

1 **Title:**

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

4
5 **Short title:**

6 Foramen magnum, locomotion and posture

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30 **ABSTRACT**

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

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

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53 INTRODUCTION

54 Primates exhibit high variability in their locomotion. Different locomotor patterns have influenced primate
55 morphological evolution and factors such as limb proportions, pelvis and long bone morphology are often
56 used to make inference about locomotion (Demes and Jungers, 1993; Profico et al., 2017; Sarringhaus et al.,
57 2016). Nevertheless, other skeletal structures such as the cranial base may have undergone important
58 locomotor adaptations, likely because of its articulation with the axial skeleton (Kimbel and Rak, 2010;
59 Lieberman et al., 2000). The foramen magnum, one of the key regions of the cranial base, allows the passage
60 of the major circulatory and neural connections between the skull and the postcranial skeleton. Also, the
61 foramen magnum is physically connected to the vertebral column, whose morphology has a remarkable
62 influence on the locomotion of a species (Kimbel and Rak, 2010; Kimbel et al., 2014; Lieberman et al., 2000;
63 Jones et al., 2018). Because of its role in linking the head with the axial skeleton, and its alleged role in
64 balancing the head atop the vertebral column in humans (Lieberman, 2011), the morphology, position and
65 orientation of foramen magnum have been linked to postural and locomotor differences in fossil hominins
66 (Ahern, 2005; Brunet et al., 2002; Neaux et al., 2017; Russo and Kirk, 2013) and primates (Luboga & Wood,
67 1990; Simons, 1967).

68 Several methods have been used to describe and estimate foramen magnum position (FMP) and orientation
69 (FMO) on the cranial base (Brunet et al., 2002; Dean and Wood, 1981; Kimbel et al., 1984; Luboga and
70 Wood, 1990; Neaux et al., 2017; Russo and Kirk, 2013, 2017; Ruth et al., 2016; Simons, 1967; White et al.,
71 1994). The early work of Topinard (1878) stressed the importance of a comparative approach to study the
72 forward migration of the foramen magnum in modern humans compared to fossil hominins. In 1925, Dart
73 assumed the bipedal posture of the Taung child (*Australopithecus africanus*) based on the "head balancing
74 index", a measure of FMP relating the basion (the anterior border of the foramen magnum) with the
75 prosthion-inion line (the line between the most anterior point on the maxilla and the occipital protuberance)
76 (Dart, 1925). Dean and Wood (1981) and Luboga and Wood (1990) used a series of indices to describe
77 differences in FMP and cranial base shape between *Homo* and the great apes, and between robust and
78 gracile australopithecines. Other authors relied on the use of similar indices to describe cranial base affinities
79 between the australopithecines and *Homo* (Kimbel et al., 1984). More recently, a series of linear indices
80 based on FMP has been used to infer bipedalism, thus the hominin status, of fossil taxa such as
81 *Sahelanthropus* (Brunet et al., 2002; Zollikofer et al., 2005) and *Ardipithecus* (Suwa et al., 2009; White et al.,
82 1994). Also, some authors have focused on the use of foramen magnum indices for discriminating posture in
83 mammals and fossil hominins (Neaux et al., 2017; Russo & Kirk, 2013, 2017).

84 Although foramen magnum indices have been widely adopted in locomotion and postural studies, their
85 interpretation is still debated due to contrasting results (Ahern, 2005; Neaux et al., 2017; Russo and Kirk,
86 2013, 2017; Ruth et al., 2016). Some limitations may be the reason for such controversies. For example,
87 some indices are based on cranial regions other than the cranial base and may reflect variations not related

88 to the basicranial morphology (Neaux et al., 2017; Ruth et al., 2016). Therefore, these indices may only
89 partially account for locomotion and posture and instead include information on other aspects of cranial
90 morphology such as mandibular and cranial vault shape modifications due to changes in diet, mastication
91 and encephalization across primates and the hominin lineage (Bastir & Rosas, 2009; Raia et al., 2018).
92 Indeed, the morphology of the cranial base and the orientation and position of the foramen magnum have
93 been observed to be affected by the growth and development of the neurocranium and facial complex as
94 well as the orientation of the latter (Anton, 1989; Cheverud & Midkiff, 1992; Cheverud et al., 1992; Bastir &
95 Rosas, 2006; Lieberman et al., 2008; Gkantidis & Halazonetis, 2011).

