Femoral neck cortical bone distribution of dryopithecin apes and the evolution of hominid locomotion

**Keywords:** Hip joint; Femur; Internal structure; Locomotion; Miocene apes; Hominoidea

**Abstract**

Only a few postcranial remains have been assigned to the Miocene great ape *Dryopithecus fontani*, leading to uncertainties in the reconstruction of its overall body plan and positional behavior. Here we shed light on the locomotor repertoire of this species through the study of the femoral neck cortical bone (FNCB) distribution of IPS41724, a partial proximal femur from the Abocador de Can Mata locality ACM/C3-Az (11.9 Ma, middle Miocene; Vallès-Penedès Basin, Spain) attributed to this taxon. This specimen was scanned through computed tomography to measure the superior (SUP) and inferior (INF) cortical thicknesses at the middle and the base of the femoral neck. Measurements were compared with a sample of extant primates and the femur IPS18800.29 from the younger great ape *Hispanopithecus laietanus* from Can Llobateres 2 (9.6 Ma, late Miocene; Vallès-Penedès Basin), previously shown to display a homogeneous FNCB distribution at the midneck section coupled with postcranial adaptations to below-branch suspensory behaviors. Our analyses indicate an asymmetric FNCB distribution for IPS41724 (SUP/INF index = ~0.4 at the midneck and base of the neck sections), comparable with that of quadrupedal primates and bipedal hominins (including early australopiths), but contrasting with the homogeneous FNCB distribution of *Hispanopithecus* and extant great apes. An asymmetrical FNCB distribution has been associated with stereotyped loads at the hip joint (as in both quadrupedal and bipedal taxa). Our results therefore support a significant quadrupedal component of the positional behavior of *Dryopithecus*, thus strengthening the argument that plesiomorphic generalized quadrupedalism was still a major locomotor behavior for Miocene great apes. If that were the case, it could have deep implications for the origins of hominin bipedalism.

**1. Introduction**

*1.1. Postcranial remains of* Dryopithecus fontani

Only a small number of postcranial remains have been assigned to the Miocene great ape[[1]](#footnote-1) *Dryopithecus fontani* (Hominoidea: Hominidae), in several instances only tentatively. A juvenile partial humerus is known from the type locality (Saint-Gaudens, France; Lartet, 1856; Pilbeam and Simons, 1971; Begun, 1992, 1994), which is correlated with the Mammal Neogene (MN) unit MN7+8 without further accuracy (Casanovas-Vilar et al., 2011). A partial distal humeral shaft from Castell de Barberà (Vallès-Penedès Basin, Spain), currently dated to 11.2 Ma (MN9; Alba et al., 2018, 2019), was also tentatively assigned to *D. fontani* by Alba et al. (2011) mostly on the basis of its size. It is possible that the thumb phalanges described by Almécija et al. (2012), also from Castell de Barberà, belong to the same taxon. Finally, Moyà-Solà et al. (2009a) attributed to *D. fontani* a proximal femur from Abocador de Can Mata (ACM) locality ACM/C3-Az (Vallès-Penedès Basin), dated to 11.9 Ma (Alba et al., 2017), which is the main focus of this study.

The assignment of the femur from ACM/C3-Az (IPS41724) to *D. fontani* is tentative for several reasons: first, no femoral remains have been recovered from the type locality of this species; second, the material of *D. fontani* from the type locality includes no upper teeth, whereas the identification of this species at ACM relies on maxillary remains from ACM/C3-Ae (Moyà-Solà et al., 2009a); and third, three distinct dryopithecin genera (*Pierolapithecus*, *Anoiapithecus* and *Dryopithecus*) have been recorded at ACM localities (see reviews in Alba, 2012; Alba et al., 2017). Discussing the alpha-taxonomy of the hominoid remains from ACM is outside the scope of this paper. However, the rationale for attributing the maxilla from ACM/C3-Ae to *D. fontani* was already discussed by Moyà-Solà et al. (2009a), while the recognition of three different genera at ACM has been further supported by subsequent analyses comparing the cranial and dental morphology of this specimen with other Vallès-Penedès hominoid craniodental remains (Moyà-Solà et al., 2009b; Alba, 2012; Alba et al., 2010b, 2013; Alba and Moyà-Solà, 2012; Pérez de los Ríos et al., 2012, 2014a,b; Fortuny et al., 2014), as well as the teeth from La Grive, France, that are also assigned to *D. fontani* (Pérez de los Ríos et al., 2012, 2013). It is noteworthy that previous criticisms on the recognition of three different great ape genera at ACM focused on the distinctiveness of *Pierolapithecus* and *Anoiapithecus* from *Dryopithecus* at the genus rank (e.g., Begun, 2009, 2010, 2015; Begun et al., 2012), but did not question the presence of the latter genus in the middle Miocene of the Vallès-Penedès Basin.

