Museum), the Morphosource database at Duke University, and NESPOS digital archive (www.nespos.org).

The hominin sample includes 8 species: *Australopithecus africanus* (STS 5, CT scan), *Paranthropus boisei* (KNM-ER 406, CT scan), *Homo habilis* (KNM-ER 1813, CT scan, available from the Digital Archive of Fossil Hominoids, University of Vienna); *H. erectus* (Sangiran 17, laser scan of cast from the anthropological museum "G. Sergi", Rome; KNM-ER 3733, CT scan, from the National Museum of Kenya)*; H. floresiensis* (LB1, CT scan, kindly provided by Prof. Peter Brown, peterbrown-palaeoanthropology.net); *H. heidelbergensis* (Kabwe 1, CT scan from the National Museum of Kenya; Petralona 1, laser scan of cast from the museum "G. Sergi"); *H. neanderthalensis* (La Chapelle-aux-Saints1, CT scan from the Digital Archive of the Muséum national d'Histoire Naturelle, Paris); Saccopastore 1, CT scan from the Digital Archive of the museum "G. Sergi"); modern humans (6 CT-scans from NESPOS digital archive, www.nespos.org).

Foramen magnum indices

For each specimen, we recorded the position of nine homologous anatomical points (landmarks) using Avizo 9.0 software (FEI Visualization): opisthocranion, opisthion, basion, spheno-basion, glabella, prosthion, left zygo-orbitale, porions and carotid foramina. We applied Generalized Procrustes Analysis (GPA) to superimpose the landmark configurations on the mean shape in three steps: translation, scaling, and rotation. The resulting landmark configurations -after the GPA- are used to compute the linear measurements necessary for the calculation of the six indices used in this study (see Supplementary S.Table 3 for further information about the landmarks). The indices are calculated after full Procrustes superimposition of the landmark configurations, thus discarding the effect of the differences in cranial absolute size.

The opisthocranion-glabella (OP-GL) and the opisthocranion-prosthion (OP-PR) indices are built as homologous of the indices in Luboga and Wood (1990) (Figure 1). After projecting the opisthocranion, opisthion, basion, glabella and prosthion landmarks along the Frankfurt plane (estimated by orienting the skull using the left-zygorbitale and left porion landmarks), the barycentre of the foramen magnum (midpoint foramen magnum or MFM) is calculated as the mean point of the opisthion-basion distance. This measurement is then used to calculate a ratio of FMP along the anterior-posterior axis by dividing the distance from MFM to opisthocranion by the distance from opisthocranion to glabella (with opisthocranion-glabella distance representing 100% of the total length) (Figure 1). The same operation is performed for the OP-PR index but using the prosthion as the most anterior point of reference, thus accounting for the total cranial length (Figure 1). Luboga and Wood (1990) use the subnasal and the opisthion landmarks instead of the prosthion and the MFM respectively. Our choice of using the MFM instead of the opisthion is meant to avoid biases due to the posterior lengthening of the foramen magnum observed in some species; another reason for preferring the MFM is that the position of basion and opisthion are influenced by factors external to locomotion such as airorhynchy (Profico et al., 2017). The OP-PR was used so to have an index in which the total length of the skull was taken into account.

The basion-biporion (BA-BP) and the basion-bicarotid (BA-BC) indices describe the length of the chord connecting basion to the bi-porionic and bi-carotid lines, respectively (Ahern, 2005; Brunet et al., 2002; Luboga and Wood, 1990; Schaefer, 1999; Suwa et al., 2009; White et al., 1994).

The FMO was tested using the foramen magnum angle (FMA). The FMA is measured as the angle between the basion-opisthion chord and the Frankfurt plane as previously used in literature (Luboga and Wood, 1990; Ruth et al., 2016; Russo and Kirk, 2017). Here, the 2D angle was estimated on 3D skulls using the angle measurement tool of Avizo 9.0 (FEI visualization) (Figure 1).

The basion-sphenoccipital ratio (BA-SF) or “Basioccipital ratio” (Dean and Wood, 1981; Russo and Kirk, 2013, 2017; Ruth et al., 2016) is calculated as the distance between the sphenoccipital synchondrosis at the midline (i.e., spheno-basion) and the basion.