96 In addition, conclusions are often drawn based on untested indices, whose relation to posture and
97 locomotion is therefore not supported by statistical evidence (Russo and Kirk, 2017). Testing should be
98 performed by taking into account extant species and possible sources of error, such as size and phylogenetic
99 relatedness among taxa. A broad comparative sample of extant and extinct species is essential to make
100 assumptions on the status of fossil hominins. Partially because of these limitations and the conflicting results,
101 the functional interpretation of the position and orientation of the foramen magnum as locomotor
102 adaptations have been doubted (White et al., 2015). A comprehensive assessment of FMP and FMO indices
103 is necessary to make order in the controversial results left behind by more than a century of studies. Such
104 assessment is even more important as the debate around posture, locomotion and the foramen magnum is
105 still ongoing, in particular for hominins. Bipedalism in fossil species is considered diagnostic of the hominin
106 status. The passage from facultative to obligate bipedalism is believed to mark an important transition to a
107 more modern lifestyle and skeletal anatomy. Nevertheless, unravelling the meaning of the skeletal variation
108 within hominins has proven difficult, also due to the fragmentary nature of the fossil record. There is still
109 disagreement about the significance of the anatomical changes occurred at the transition between
110 australopithecines and *Homo*, and the locomotor behaviour of the early hominins, particularly *Homo habilis*,
111 is still poorly understood and highly debated (Harcourt-Smith & Aiello, 2004; Ruff, 2009; Harcourt-Smith,
112 2015). A better understanding of FMP and FMO indices would help timing the evolutionary shift that led to
113 hominins exhibiting a modern locomotor style.

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

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

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

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

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126

127 METHODS

128 Ethical statement

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

135

136 Sample

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

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

154 Foramen magnum indices

155 For each specimen, we recorded the position of nine homologous anatomical points (landmarks) using Avizo
156 9.0 software (FEI Visualization): opisthocranium, opisthion, basion, spheno-basion, glabella, prosthion, left
157 zygo-orbitale, porions and carotid foramina. We applied Generalized Procrustes Analysis (GPA) to
158 superimpose the landmark configurations on the mean shape in three steps: translation, scaling, and
159 rotation. The resulting landmark configurations -after the GPA- are used to compute the linear
160 measurements necessary for the calculation of the six indices used in this study (see Supplementary S.Table
161 3 for further information about the landmarks). The indices are calculated after full Procrustes
162 superimposition of the landmark configurations, thus discarding the effect of the differences in cranial
163 absolute size.

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

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

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

186 The basion-sphenoccipital ratio (BA-SF) or “Basioccipital ratio” (Dean and Wood, 1981; Russo and Kirk, 2013,
187 2017; Ruth et al., 2016) is calculated as the distance between the sphenoccipital synchondrosis at the
188 midline (i.e., spheno-basion) and the basion.