The presence of several dryopithecine genera at ACM within a restricted time span that overlaps with the record of IPS41724 is the most serious problem that precludes a conclusive assignment of this specimen to *D. fontani*. Moyà-Solà et al. (2009a) relied on inferred body mass to support an assignment to *D. fontani*, since the male palate from ACM/C3-Ae is larger dentally than other Vallès-Penedès hominoids (including the male holotypes of *Pierolapithecus catalaunicus* and *Anoiapithecus brevirostris*; Moyà-Solà et al., 2004, 2009b). Moreover, the body mass inferred for the IPS41724 femur (Moyà-Solà et al., 2009a) is also larger than that inferred by Moyà-Solà et al. (2004) from the lumbar vertebra of the holotype of *P. catalaunicus*. The same reasoning was followed by Alba et al. (2011) to favor a tentative assignment of the humeral shaft from Castell de Barberà to cf. *D. fontani*. A more conclusive taxonomic assignment will not be possible for IPS41724 until new femoral hominoid remains are recovered in association with craniodental dryopithecin specimens at ACM or elsewhere.

*1.2. Positional behavior of* D. fontani

As a result of the scarcity of postcranial elements attributed to *D. fontani*, its positional behavior and body plan (pronograde vs. orthograde) remain poorly understood, although some inferences have been previously drawn. The general appearance of the two aforementioned humeri from Saint-Gaudens and Castell de Barberà is hominoid-like (e.g., with a rounded diaphyseal cross-section and deep olecranon and coronoid fossae; Alba et al., 2011, and references therein). Based on these and other features displayed by the St. Gaudens humerus, including an inferred chimpanzee-like degree of humeral torsion, Begun (1992:334) concluded that *D. fontani* displayed, like *Rudapithecus hungaricus* from Rudabánya, Hungary, “habitually suspended postural and locomotor behavior”. However, as stressed by Alba et al. (2011), subsequent studies indicated a much lesser degree of torsion for the specimen (Rose, 1994; Larson, 1996)—suggesting that quadrupedalism still represented a significant component of the *Dryopithecus* locomotor repertoire. Furthermore, it is worth noting that some features of these humeri that resemble the modern hominoid condition, such as the deep olecranon and coronoid fossae, are indicative of a broad range of elbow flexion/extension, but cannot be unambiguously functionally linked to suspensory behaviors to the exclusion of above-branch quadrupedalism, since on functional grounds they merely preserve joint stability at very different elbow postures, which is also necessary in vertical climbing (e.g., Alba et al., 2011). In this regard, we concur with Richmond and Whalen (2001) that, even if the animal to which the Saint Gaudens humerus belongs used orthograde postures to some extent, at least it would have lacked the suspensory specializations displayed by extant apes.

Locomotor differences between Miocene great apes such as dryopithecins and extant great apes are further reflected in phalangeal morphology, which in the former most closely resembles that of early Miocene stem hominoids such as proconsulids and is indicative of powerful-grasping capabilities during above-branch quadrupedalism and cautious climbing (Begun, 1993; Begun et al., 1994; Madar et al., 2002; Nakatsukasa et al., 2003; Almécija et al., 2007, 2009, 2012; Alba et al., 2010a). Among dryopithecines, *Hispanopithecus* is an exception since its phalanges are longer and more curved than in *Pierolapithecus* (Almécija et al., 2007; Alba et al., 2010), also from the Vallès-Penedès Basin and with a similar inferred body mass as *Hispanopithecus* (Moyà-Solà et al., 2004, 2005). In any case, the similarities between the phalangeal morphology of proconsulids and the middle Miocene dryopithecines fit well with the morphology of the pollical phalanges from Castell de Barberà, potentially attributable to *D. fontani*, as shown by the relatively long, slender and curved proximal pollical phalanx with marked muscular insertions that are generally indicative of thumb-assisted powerful grasping (Almécija et al., 2012).