#Figure 1

Locomotor and postural categories

The categories used in this study describe postural and locomotor behaviours. There is a recent tendency toward the use of postural categories in locomotion studies (Russo and Kirk, 2013, 2017; Ruth et al., 2016). However, we believe that considering only the postural classification may underestimate the locomotor variability of primates. Therefore, the locomotor categories we used are as follows: vertical clingers, arboreal quadrupeds, terrestrial quadrupeds, brachiators, knuckle walkers, facultative bipedals, and obligate bipedals. Vertical clinging is a type of arboreal locomotion prevalently adopted by some prosimians and performed by clinging to vertical supports and leaping between supports (Fleagle, 2013). Anatomically specialised vertical clingers bear adaptations in the pelvic girdle and the lower part of the body, such as a lower forelimb to hindlimb ratios (intermembral index) (Granatosky, 2018): the longer hindlimbs bear the weight during clinging and are necessary to propel leaping between vertical substrates. Other morphological adaptations are shared among vertical clingers, such as the hindlimb bone cross-sectional geometry, which is more robust than in the forelimbs (Demes et al., 1991). In the pelvis, the ilium tends to be relatively wider than in quadrupedal strepsirrhines, although this feature has positive allometry with body size and holds for large species only (Lewton, 2015). In arboreal and terrestrial quadrupedalism, all four limbs are used with a regular gait walking (Fleagle, 2013). Quadrupedal species tend to have hindlimbs and forelimbs of similar length (Fleagle, 2013), reflecting their equal importance for locomotion. Differently from clinging and leaping primates, the femoral head of quadrupedal species is deeply enclosed in the pelvic socket, which reduces the range of movements allowed to the articulation (Ankel-Simons, 2010). Despite the similarities in limb proportions, the functional demands of terrestrial and arboreal quadrupedalism are different. In fact, prevalently arboreal species exhibit limbs that are relatively shorter than those of terrestrial quadrupeds, which helps maintaining the centre of mass closer to the branch (Rose, 1973). Brachiation relies on specialised forelimbs for moving between branches, usually producing a pendulum-like swinging alternating each arm as a fulcrum (Fleagle, 2013). Forelimbs are considerably longer than hindlimbs (Fleagle, 2013) and the humerus is straighter than in other primates, probably to resist torsion during brachiation (Swartz, 1990). The elongated and narrow scapulae together with the small and shallow glenoid fossa of ovate or spherical shape allow higher mobility to the forelimbs (Jenkins, 1974). Knuckle walking is a form of terrestrial, quadrupedal locomotion observed in the genera *Gorilla* and *Pan*, characterised by bearing the weight of the upper body on the dorsal surface of the third and fourth digits of the hand (Schmitt, 2010). As other quadrupeds, forelimbs and hindlimbs are of similar length, although the formers tend to be slightly longer than the latter (Fleagle, 2013). The articular surfaces of forelimb bones are relatively larger than in other primates, with the exception of hylobatids (Ankel-Simons, 2010). In addition, the thumb is not completely opposable (Ankel-Simons, 2010). Bipedalism is characteristic of modern humans and fossil hominins, although a distinction can be made between species that have lost all other form of terrestrial and arboreal locomotion (obligate bipedalism) and those (fossil) species who may have retained semi-arboreal habits butadopt bipedal stance non occasionally (facultative bipedalism) (Harcour-Smith, 2007; Prost, 1980). Due to the lack of extant representatives of facultative bipedalism, and since humans are the only extant obligate bipedals, setting an abrupt cutoff between the two forms of bipedalism has proven difficult. Both forms are characterised by hindlimbs longer than the forelimbs (Jungers, 2009) and hindlimb articular surfaces larger than in other primates (Jungers, 1988), thus reflecting the high loads acting on the lower body. In facultative bipedals, articular surfaces tend to be larger than in quadruped and suspensory primates but smaller than in humans (Jungers, 1988). Bipedalism likely triggered pelvic and vertebral adaptations to improve balance, such as curvature patterns in the column and reduced iliac blades (Gruss and Schmitt, 2015). Facultative bipedals exhibit skeletal features suggesting the retention of semi-arboreal habit in the formers, for example the phalangeal curvature (Richmond, 2007).

The postural categories adopted in this study are orthogrades, pronogrades, clinogrades, antipronogrades. These categories are not defined based on movement pattern or specific anatomical adaptations but rather on the relative position of the head and trunk during habitual stance or movement. Each postural group (except antipronogrades) includes species taxonomically and anatomically diverse. In orthograde posture, the spine is habitually vertical to the ground (Shapiro & Simons, 2002), a condition observed in vertical clinging strepsirrhines, brachiators and bipedal species. The pronograde posture is characterised by the spine being prevalently parallel to the ground during locomotion (Shapiro & Simons, 2002). Most arboreal and terrestrial quadrupeds adopt this posture while moving. In clinograde species, the forelimbs are elongated and the hindlimbs are flexed, the trunk is angled in relation to the ground and forms a triangle with the limbs (Anquetin & Tassy, 2007). The antipronograde group includes some species belonging to the *Lorisidae* family whose posture is not consistently pronograde or orthograde but changes orientation and bends frequently in more than one plane (Shapiro & Simons, 2002).

In Table 1, we report the definitions of the locomotor and postural categories used in this study (further information about the species assigned to each category are available in the Supplementary Tables 1 and 2). Each of the species in the sample is assigned to the locomotor and postural category that is the most used by each species according to literature.

Analytical approaches

The FMP and FMO indices are tested for their power in discriminating locomotor and postural habits in primates and fossil hominins considering the null hypothesis of independence between indices and categories. Two different approaches are used: univariate and multivariate. In the multivariate approach, the indices are combined in a single data matrix and their relative contributions are analysed. The multivariate analysis allows increasing the information to be tested by reducing its redundancy, as each variable contributes to the final result only partially. Unfortunately, fossil specimens are rarely blessed with completeness and it is unlikely that several indices are measurable on the same fragmentary specimen. It is, therefore, useful to address the issue of which single index could provide the best information and we also perform a univariate analysis for assessing the efficacy of each index in discriminating locomotion and posture. To account for phylogeny, we use the primate phylogenetic tree available in the “10ktrees” database (Arnold et al., 2010). For the hominin phylogeny, we use the topology published by Dembo et al. (2015), based on a Bayesian statistical approach applied on a matrix of morphological traits of hominins (Berger et al., 2015; Young et al., 2015). Palaeontological data of First and Last Appearance Datum (FAD and LAD) of fossil hominins is used to reconstruct plausible times of divergence between taxa. Potts (2013) provides a list of FAD and LAD data from several literature sources. Branch lengths are scaled to fit the time of divergence between *P. troglodytes* and *H. sapiens* in the non-hominin phylogenetic tree, by using the R package “ape” (Paradis et al., 2004). The phylogenetic tree is shown in Supplementary S.Figure 1.

Statistical analysis

As a preliminary step, FMP and FMO indices are normalized by subtracting mean and dividing by the standard deviations, to ease comparisons. We compute the phylogenetic signal for the multivariate sample and each index separately. The phylogenetic signal is calculated as the K statistics (Blomberg et al., 2003), which measures trait similarity between related species according to Brownian Motion (BM) conditions of trait evolution. Values of K close to zero suggest absence of phylogenetic constraints between related species, while K equal or higher than one indicates trait similarities as strong as expected under BM or stronger, respectively. The multivariate information of FMP and FMO indices is first analysed using Principal Component Analysis (PCA). Standard and phylogenetic PCAs are performed to explore the variability of the locomotor and postural groups and the relative importance of each index. Comparison of the standard and phylogenetic PCAs also address the relevance of phylogenetic effect on the variability of locomotor and postural indices. PCA loadings are used to determine the relative contribution of each index to the variations revealed by the PCA.