189

190 #Figure 1

191

192 **Locomotor and postural categories**

193 The categories used in this study describe postural and locomotor behaviours. There is a recent tendency
194 toward the use of postural categories in locomotion studies (Russo and Kirk, 2013, 2017; Ruth et al., 2016).
195 However, we believe that considering only the postural classification may underestimate the locomotor
196 variability of primates. Therefore, the locomotor categories we used are as follows: vertical clingers, arboreal
197 quadrupeds, terrestrial quadrupeds, brachiators, knuckle walkers, facultative bipedals, and obligate bipedals.
198 Vertical clinging is a type of arboreal locomotion prevalently adopted by some prosimians and performed by
199 clinging to vertical supports and leaping between supports (Fleagle, 2013). Anatomically specialised vertical
200 clingers bear adaptations in the pelvic girdle and the lower part of the body, such as a lower forelimb to
201 hindlimb ratios (intermembral index) (Granatosky, 2018): the longer hindlimbs bear the weight during
202 clinging and are necessary to propel leaping between vertical substrates. Other morphological adaptations
203 are shared among vertical clingers, such as the hindlimb bone cross-sectional geometry, which is more
204 robust than in the forelimbs (Demes et al., 1991). In the pelvis, the ilium tends to be relatively wider than in
205 quadrupedal strepsirrhines, although this feature has positive allometry with body size and holds for large
206 species only (Lewton, 2015). In arboreal and terrestrial quadrupedalism, all four limbs are used with a regular
207 gait walking (Fleagle, 2013). Quadrupedal species tend to have hindlimbs and forelimbs of similar length
208 (Fleagle, 2013), reflecting their equal importance for locomotion. Differently from clinging and leaping
209 primates, the femoral head of quadrupedal species is deeply enclosed in the pelvic socket, which reduces the
210 range of movements allowed to the articulation (Ankel-Simons, 2010). Despite the similarities in limb
211 proportions, the functional demands of terrestrial and arboreal quadrupedalism are different. In fact,
212 prevalently arboreal species exhibit limbs that are relatively shorter than those of terrestrial quadrupeds,
213 which helps maintaining the centre of mass closer to the branch (Rose, 1973). Brachiation relies on
214 specialised forelimbs for moving between branches, usually producing a pendulum-like swinging alternating
215 each arm as a fulcrum (Fleagle, 2013). Forelimbs are considerably longer than hindlimbs (Fleagle, 2013) and
216 the humerus is straighter than in other primates, probably to resist torsion during brachiation (Swartz, 1990).
217 The elongated and narrow scapulae together with the small and shallow glenoid fossa of ovate or spherical
218 shape allow higher mobility to the forelimbs (Jenkins, 1974). Knuckle walking is a form of terrestrial,
219 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 but adopt 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.

253

254 Analytical approaches

255 The FMP and FMO indices are tested for their power in discriminating locomotor and postural habits in
256 primates and fossil hominins considering the null hypothesis of independence between indices and
257 categories. Two different approaches are used: univariate and multivariate. In the multivariate approach, the
258 indices are combined in a single data matrix and their relative contributions are analysed. The multivariate
259 analysis allows increasing the information to be tested by reducing its redundancy, as each variable
260 contributes to the final result only partially. Unfortunately, fossil specimens are rarely blessed with
261 completeness and it is unlikely that several indices are measurable on the same fragmentary specimen. It is,
262 therefore, useful to address the issue of which single index could provide the best information and we also
263 perform a univariate analysis for assessing the efficacy of each index in discriminating locomotion and
264 posture. To account for phylogeny, we use the primate phylogenetic tree available in the “10ktrees”
265 database (Arnold et al., 2010). For the hominin phylogeny, we use the topology published by Dembo et al.
266 (2015), based on a Bayesian statistical approach applied on a matrix of morphological traits of hominins
267 (Berger et al., 2015; Young et al., 2015). Palaeontological data of First and Last Appearance Datum (FAD and
268 LAD) of fossil hominins is used to reconstruct plausible times of divergence between taxa. Potts (2013)
269 provides a list of FAD and LAD data from several literature sources. Branch lengths are scaled to fit the time
270 of divergence between *P. troglodytes* and *H. sapiens* in the non-hominin phylogenetic tree, by using the R
271 package “ape” (Paradis et al., 2004). The phylogenetic tree is shown in Supplementary S.Figure 1.

273 Statistical analysis

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

286 We then use pairwise comparisons between groups to test which groups differ with respects to which
287 indices. The tests are performed on the multivariate sample (all indices) and each index separately. The

288 differences between groups are measured as distances between group variances, calculated as the sum of
289 the diagonal elements of the group covariance matrix divided by the number of observations in the group
290 (Zelditch et al., 2012). The pairwise comparisons take into account the phylogenetic relatedness among taxa
291 by assuming Brownian Motion model of trait evolution. Significance is two-tailed and is assessed using a
292 residual randomization procedure (Collyer et al., 2015). A P value equal to or less than 0.05 was considered
293 to be statistically significant. Phylogenetic signal and pairwise comparisons are performed using the R
294 package “geomorph” (Adams and Otárola-Castillo, 2013).

295

296

297 RESULTS

298 Phylogenetic signal and Principal Component Analysis

299 The variability of the FMP and FMO across locomotor and postural groups is reported in the boxplot in Figure
300 2, where the data is not corrected phylogenetically. The indices produce overlapping results for most of the
301 locomotor and postural categories, except for the obligate bipeds, which show a quite distinctive locomotion
302 when applying the OP-PR, OP-GL and FMA indices.