Taken overall, available postcranial remains more or less confidently attributed to *Dryopithecus* are consistent with a positional repertoire including a significant component of above-branch quadrupedalism and cautious climbing, potentially combined with antipronograde behaviors such as vertical climbing, but lacking specific adaptations to suspensory behaviors. Similar views have been advocated for the roughly coeval (12.0 Ma; Alba et al., 2017) dryopithecine *Pierolapithecus catalaunicus* from ACM/BCV1 (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009; Alba et al., 2010a; Alba, 2012), as well as for the older (ca. 16–15 Ma) *Nacholapithecus kerioi* (Nakatsukasa et al., 2003; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009), further considered a putative stem hominid (Alba, 2012; Kunimatsu et al., 2019). The inference that *Pierolapithecus* lacked specific suspensory adaptations in spite of possessing an orthograde body plan (Moyà-Solà et al., 2004) was mostly based on differences in phalangeal morphology and relative proportions to body mass, as compared to *Hispanopithecus* and extant apes. Such a contention was subsequently challenged by some authors (Begun and Ward, 2005; Deane and Begun, 2008) but supported by additional evidence by Moyà-Solà and coworkers (Moyà-Solà et al., 2005; Almécija et al., 2009, 2010b). Regarding suspensory adaptations, both *Dryopithecus* and *Pierolapithecus* (besides *Nacholapithecus* and most other middle Miocene apes) would differ from the late Miocene *Hispanopithecus laietanus* from Can Llobateres 2, which already shows clear adaptations to below-branch suspension (Moyà-Solà and Köhler, 1996; Almécija et al., 2007; Alba et al., 2010, 2012; Alba, 2012; Pina et al., 2012) in spite of still retaining some primitive features consistent with some degree of above-branch quadrupedalism (Almécija et al., 2007; Alba et al., 2010, 2012; Tallman et al., 2013).

*1.3. Femoral neck cortical bone distribution*

Given the aforementioned controversies regarding the possession of suspensory adaptations in both *Dryopithecus* and *Pierolapithecus*, the study of the internal anatomy of the IPS41724 femur from ACM/C3-Az offers an opportunity to provide additional insight into the locomotor repertoire of dryopithecins. Indeed, preliminary analyses of this femur have suggested a mixture of primitive and derived features compatible with the performance of quadrupedal behaviors (Moyà-Solà et al., 2009a; Pina et al., 2015; Pina, 2016).

The specific aims of this paper are twofold: (1) to add new mechanical information about the locomotor repertoire inferred for *D. fontani*; and (2) to test the hypothesis that the positional behavior of *D. fontani* was significantly different from that of taxa such as *H. laietanus*, which are clearly committed to suspensory behaviors. To do so, here we focus on the study of the internal structure of the partial proximal femur (IPS41724) from ACM/C3-Az and also report new data for the partial femur (IPS18800.29) of *H. laietanus* from Can Llobateres 2.

From a biomechanical point of view, the femoral neck is an important structure that transmits body weight and bears loadings from the muscles of the hip joint complex (e.g., Lovejoy et al., 1973; Ruff, 1995, 1998). We investigate here the femoral neck cortical bone (FNCB) distribution, which differs among primates depending on their type of locomotion (Rafferty, 1998; Pina et al., 2012). It has been proposed that differences in FNCB distribution are related to differential loading patterns at the hip joint, and that the organization of the internal structure of the femoral neck responds to differences in locomotor demands (main direction of the stresses; Rafferty, 1998; Demes et al., 2000; Ruff, 2002; Scherf, 2008). Moreover, comparisons between wild and captive chimpanzees (Matsumura et al., 2010), as well as between young and adult chimpanzees (Claxton, 2015), indicate that the FNCB distribution is to some extent an ecophenotypic feature (i.e., environmentally driven due to bone plasticity). This makes this feature particularly suitable to paleobiological inferences, as it does not merely reflect adaptation but also actual behavior to some degree.