We then use pairwise comparisons between groups to test which groups differ with respects to which indices. The tests are performed on the multivariate sample (all indices) and each index separately. The differences between groups are measured as distances between group variances, calculated as the sum of the diagonal elements of the group covariance matrix divided by the number of observations in the group (Zelditch et al., 2012). The pairwise comparisons take into account the phylogenetic relatedness among taxa by assuming Brownian Motion model of trait evolution. Significance is two-tailed and is assessed using a residual randomization procedure (Collyer et al., 2015). A P value equal to or less than 0.05 was considered to be statistically significant. Phylogenetic signal and pairwise comparisons are performed using the R package “geomorph” (Adams and Otárola-Castillo, 2013).

RESULTS

Phylogenetic signal and Principal Component Analysis

The variability of the FMP and FMO across locomotor and postural groups is reported in the boxplot in Figure 2, where the data is not corrected phylogenetically. The indices produce overlapping results for most of the locomotor and postural categories, except for the obligate bipeds, which show a quite distinctive locomotion when applying the OP-PR, OP-GL and FMA indices.

#Figure 2

Table 2 shows that the Blomberg’s K is significant and consistently low for most indices, except for the BA-SF ratio (K: 0.83, p<0.001). In the case of BA-BP and BA-BC the signal is not significant, thus indicating lower or absent phylogenetic patterning on these indices. When all the indices are considered in a multivariate dataset, Blomberg’s K is low but significant (K: 0.20, p<0.001). Overall the results justify the use of a phylogenetic approach for the Principal Component Analysis (PCA). Because of the low phylogenetic signal, standard and phylogenetic PCAs performed similarly and here only the latter is discussed. Locomotor and postural Phylogenetic PCAs are shown in Figure 3, which shows scatterplots of scores and bar plots of loadings for the first and second principal components (the non-phylogenetic PCA is shown in supplementary S. Figure 2). For what concerns locomotion (PCA top left), results show a high variance in FMP and FMO indices for the arboreal quadruped group, which overlap to most other locomotor categories. Overlap is minimal or absent across terrestrial quadrupeds, brachiators, knuckle-walkers and vertical clingers. The genus *Homo* (obligate bipeds) is isolated from the other groups along the PC1 (% variance: 57.8) and partially along the PC2 (% variance: 16.8), as also evident from the separation of obligate bipeds from the other groups in the boxplot in Figure 2. The indices OP-PR, OP-GL and FMA contribute the most to the PC1 variations. Nonetheless, the influence of other indices is not negligible. Along the PC1, the genus *Homo* is also separated from the australopithecines, which lie close to knuckle-walkers, a trend already visible when comparing their boxplots for some of the indices in Figure 2.

When looking at posture, the PCA exhibits a wide overlap between orthograde and pronograde species. Such overlap already exists in the variability of FMP and FMO indices before phylogenetic correction (boxplot in Figure 2). Clinograde species are separated from pronograde taxa but not from orthograde ones both in the multivariate dataset (PCA in Figure 3) and for most indices (boxplot in Figure 2). Antipronograde species are isolated from the other groups along the PC1 (Figure 3) and when looking at the boxplots (Figure 2), lying outside of the variability of the other postural groups. In the PCA, hominins, and particularly the genus *Homo*, occupy an extreme position in the orthograde variability.

#Figure 3

Pairwise comparisons

The multivariate pairwise comparisons revealed that knuckle-walkers and bipeds are significantly different from quadrupeds and vertical clingers (Table 3) as also shown by the absence of overlap in the PCA (Figure 3). Obligate and facultative bipeds also differ from each other (d: 11.21, p: 0.035) but not from knuckle-walkers. When pairwise comparisons are performed using OP-PR, we only observe significant differences between obligate bipeds and terrestrial quadrupeds (d: 1.02, p: 0.022) and no significance at all is achieved with OP-GL. Bipeds are not different from other groups when testing BA-BC and BA-SF, while interesting trends occur for BA-BP and FMA. Indeed, the BA-BP index discriminates facultative bipeds from all groups, including knuckle-walkers (d: 5.04, p: 0.019) and obligate bipeds (d: 6.44, p: 0.002). Obligate bipeds are instead different from all other groups when FMA is considered. Overall FMP and FMO indices do not show consistent levels of discrimination between locomotor groups in primates.

The pairwise multivariate comparisons of postural groups show significant differences solely between pronograde and orthograde species (d: 6.19, p: 0.002), a difference that is found also for OP-PR (d: 1.74, $p<0.001$), OP-GL (d: 1.33, p: 0.002) and FMA (d: 1.67, $p<0.001$). Antipronograde species, as expected from the peculiar set of FMP and FMO values shown in the boxplots (Figure 2), are consistently different from other postural groups when OP-GL, BA-BP, BA-BC and BA-SF are compared (Table 4). Clinograde species do not show differences from other groups but antipronogrades.

DISCUSSION

For decades, the position of the foramen magnum and its orientation have been considered proxies for locomotion and used to infer locomotor and postural habits in several taxa (Ahern, 2005; Brunet et al., 2002; Dart, 1925; Kimbel et al., 1984, 2014; Russo and Kirk, 2013, 2017; Suwa et al., 2009; Zollikofer et al., 2005). In particular, the bipedal status of early hominins has often been inferred based on a more anteriorly placed foramen magnum when compared to other primates (Ahern, 2005; Brunet et al., 2002; Dart, 1925; Suwa et al., 2009; White et al., 1994; Zollikofer et al., 2005). Recently, the validity of some FMP and FMO indices was tested and contrasting results were obtained, depending on the sample used and methods applied (Neaux et al., 2017; Russo and Kirk, 2013, 2017; Ruth et al., 2016). The contradictory nature of the results arises from the scarcity of fossil hominin postcranial remains (Haeusler and McHenry, 2004), usually better suited than the cranium to address issues related to locomotion.