303

304 #Figure 2

305

306 Table 2 shows that the Blomberg’s K is significant and consistently low for most indices, except for the BA-SF
307 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
308 absent phylogenetic patterning on these indices. When all the indices are considered in a multivariate
309 dataset, Blomberg’s K is low but significant (K: 0.20, $p < 0.001$). Overall the results justify the use of a
310 phylogenetic approach for the Principal Component Analysis (PCA). Because of the low phylogenetic signal,
311 standard and phylogenetic PCAs performed similarly and here only the latter is discussed. Locomotor and
312 postural Phylogenetic PCAs are shown in Figure 3, which shows scatterplots of scores and bar plots of
313 loadings for the first and second principal components (the non-phylogenetic PCA is shown in supplementary
314 S. Figure 2). For what concerns locomotion (PCA top left), results show a high variance in FMP and FMO
315 indices for the arboreal quadruped group, which overlap to most other locomotor categories. Overlap is
316 minimal or absent across terrestrial quadrupeds, brachiators, knuckle-walkers and vertical clingers. The
317 genus *Homo* (obligate bipeds) is isolated from the other groups along the PC1 (% variance: 57.8) and partially
318 along the PC2 (% variance: 16.8), as also evident from the separation of obligate bipeds from the other
319 groups in the boxplot in Figure 2. The indices OP-PR, OP-GL and FMA contribute the most to the PC1

320 variations. Nonetheless, the influence of other indices is not negligible. Along the PC1, the genus *Homo* is
321 also separated from the australopithecines, which lie close to knuckle-walkers, a trend already visible when
322 comparing their boxplots for some of the indices in Figure 2.

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

330

331 #Figure 3

332

333 **Pairwise comparisons**

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

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

350

351

352 DISCUSSION

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

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

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

376 The low phylogenetic signals (Table 2) suggest a low taxonomic value for most indices (except BA-SF), which
377 is a desirable feature for functional proxies (Nunn & Barton, 2001; O'Neill & Dobson, 2008). The functional
378 significance of the indices seems clear when they are considered in a multivariate fashion. In fact, in the PCA
379 (Figure 3), the data part accordingly to locomotion, except for arboreal quadrupeds, which overlap with
380 brachiators, terrestrial quadrupeds and vertical clingers likely because of their higher locomotor plasticity
381 (Larson, 2018). Nevertheless, the multivariate pairwise test between groups (Table 3) overturns the situation
382 depicted in the PCA and no significant difference is observed across most locomotor groups. However,
383 knuckle-walkers and bipeds (facultative and obligate) differ significantly from other groups and between
384 each other, suggesting that certain locomotor habits can be discriminated by combining multiple indices.
385 Although this result may appear insightful, it has to be considered carefully. In fact, by combining the indices

386 in the multivariate space, the resulting new axes of variation may boost the importance of those indices that
387 are referenced to cranial regions other than the foramen magnum and the base. This is evident from the
388 loadings of the PCA (Figure 3), where OP-PR and OP-GL contribute highly to the first and second components
389 (74.6 % of total variance). Such indices identify the anteroposterior placement of the foramen magnum in
390 respect of the maxilla and the brow ridge, respectively. Both areas witnessed important changes during the
391 evolution of hominins (Bastir & Rosas, 2016; Godinho et al., 2018; Lacruz et al, 2019), and their variability
392 may be associated to factors other than locomotion, such as encephalization or prognathism. The same
393 consideration holds for posture. Based on these observations, we suggest that the multivariate approach
394 enhances the non-locomotor signal in the analysis and it is, therefore, not applicable for discriminating
395 locomotion and posture across primates in general.

396 When looking at the univariate pairwise analysis for locomotion, most indices fail to discriminate between
397 one or more pairs of locomotor categories (Table 3) except for the BA-BP index and the foramen magnum
398 angle (FMA). Interestingly, the BA-BP index discriminates the facultative bipeds from all the other locomotor
399 categories, while the FMA show that the obligate bipeds possess significantly different angle values from all
400 the other locomotor groups. The results given by these two indices may rely on their functional significance
401 for head balance. Indeed, BA-BP involves the distance between the foramen magnum and the ear canals,
402 which are functionally and structurally linked to the inner ear and, therefore, the balance system
403 (Lieberman, 2011); the FMA is an indirect proxy of the spatial relationship between the cranium and the
404 vertebral column, whose modifications have been remarkable during the evolution of bipedalism (Lovejoy,
405 2005; Williams and Russo, 2015). As a result, BA-BP and FMA are likely to represent evolutionary adaptations
406 occurred in response to the integration of the cranial base with the auditory system and the vertebral
407 column, respectively; the other indices, instead, mainly represent the antero-posterior displacement of the
408 foramen magnum and probably exhibit a lower locomotor signal as the result of other trends in the
409 evolution of the cranium.