Previous studies have shown that quadrupeds and bipeds share an asymmetrical FNCB distribution, with the superior cortex being thinner than the inferior (e.g., Lovejoy, 1988; Rafferty, 1998; Scherf, 2008; Pina et al., 2012), reflecting stereotypical loadings on their hip joint. In contrast, extant apes display a homogenous FNCB distribution (i.e., the superior and inferior thicknesses are similar) as a result of non-stereotypical loads (Lovejoy, 1988; Rafferty, 1998; Scherf, 2008; Pina et al., 2012). Therefore, FNCB distribution is useful to infer broad locomotor adaptations in fossil primates, particularly to distinguish taxa with antipronograde (suspensory and/or vertical-climbing) behaviors from those that are mainly pronograde (Ohman et al., 1997; Rafferty, 1998; Demes et al., 2000; Ruff and Higgins, 2013). Therefore, we investigate the FNCB distribution in the proximal femur IPS41724 tentatively assigned to *D. fontani*, in order to make paleobiological inferences about how this taxon loaded its hip joint and compare it with the younger *H. laietanus*. The internal structure of this Miocene ape is here reported for the first time, and new measurements for the right femur of *H. laietanus* are also provided for the base of the neck section.

**2. Materials and methods**

*2.1. Comparative sample*

The studied specimen (IPS41724) is housed at the Institut Català de Paleontologia Miquel Crusafont (IPS) in Sabadell, Spain. The estimated body mass (BM) for *D. fontani* is 44.4 kg (see below; Moyà-Solà et al., 2009a:Table 7). Superior (SUP) and inferior (INF) femoral neck cortical thicknesses of IPS41724 were originally measured (to the nearest 0.01 mm) at the greatest superoinferior axis of the selected sections (from the periosteum to the endocortical limit along this axis; see below for further details on the computed tomography, CT, scanning and thresholding process). The cortical thicknesses of IPS41724 were compared with published data of extant primates. The sample of living taxa includes humans (*Homo sapiens*), apes (*Pan* sp., *Gorilla gorilla*, *Pongo pygmaeus*, *Symphalangus syndactylus*, and *Hylobates lar*), cercopithecines (*Papio* sp., *Mandrillus* sp., and *Macaca* sp.), colobines (*Nasalis larvatus*, *Presbytis rubicunda*, *Trachypithecus cristatus*, *Colobus guereza*, and *Lophocebus albigena*), atelids (*Ateles* sp., and *Alouatta seniculus*), and 20 different genera of strepsirrhines (SUP and INF data from Rafferty, 1998; Demes et al., 2000; Matsumara et al., 2010; Lovejoy, pers. comm.; see Pina et al., 2012 and SOM Table S1 for further details).

*2.2. Computed tomography scans and cortical thicknesses measurements*

The FNCB thicknesses of IPS41724 were computed based on high-resolution CT scans, which were processed using VSG-Avizo v. 7.0 (FEI Visualization Sciences Group, Hillsboro). Exploring the FNCB distribution (SUP and INF) of IPS41724 is challenging due to the strong mineralization found at its femoral head and greater trochanter (Fig. 1), which results in low quality CT images with extremely bright (white) areas (“bulb effect”; e.g., see Solomon et al., 1991; Gielen and Van Dyck, 2015). Moreover, the interaction of these two bright points creates an area of shadow that crosses from the inferior-most medial part of the femoral neck to its superior edge (i.e., superior half of the femoral neck), just where SUP should be measured (Fig. 1). As a result, approximately the superior third of the neck is not well resolved in the final CT images. To obtain reliable measurements of this variable in IPS41724, this fossil was scanned several times using different CT devices and settings (Table 2). This approach allowed us to obtain CT scans with increasing resolution, although the definition of the cortical bone boundaries was still relatively low (Table 2; Fig. 2). Unfortunately, the brightness of the femoral head and the greater trochanter made difficult to define cortical bone boundaries in the femoral neck. Therefore, IPS41724 was scanned after physically removing the femoral head along a natural break situated about its base (Fig. 2d). The most distal part of the preserved shaft was also removed by manually separating it through another natural break (just below the lesser trochanter; see Moyà-Solà et al., 2009a: Fig. 11). CT images acquired from the resulting scan had less resolution, but a slightly better definition of cortical bone boundaries (SOM Fig. S1). For CT settings and further details about IPS18800.29, see Pina et al. (2012).