In this paper, we assess the effectiveness of FMP and FMO indices in discriminating locomotion and posture in non-human primates and hominins. Uniquely, this study takes into account both phylogeny and cranial absolute size when testing the indices. Furthermore, the hominin sample was analysed in the framework of a wide primate perspective, while previous studies have focused on broader samples of mammals (Russo and Kirk, 2017) or specific primate groups, such as Hominoidea (Neaux et al., 2017).

It has to be considered that whenever one of the variables tested in this study fails to discriminate postural or locomotor categories it may reflect that the variable is not a good proxy for FMO and FMP or that the differences in position and orientation of the foramen magnum between different locomotor groups are negligible, making therefore possible to argue that the foramen magnum position and orientation are not strictly linked to locomotion or posture. Although this is difficult to determine when looking at one single index, the application and comparison of several indices, together with their combination in a multivariate approach, maximises the chances of detecting a functional signal or of identifying the factors hindering the use of such indices.

The low phylogenetic signals (Table 2) suggest a low taxonomic value for most indices (except BA-SF), which is a desirable feature for functional proxies (Nunn & Barton, 2001; O'neill & Dobson, 2008). The functional significance of the indices seems clear when they are considered in a multivariate fashion. In fact, in the PCA (Figure 3), the data part accordingly to locomotion, except for arboreal quadrupeds, which overlap with brachiators, terrestrial quadrupeds and vertical clingers likely because of their higher locomotor plasticity (Larson, 2018). Nevertheless, the multivariate pairwise test between groups (Table 3) overturns the situation depicted in the PCA and no significant difference is observed across most locomotor groups. However, knuckle-walkers and bipeds (facultative and obligate) differ significantly from other groups and between each other, suggesting that certain locomotor habits can be discriminated by combining multiple indices. Although this result may appear insightful, it has to be considered carefully. In fact, by combining the indices in the multivariate space, the resulting new axes of variation may boost the importance of those indices that are referenced to cranial regions other than the foramen magnum and the base. This is evident from the loadings of the PCA (Figure 3), where OP-PR and OP-GL contribute highly to the first and second components (74.6 % of total variance). Such indices identify the anteroposterior placement of the foramen magnum in respect of the maxilla and the brow ridge, respectively. Both areas witnessed important changes during the evolution of hominins (Bastir & Rosas, 2016; Godinho et al., 2018; Lacruz et al, 2019), and their variability may be associated to factors other than locomotion, such as encephalization or prognathism. The same consideration holds for posture. Based on these observations, we suggest that the multivariate approach enhances the non-locomotor signal in the analysis and it is, therefore, not applicable for discriminating locomotion and posture across primates in general.

When looking at the univariate pairwise analysis for locomotion, most indices fail to discriminate between one or more pairs of locomotor categories (Table 3) except for the BA-BP index and the foramen magnum angle (FMA). Interestingly, the BA-BP index discriminates the facultative bipeds from all the other locomotor categories, while the FMA show that the obligate bipeds possess significantly different angle values from all the other locomotor groups. The results given by these two indices may rely on their functional significance for head balance. Indeed, BA-BP involves the distance between the foramen magnum and the ear canals, which are functionally and structurally linked to the inner ear and, therefore, the balance system (Lieberman, 2011); the FMA is an indirect proxy of the spatial relationship between the cranium and the vertebral column, whose modifications have been remarkable during the evolution of bipedalism (Lovejoy, 2005; Williams and Russo, 2015). As a result, BA-BP and FMA are likely to represent evolutionary adaptations occurred in response to the integration of the cranial base with the auditory system and the vertebral column, respectively; the other indices, instead, mainly represent the antero-posterior displacement of the foramen magnum and probably exhibit a lower locomotor signal as the result of other trends in the evolution of the cranium.

Overall, our results suggest that most FMP and FMO indices might be unreliable to detect differences in locomotion. This may occur for several reasons. Most FMP and FMO indices have been designed for addressing the morphological variability of hominins and their closest living relatives; therefore, they may not be representative of non-hominoid variability. In addition, some indices are measured using points outside of the cranial base region and may therefore represent variations not related to locomotion but rather linked to other sources of variability. An alternative explanation would be that differences across locomotor categories exist as gradients rather than abrupt changes. This view agrees with the observation of highly varied sets of locomotor skills exhibited by most primate species, which can switch easily between different locomotor styles (Fleagle, 1980; 2013; Gebo, 1987). Also, these gradients would constitute the major reason why it is often difficult to categorise primate locomotor habits unequivocally. Differences are more easily detected when it comes to extreme morphological changes, such as in bipeds.

When looking at the univariate pairwise analysis for posture (Table 3), OP-PR, OP-GL and FMA indices significantly discriminate orthogrades from pronogrades. Antipronograde species are often observed as different from at least one (for the OP-PR index) or more (for the OP-GL, BA-BC, BA-BP and BA-SF indices) postural groups (Table 3). It has to be reminded that OP-PR and OP-GL are referenced on regions outside of the cranial base and are prone of adding non-locomotor variation to the analysis. Therefore, any inference based on those indices should be taken cautiously. The results observed for FMA and posture seem to contradict previous results from Ruth et al. (2016), which suggested that this index is not useful to distinguish between the orthograde and pronograde conditions in mammals. None of the indices tested was associated to significant differences across all postural groups, thus demonstrating that the complex anatomical response to changes in posture cannot be summarized by one single measurement.

Regarding the hypotheses tested in this study, our results show that none of the indices tested is effective in discriminating among all locomotor and postural habits in extant and extinct primates, therefore the first hypothesis (I) is rejected. Furthermore, the multivariate approach results showed that this method should be used cautiously. Indeed, when looking at the PCA and its loadings it appears that indices that take into considerations regions of the skull other than the cranial base could impact on the resulting distribution along the PCA components and therefore may be shadowing the detection of any locomotor signal. Therefore, our second hypothesis (II) is rejected.