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

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

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

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

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

454 more on the morphology of postcranial bony elements than on the foramen magnum position and
455 orientation.

456

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461

462 **Author contributions**

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

465

466 **Data availability**

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

469

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659 **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

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664 **Table 2** Phylogenetic signal measured as Blomberg’s K statistics for the multivariate sample and for each
665 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

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

667 ^b OP-PR: opisthocranium-prosthion axis, OP-GL: opisthocranium-glabella axis, BA-BC: basion-bicarotid chord, BA-BP: basion-biporionic
668 chord, BA-SF: basion-sphenoccipital ratio, FMA: foramen magnum angle.

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

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Pairwise (p\d): Multivariate								Pairwise (p\d): OP-PR ^b							
	VC	AQ	TQ	BR	KW	FB	OB		VC	AQ	TQ	BR	KW	FB	OB
VC ^a	-	0.72	1.63	3.43	10.13	20.91	9.76	VC	-	0.03	0.18	0.29	0.07	0.24	0.84
AQ	0.851	-	2.34	2.75	9.45	20.32	9.19	AQ	0.954	-	0.21	0.26	0.09	0.21	0.81
TQ	0.642	0.209	-	5.17	11.78	22.63	11.34	TQ	0.729	0.446	-	0.47	0.11	0.42	1.02
BR	0.357	0.270	0.051	-	6.76	17.65	6.35	BR	0.584	0.477	0.231	-	0.36	0.05	0.55
KW	0.036	0.023	0.009	0.115	-	10.91	0.42	KW	0.916	0.883	0.873	0.574	-	0.31	0.91
FB	<0.001	<0.001	<0.001	0.003	0.073	-	11.21	FB	0.752	0.811	0.584	0.952	0.666	-	0.61
OB	0.016	0.004	<0.001	0.070	0.937	0.035	-	OB	0.153	0.051	0.022	0.295	0.184	0.419	-
Pairwise (p\d): OP-GL								Pairwise (p\d): BA-BC							
	VC	AQ	TQ	BR	KW	FB	OB		VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.12	0.39	0.01	0.52	0.01	0.43	VC	-	0.78	0.12	0.89	1.15	0.04	1.08
AQ	0.845	-	0.51	0.11	0.64	0.11	0.31	AQ	0.288	-	0.91	0.11	0.37	0.75	0.29
TQ	0.495	0.105	-	0.39	0.13	0.39	0.82	TQ	0.879	0.047	-	1.00	1.27	0.16	1.20
BR	0.992	0.797	0.395	-	0.53	0.01	0.42	BR	0.313	0.872	0.132	-	0.26	0.85	0.19
KW	0.484	0.293	0.872	0.459	-	0.53	0.95	KW	0.282	0.715	0.152	0.793	-	1.11	0.07
FB	0.986	0.919	0.654	0.995	0.507	-	0.42	FB	0.968	0.497	0.907	0.426	0.358	-	1.04
OB	0.502	0.556	0.111	0.471	0.219	0.605	-	OB	0.265	0.686	0.112	0.811	0.937	0.345	-
Pairwise (p\d): BA-BP								Pairwise (p\d): BA-SF							
	VC	AQ	TQ	BR	KW	FB	OB		VC	AQ	TQ	BR	KW	FB	OB
VC	-	0.34	0.58	0.39	1.01	6.05	0.39	VC	-	0.13	0.61	0.83	0.78	0.92	0.29
AQ	0.748	-	0.25	0.06	1.35	6.39	0.05	AQ	0.829	-	0.49	0.95	0.91	1.04	0.41
TQ	0.554	0.676	-	0.19	1.59	6.64	0.19	TQ	0.317	0.156	-	1.44	1.39	1.53	0.90
BR	0.689	0.945	0.819	-	1.40	6.45	0.00	BR	0.228	0.037	0.005	-	0.05	0.09	0.54
KW	0.396	0.156	0.138	0.232	-	5.04	1.39	KW	0.369	0.185	0.062	0.956	-	0.14	0.49
FB	0.003	0.002	0.002	0.003	0.019	-	6.44	FB	0.351	0.167	0.071	0.930	0.888	-	0.63
OB	0.704	0.963	0.842	0.997	0.275	0.002	-	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	-								