Two slices from the femoral neck, orthogonal to the main axis of the neck were selected for each fossil specimen, following Ruff and Higgins (2013). One of the sections was placed at the base of the neck, just medial to the intertrochanteric line, and the other at the midpoint of the femoral neck between the base of neck section and the most lateral edge of the femoral head (Fig. 3). The cross-sectional thresholding was carried out in Fiji 1.50e (Schindelin et al., 2012) with the help of an image histogram and following changes in the Hounsfield units to differentiate fluctuations in the gray scale densities (Hounsfield, 1973, 1976; Ohman et al., 1997). IPS41724 was scanned four times in total at different institutions with different CT devices and settings (Table 2). Images extracted from the scan performed at the American Museum of Natural History (AMNH; New York, USA) and “Abdus Salam” International Centre for Theoretical Physics (Trieste, Italy)—which display the best final resolution and tissue definition—were used as the main basis to delineate the cortical boundaries (Fig. 4). When boundaries were not clear enough (mainly at the superior part of the base of the neck section), the remaining CT scans were visualized in parallel to further help in this process; in these cases, some filters were applied to the images (e.g., gamma correction and Laplacian) and/or brightness/contrast were dynamically changed to more clearly discern the cortical boundary. The resulting drawings were mostly based on the AMNH and Trieste scans, in which SUP and INF measurements, respectively, were originally taken by one of us (M.P.) along the greatest superoinferior height of the femoral neck (Ruff and Higgins, 2013).

Given that the low quality of the images of the final CT images of IPS41724 may have impacted the measurement of SUP and INF, an interobserver test was performed in order to quantify the measurement error. Three different observers measured SUP and INF in three consecutive days in the two images obtained from the four scans (both for the midneck and the base of the neck, i.e., a total of 16 measurements). The details and results of the interobserver test are reported in SOM S1 and SOM Tables S2 and S3. In most instances, measurements of SUP and INF in IPS41724 do not significantly differ among experienced observers (*p* > 0.05). Significant differences are only found for INF at the base of the neck section (*p* = 0.006), although the associated interobserver error in the performed test is quite low (2.51%). Moreover, when the measurements of the three observers of the additional test are compared with the measurements taken originally by M.P. (those reported in the main text), the error is only 5.37%. Based on these results, we consider that the SUP and INF values reported in the main text are reliable and reproducible, and hence amenable to further analysis.

*2.3. Statistical analyses*

Statistical comparisons were performed following the procedure detailed in Pina et al. (2012). For the allometric analyses, apes and humans were considered by genera and non-hominoid taxa were grouped into strepsirrhines, atelids, colobines, and cercopithecines. For comparative analyses, taxa were grouped by locomotor types following Rafferty (1998). The right partial femur IPS18800.29 of *H. laietanus*, also housed at the ICP, was also included in the comparative sample (BM = 38.6 kg; Moyà-Solà et al., 2009a: Table 7). SUP and INF data for IPS18800.29 was obtained from Pina et al. (2012) for the midneck; whereas cortical thicknesses for the base of the neck were originally collected for this study.

For the statistical analysis, we first computed a dimensionless ratio between SUP and INF (SUP/INF), since this index has been related to locomotor types (Rafferty, 1998). To also control for size-related scaling effects, we relied on allometric techniques as a criterion of subtraction (Gould, 1966). Log-transformed means (with natural logarithms, ln) for SUP and INF were regressed against each other using the ordinary least-squares method (OLS; Smith, 1994, 2009). Subsequently, allometric residuals (RES) obtained from the SUP vs. INF regressions (which do not include the extinct taxa) were computed as a metric of intrinsic relative cortical thickness (with the non-hominoid regression as the baseline, since apes have previously been found to be outliers; Pina et al., 2012). The least squares residuals from the regression of SUP vs. body mass (BM, in kg; data taken from Smith and Jungers, 1997; Rafferty, 1998; Demes et al., 2000) were also used as another size-corrected measure of SUP (RESBM). Allometric regressions were replicated from Pina et al. (2012), hence, we only show the final comparative boxplots in this work, in which new results are displayed. Given that the comparative data used in this study was mainly extracted from the literature (see above), the information we can provide here is limited and analyses were restricted to reproduce those provided in the original references (Rafferty, 1998; Ruff and Higgins, 2013). Thus, for the midneck section, SUP/INF, RES and RESBM were grouped by locomotor modes. The following groups were considered: bipeds (humans), knuckle-walkers (gorillas and chimpanzees), suspensory taxa (orangutans, hylobatids, and atelids), slow climbers (loris), quadrupeds (cercopithecoids, some galagos), and vertical clingers and leapers (VCL; lemurs, sifakas, and indris; SOM Table S1; see also Rafferty, 1998; Pina et al., 2012 and references therein).