Given the results of this work, locomotor adaptations may not be the sole factors responsible for the antero-posterior displacement of the foramen magnum in primates and hominins (Raia et al., 2018). Although the more anterior positioning of the foramen magnum in *Homo* compared to other primates may be linked to reduced locomotor versatility and head balancing due to obligate bipedalism, other factors influencing cranial base morphology cannot be discarded. A possible explanation for the anterior position of the foramen magnum in *Homo* could be found in the structural reorganization of the brain (Gunz et al., 2019; Lieberman et al., 2008; Veneziano et al., 2018), which caused a “spatial packing” problem, possibly solved by the flexion of the basicranium and the anterior displacement of the foramen magnum along the midsagittal plane (Ross & Ravosa, 1993). Ruth and colleagues (Ruth et al., 2016) tested the potential correlation between brain size and foramen magnum position and orientation in Strepsirrhines and found it to be significant.

The findings of this study suggest using caution when inferring bipedalism in early hominins based solely on one of the several indices used in literature for the position of the foramen magnum. Our findings also suggest that locomotion may not be the sole factor influencing the position of the foramen magnum in extant and extinct primates, and hypotheses concerning encephalization should be considered (Melchionna et al. 2020). Further studies inferring about locomotion and posture in fossil hominin species should focus more on the morphology of postcranial bony elements than on the foramen magnum position and orientation.

Acknowledgments

Special thanks to the National Museum of Natural History (NMNH), the Kyoto University Primate Research Institute (KUPRI, Digital Morphology Museum), Morphosource database at Duke University and NESPOS digital archive.

Author contributions

F.L., A.P., and G.M. designed the work; F.L. data curation; F.L., A.P., A.V. methodology and statistical analysis; F.L., A.P., A.V. original draft; F.L., A.P., A.V., I.D.G., G.M. review and editing.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Table 1 Definition of postural and locomotor categories according to literature as used in this study.

Postural/Locomotor category	Definition	Reference
Antipronograde	The posture is not consistently pronograde or orthograde but is subject to changing orientation and frequent bending in more than one plane.	Shapiro & Simons, 2002
Orthograde	A posture in which the spine is habitually vertical.	Shapiro & Simons, 2002
Pronograde	A posture in which the spine is consistently horizontal.	Shapiro & Simons, 2002
Clinograde	A posture in which the forelimbs are elongated and the hindlimbs are shortened and flexed. The trunk is angled and forms a triangle with respect to the lower limbs.	Anquetin & Tassy, 2007
Knuckle walking	Type of quadrupedal locomotion in which the weight of the upper body is borne on the backs of the middle phalanges with specializations of hand and wrist.	Schmitt, 2010
Obligate bipedalism	A type of locomotion that is exclusively bipedal and had lost all other forms of terrestrial and arboreal locomotor variants.	Harcour-Smith, 2007
Facultative bipedalism	Locomotion is not exclusively bipedal and terrestrial but retains some arboreal elements.	Prost, 1980
Vertical clinging	A type of locomotion and posture in which animals cling to vertical supports and move by leaping between these vertical supports.	Fleagle, 2013
Arboreal quadrupedalism	A mode of locomotion in which the animal moves along horizontal branches with a regular gait pattern involving all four limb.	Fleagle, 2013
Terrestrial quadrupedalism	A four-limbed locomotion on the ground.	Fleagle, 2013
Brachiation	Swinging from tree to tree by two arms.	Fleagle, 2013

Table 2 Phylogenetic signal measured as Blomberg's K statistics for the multivariate sample and for each index separately.

	Multivariate	OP-PR [b]	OP-GL	BA-BC	BA-BP	BA-SF	FMA
Blomberg's K	0.20	0.24	0.26	0.10	0.12	0.83	0.17
P-value [a]	**<0.001**	**0.001**	**<0.001**	0.140	0.057	**<0.001**	**0.005**

[a] P-values equal or minor than 0.05 are considered significant and are shown in bold.

[b] OP-PR: opisthocranion-prosthion axis, OP-PR: opisthocranion-glabella axis, BA-BC: basion-bicarotid chord, BA-BP: basion-biporionic chord, BA-SF: basion-sphenoccipital ratio, FMA: foramen magnum angle.

Table 3 Pairwise comparisons for the locomotion groups based on distances between group variances (**d**: upper triangles) and relative P-values (**p**: lower triangles).

Pairwise (p\d): Multivariate

	VC	AQ	TQ	BR	KW	FB	OB
VC[a]	-	0.72	1.63	3.43	10.13	20.91	9.76
AQ	0.851	-	2.34	2.75	9.45	20.32	9.19
TQ	0.642	0.209	-	5.17	11.78	22.63	11.34
BR	0.357	0.270	0.051	-	6.76	17.65	6.35
KW	**0.036**	**0.023**	**0.009**	0.115	-	10.91	0.42
FB	**<0.001**	**<0.001**	**<0.001**	**0.003**	0.073	-	11.21
OB	**0.016**	**0.004**	**<0.001**	0.070	0.937	**0.035**	-

Pairwise (p\d): OP-PR[b]

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.03	0.18	0.29	0.07	0.24	0.84
AQ	0.954	-	0.21	0.26	0.09	0.21	0.81
TQ	0.729	0.446	-	0.47	0.11	0.42	1.02
BR	0.584	0.477	0.231	-	0.36	0.05	0.55
KW	0.916	0.883	0.873	0.574	-	0.31	0.91
FB	0.752	0.811	0.584	0.952	0.666	-	0.61
OB	0.153	0.051	**0.022**	0.295	0.184	0.419	-

Pairwise (p\d): OP-GL

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.12	0.39	0.01	0.52	0.01	0.43
AQ	0.845	-	0.51	0.11	0.64	0.11	0.31
TQ	0.495	0.105	-	0.39	0.13	0.39	0.82
BR	0.992	0.797	0.395	-	0.53	0.01	0.42
KW	0.484	0.293	0.872	0.459	-	0.53	0.95
FB	0.986	0.919	0.654	0.995	0.507	-	0.42
OB	0.502	0.556	0.111	0.471	0.219	0.605	-