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

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

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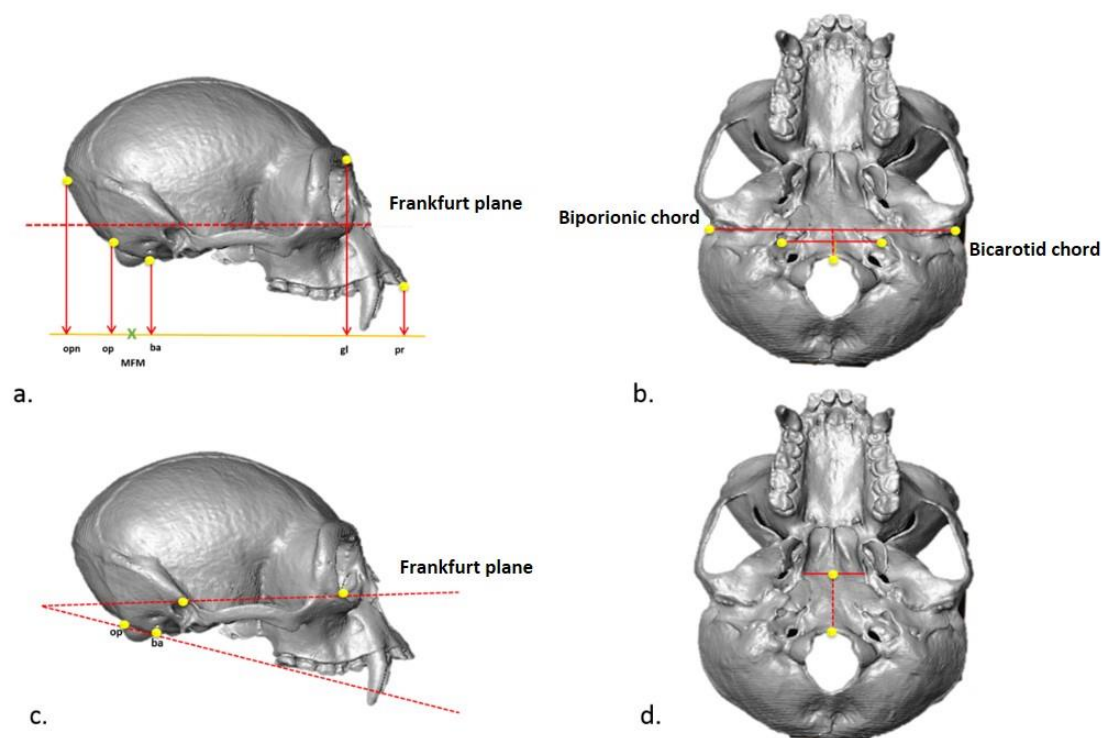
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Table 4 Pairwise comparisons for the Posture groups based on distances between group variances (d: upper triangles) and relative P-values (p: lower triangles).

Pairwise (p\d): Multivariate					Pairwise (p\d): OP-PR ^b				
	ANTI	CLIN	PRON	ORTH		ANTI	CLIN	PRON	ORTH
ANTI ^a	-	5.20	1.71	7.91		ANTI	-	3.48	1.32
CLIN	0.337	-	3.49	2.71		CLIN	0.057	-	2.15
PRON	0.711	0.382	-	6.19		PRON	0.038	0.715	-
ORTH	0.101	0.536	0.002	-		ORTH	0.176	0.059	<0.001
Pairwise (p\d): OP-GL					Pairwise (p\d): BA-BC				
	ANTI	CLIN	PRON	ORTH		ANTI	CLIN	PRON	ORTH
ANTI	-	3.89	3.83	2.50		ANTI	-	2.37	3.01
CLIN	0.013	-	0.06	1.39		CLIN	0.105	-	1.09
PRON	0.004	0.955	-	1.33		PRON	0.008	0.141	-
ORTH	0.035	0.132	0.002	-		ORTH	0.018	0.479	0.294
Pairwise (p\d): BA-BP					Pairwise (p\d): BA-SF				
	ANTI	CLIN	PRON	ORTH		ANTI	CLIN	PRON	ORTH
ANTI	-	11.74	13.25	12.37		ANTI	-	11.22	11.70
CLIN	<0.001	-	1.51	0.63		CLIN	<0.001	-	0.47
PRON	<0.001	0.126	-	0.88		PRON	<0.001	0.712	-
ORTH	<0.001	0.642	0.229	-		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.