Pairwise (p\d): BA-BC

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.78	0.12	0.89	1.15	0.04	1.08
AQ	0.288	-	0.91	0.11	0.37	0.75	0.29
TQ	0.879	**0.047**	-	1.00	1.27	0.16	1.20
BR	0.313	0.872	0.132	-	0.26	0.85	0.19
KW	0.282	0.715	0.152	0.793	-	1.11	0.07
FB	0.968	0.497	0.907	0.426	0.358	-	1.04
OB	0.265	0.686	0.112	0.811	0.937	0.345	-

Pairwise (p\d): BA-BP

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.34	0.58	0.39	1.01	6.05	0.39
AQ	0.748	-	0.25	0.06	1.35	6.39	0.05
TQ	0.554	0.676	-	0.19	1.59	6.64	0.19
BR	0.689	0.945	0.819	-	1.40	6.45	0.00
KW	0.396	0.156	0.138	0.232	-	5.04	1.39
FB	**0.003**	**0.002**	**0.002**	**0.003**	**0.019**	-	6.44
OB	0.704	0.963	0.842	0.997	0.275	**0.002**	-

Pairwise (p\d): BA-SF

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.13	0.61	0.83	0.78	0.92	0.29
AQ	0.829	-	0.49	0.95	0.91	1.04	0.41
TQ	0.317	0.156	-	1.44	1.39	1.53	0.90
BR	0.228	**0.037**	**0.005**	-	0.05	0.09	0.54
KW	0.369	0.185	0.062	0.956	-	0.14	0.49
FB	0.351	0.167	0.071	0.930	0.888	-	0.63
OB	0.703	0.455	0.113	0.416	0.560	0.509	-

Pairwise (p\d): FMA

	VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.36	0.99	0.55	1.01	0.49	3.57
AQ	0.759	-	0.63	0.19	0.65	0.14	3.93
TQ	0.255	0.215	-	0.44	0.01	0.50	4.56
BR	0.569	0.793	0.557	-	0.46	0.06	4.12
KW	0.410	0.581	0.993	0.665	-	0.51	4.58
FB	0.606	0.937	0.691	0.958	0.556	-	4.06
OB	**0.002**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.012**	-

[a] VC: vertical clingers, AQ: arboreal quadrupeds, TQ: terrestrial quadrupeds, BR: brachiators, KW: knucle-walkers, FB: facultative bipeds, OB: obligate bipeds.

[b] OP-PR: opisthocranion-prosthion axis, OP-PR: opisthocranion-glabella axis, BA-BC: basion-bicarotid chord, BA-BP: basion-biporionic chord, BA-SF: basion-sphenoccipital ratio, FMA: foramen magnum angle.

Table 4 Pairwise comparisons for the Posture groups based on distances between group variances (**d**: upper triangles) and relative P-values (**p**: lower triangles).

Pairwise (p\d): Multivariate

	ANTI	CLIN	PRON	ORTH
ANTI [a]	-	5.20	1.71	7.91
CLIN	0.337	-	3.49	2.71
PRON	0.711	0.382	-	6.19
ORTH	0.101	0.536	**0.002**	-

Pairwise (p\d): OP-PR [b]

	ANTI	CLIN	PRON	ORTH
ANTI	-	3.48	3.07	1.32
CLIN	0.057	-	0.41	2.15
PRON	**0.038**	0.715	-	1.74
ORTH	0.176	0.059	**<0.001**	-

Pairwise (p\d): OP-GL

	ANTI	CLIN	PRON	ORTH
ANTI	-	3.89	3.83	2.50
CLIN	**0.013**	-	0.06	1.39
PRON	**0.004**	0.955	-	1.33
ORTH	**0.035**	0.132	**0.002**	-

Pairwise (p\d): BA-BC

	ANTI	CLIN	PRON	ORTH
ANTI	-	2.37	3.46	3.01
CLIN	0.105	-	1.09	0.64
PRON	**0.008**	0.141	-	0.46
ORTH	**0.018**	0.479	0.294	-

Pairwise (p\d): BA-BP

	ANTI	CLIN	PRON	ORTH
ANTI	-	11.74	13.25	12.37
CLIN	**<0.001**	-	1.51	0.63
PRON	**<0.001**	0.126	-	0.88
ORTH	**<0.001**	0.642	0.229	-

Pairwise (p\d): BA-SF

	ANTI	CLIN	PRON	ORTH
ANTI	-	11.22	11.70	10.99
CLIN	**<0.001**	-	0.47	0.23
PRON	**<0.001**	0.712	-	0.70
ORTH	**<0.001**	0.861	0.339	-

Pairwise (p\d): FMA

	ANTI	CLIN	PRON	ORTH
ANTI	-	1.12	1.19	0.47
CLIN	0.359	-	0.07	1.59
PRON	0.153	0.951	-	1.67
ORTH	0.653	0.101	**<0.001**	-

[a] ANTI: antipronograde, CLIN: clinograde, PRON: pronograde, ORTH: orthograde.

[b] OP-PR: opisthocranion-prosthion axis, OP-PR: opisthocranion-glabella axis, BA-BC: basion-bicarotid chord, BA-BP: basion-biporionic chord, BA-SF: basion-sphenoccipital ratio, FMA: foramen magnum angle.

Figures and captions

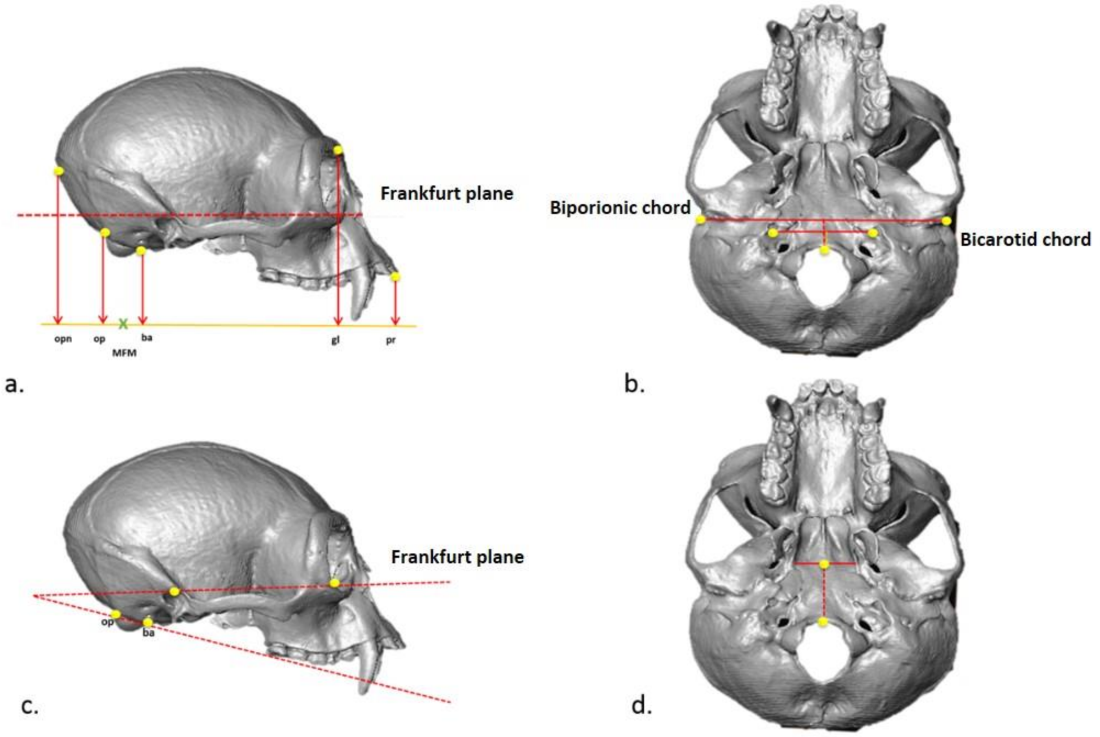

Figure 1. Methods applied for recording foramen magnum position and orientation. **a**. OP-GL (opisthocranion-glabella) and OP-PR (opisthocranion-prosthion) indices: projection of five anatomical points (opisthocranion, opisthion, basion, glabella, prosthion) on the Frankfurt plane. Basion and opisthion were used to calculate the midpoint position of the foramen magnum (midpoint foramen magnum or MFM, green cross). MFM was then used to calculate a ratio for the foramen magnum position along the anterior-posterior axis by dividing the distance from MFM to opisthocranion by the distance from opisthocranion to glabella. **b**. BA-BP (basion-biporion) index: basion-biporion chord used to estimate the FMP; BA-BC (basion-bicarotid) index: basion-bicarotid chord used to estimate the FMP. **c.** FMA (foramen magnum angle): angle between a chord connecting basion and opisthion landmarks, and the Frankfurt horizontal plane. **d.** BA-SF ratio (basion-sphenoccipital): distance from basion to sphenobasion landmarks (along the the sphenoccipital synchrondrosis), divided by cranial size.