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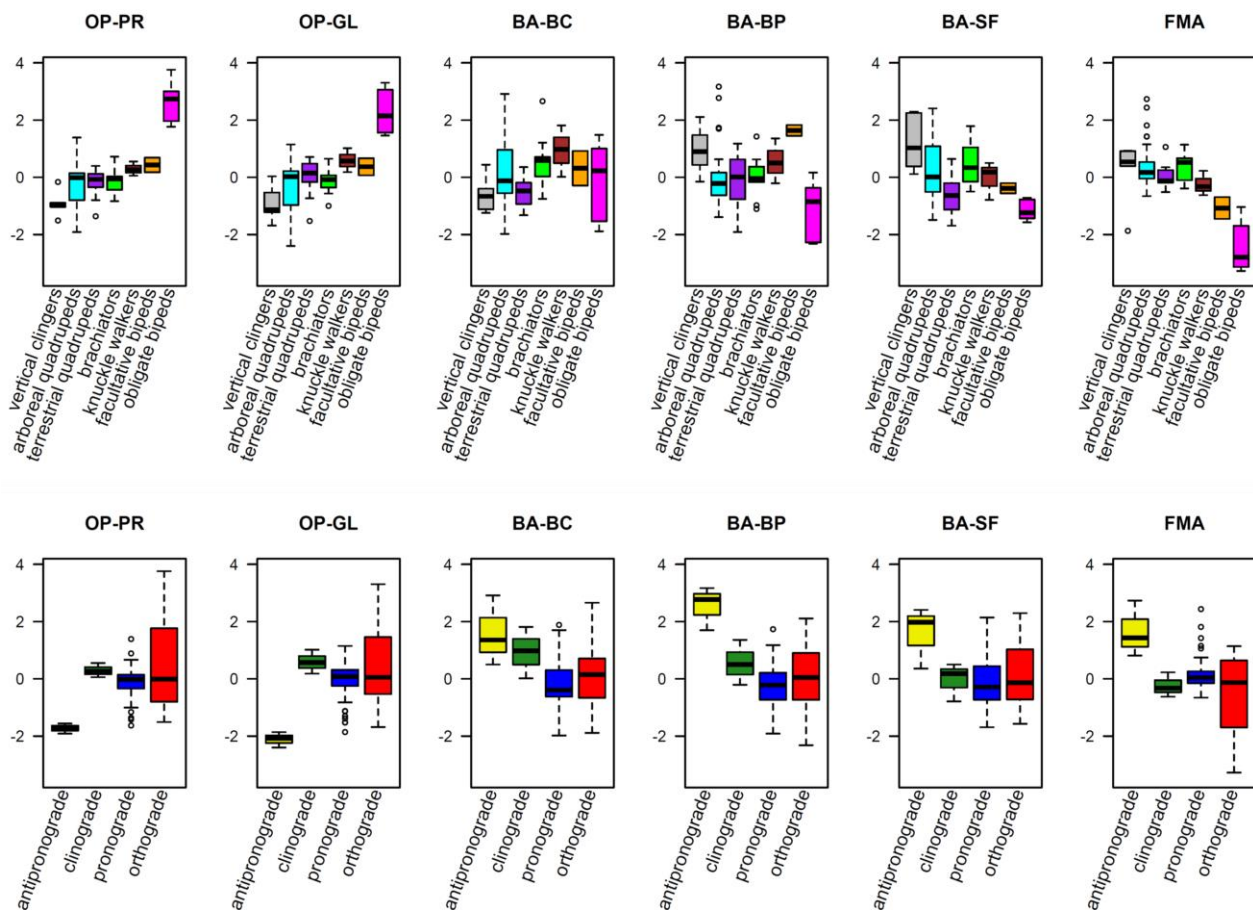


Figure 2. Boxplots showing the variability of foramen magnum indices across locomotor and postural categories (no phylogenetic correction applied). Bottom and top of the boxes are the first and third quartiles, the horizontal black lines represent the median, the whiskers represent the minimum and maximum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

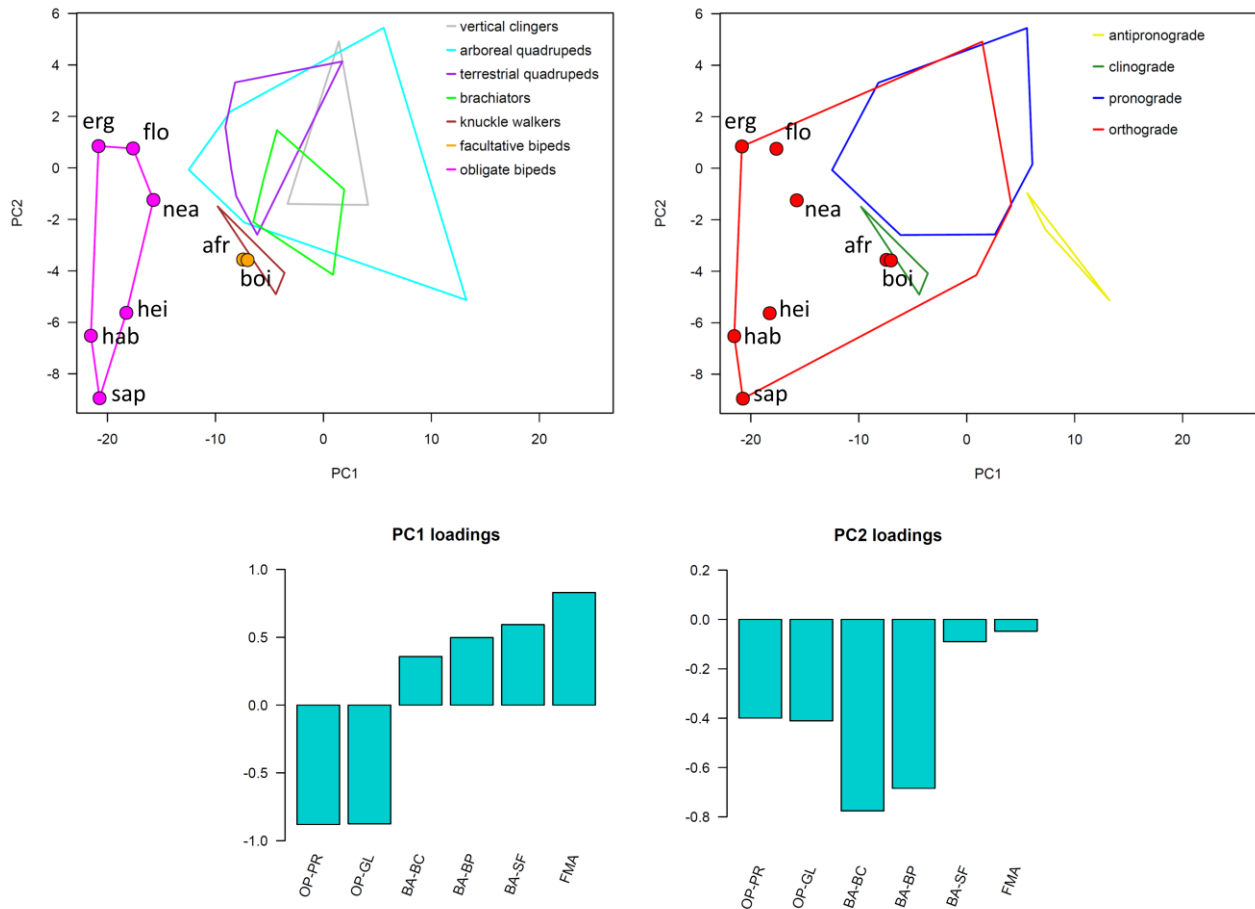


Figure 3. Phylogenetic Principal Component Analysis including all the indices tested in the work. The data is grouped by locomotion (top left) and posture (top right). The loadings (bottom) for the first (PC1) and second (PC2) components report the relative contributions. Phylogenetic correction is performed. (**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*).