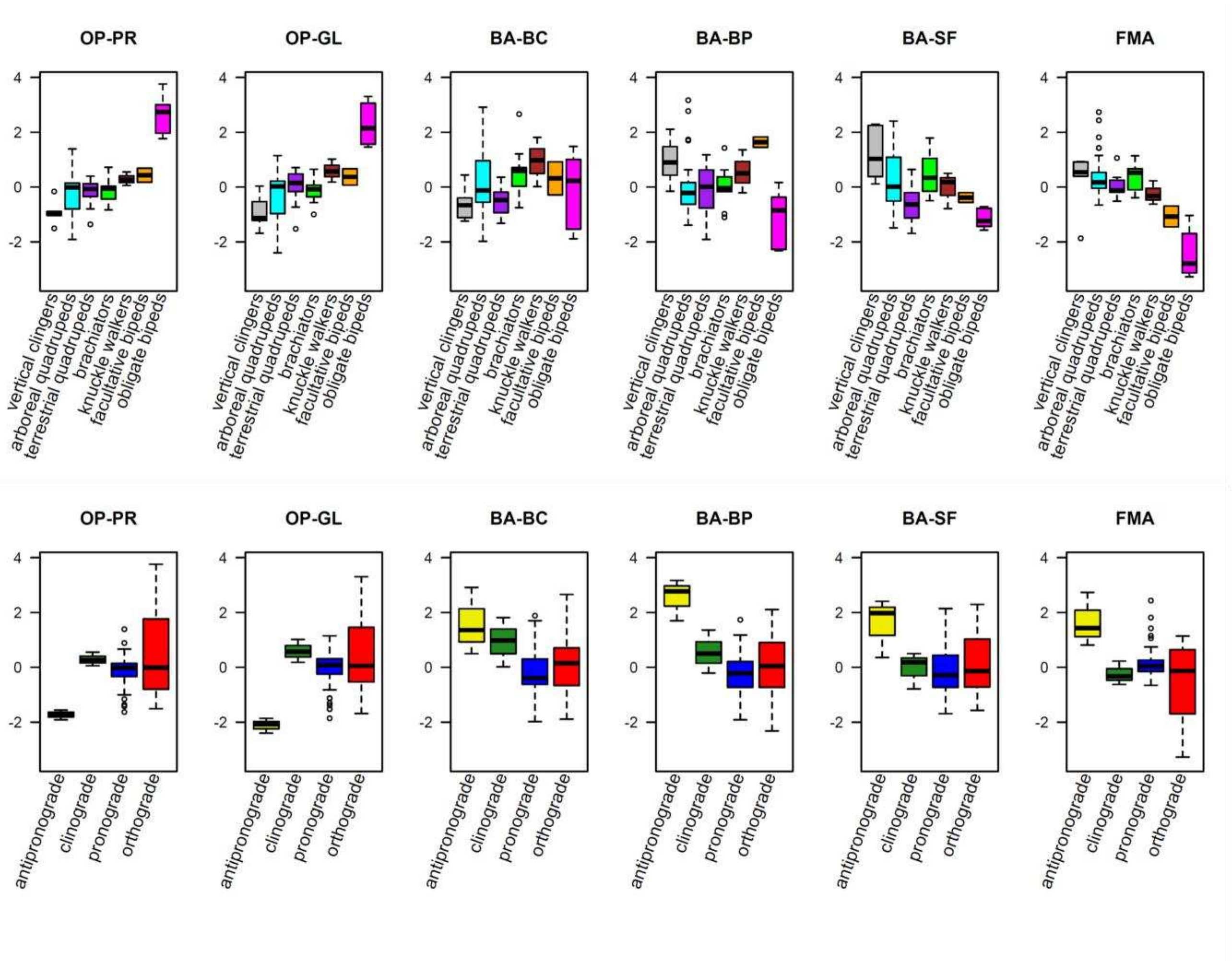

Figure 2. Boxplots showing the variability of foramen magnum indices across locomotor and postural categories (no phylogenetic correction applied). Bottom and top of the boxes are the first and third quartiles, the horizontal black lines represent the median, the whiskers represent the minimum and maximum values, the dots are outliers. (**OP-PR**: opisthocranion-prosthion axis, **OP-PR**: opisthocranion-glabella axis, **BA-BC**: basion-bicarotid chord, **BA-BP**: basion-biporionic chord, **BA-SF**: basion-sphenoccipital ratio, **FMA**: foramen magnum angle).

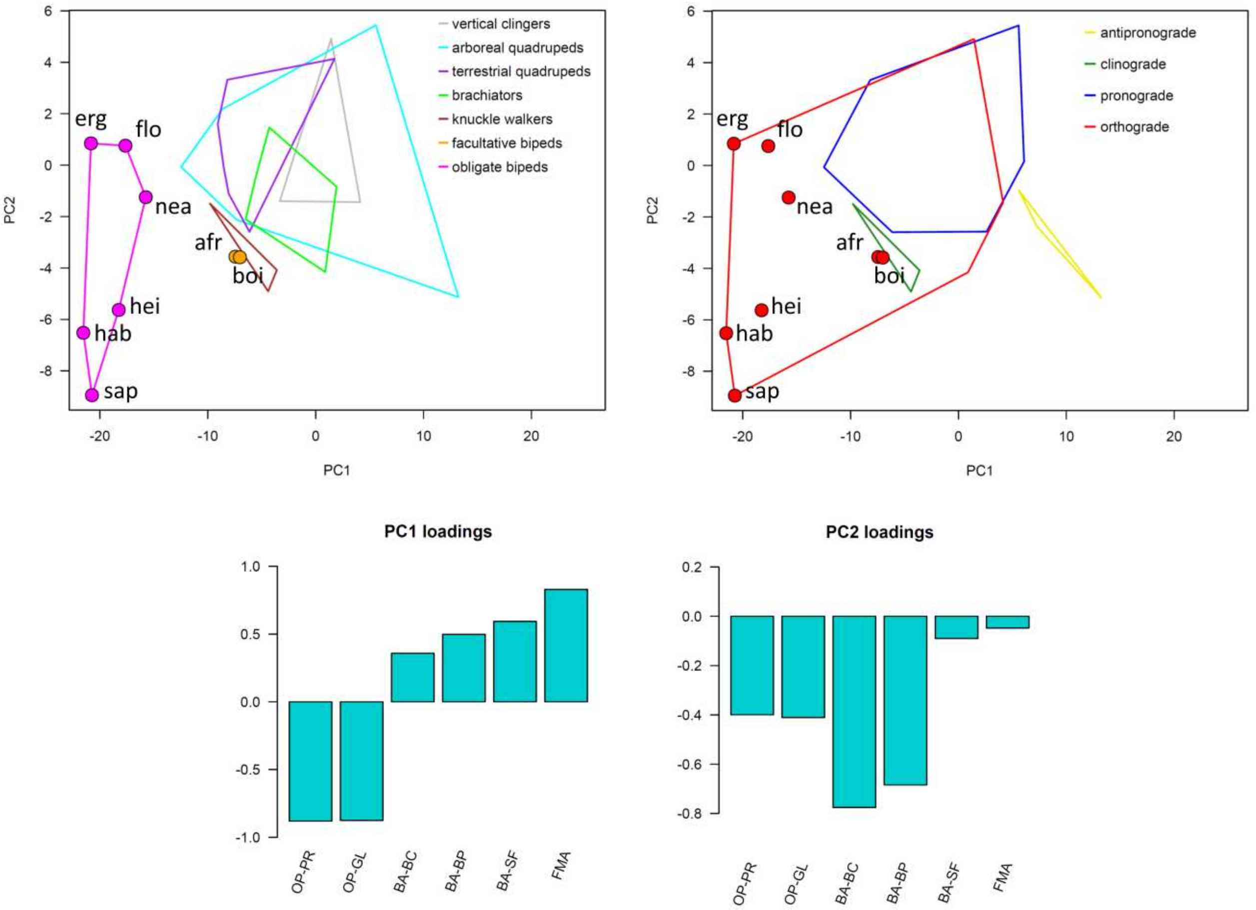

Figure 3. Phylogenetic Principal Component Analysis including all the indices tested in the work. The data is grouped by locomotion (top left) and posture (top right). The loadings (bottom) for the first (PC1) and second (PC2) components report the relative contributions. Phylogenetic correction is performed. (**OP-PR**: opisthocranion-prosthion axis, **OP-PR**: opisthocranion-glabella axis, **BA-BC**: basion-bicarotid chord, **BA-BP**: basion-biporionic chord, **BA-SF**: basion-sphenoccipital ratio, **FMA**: foramen magnum angle; **afr**: *Australopithecus africanus*, **erg**: *Homo ergaster*, **flo**: *Homo floresiensis*, **hab**: *Homo habilis*, **hei**: *Homo heidelbergensis*, **nea**: *Homo neanderthalensis*, **boi**: *Paranthropus boisei*, **sap**: *Homo sapiens*).