Additionally, given that Ruff and Higgins (2013; see also Ohman et al., 1997) highlighted in their study that the main differences between humans (and their fossil relatives) and great apes are mainly at the base of the neck instead of the midneck, we used their data to compare the SUP/INF ratios of IPS41724 and IPS18800.29 at both the midneck and base of neck sections. Taxa analyzed by Ruff and Higgins (2013) include only extant apes (*Symphalangus syndactylus*, *Pongo pygmaeus*, *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*) and humans (*Homo sapiens*), as well as several specimens of *Australopithecus* and *Paranthropus* (Table 1). In this case, SUP/INF results for the midneck and base of the neck sections are shown by species (unless for fossil femora) following Ruff and Higgins (2013).

BM estimates of *D. fontani* and *H. laietanus* were used for the analyses. These BM estimates were derived by Moyà-Solà et al. (2009a) using Ruff’s (2003) regression equations based on superoinferior height of the femoral head (FHSI) and the femoral head surface area (FHSA) and subsequently applying the quasimaximum likelihood estimator (QMLE) correction factor (QMLE = exp [SEE2/2], where SEE is the standard error of estimate) to account for logarithmic detransformation bias (Ruff, 2003). The BM estimates for *D. fontani* and *H. laietanus* used in this paper are the average between the estimations based on FHSI and FHSA (Moyà-Solà et al., 2009a), but to ensure that results were not an artifact of body size estimation uncertainties, statistical analyses were repeated by taking into account the 50% confidence intervals for their predicted BM (IPS41724: 40.1–49.5 kg; IPS18800.29: 34.3–43.1 kg; Moyà-Solà et al., 2009a: Table 7).

Analyses were performed using SPSS v.15.0 (SPSS Inc., 2006) and the R statistical environment (R Core Team, 2017).

**3. Results**

*3.1. External morphology of IPS41724*

IPS41724 was originally described by Moyà-Solà et al. (2009a). It is a well-preserved partial right proximal femur that displays a spherical femoral head, which is small relative to the neck (Almécija et al., 2013; Pina, 2016). The femoral head articular surface is mediolaterally broad in anterior view and expands onto the neck on its posterior side (Fig. 5d, e). The head exhibits a well-marked fovea capitis, which is large, shallow, and located superoposteriorly (Fig. 5a). The femoral neck is anteroposteriorly flattened and displays an elliptical cross-section (Fig. 4c, d). Its biomechanical length is relatively long (Almécija et al., 2013), and its neck-shaft angle is 124º (Pina, 2016). The proximal epiphysis shows a slight anteversion (Fig. 5a). The greater trochanter is markedly projected proximally, although situated somewhat below the femoral head, and displays a slight lateral flare. The greater trochanter is proximodistally short and anteroposteriorly narrow. The trochanteric fossa is deep and broad, as is the femoral notch. The trochanteric crest is slightly prominent and the quadrate tubercle is clearly marked. The lesser trochanter is well developed and faces posteriorly (Fig. 5b). The proximal shaft is anteroposteriorly flattened, and shows a well-marked gluteal tuberosity in its lateral side, which is clearly separated from the greater trochanter (Fig. 5c).

*3.2. Internal structure of the IPS41724 femoral neck*

INF was measured at the Trieste scan at both the midneck (5.42 mm) and the base of the neck (4.84 mm; Table 1). SUP values for IPS41724 are somewhat tentative due to the low quality of the CT images, and are estimated to be ~2.40 mm for the midneck section and ~2.16 mm for the base of neck section on the basis of the AMNH scan in both cases (Table 1). INF progressively decreases towards the anterior and posterior edges, showing a thinner cortex superiorly. Hence, on qualitative grounds IPS41724 clearly displays an asymmetric FNCB distribution (Fig. 4). The SUP/INF indices along the neck are approximately 0.4 (Table 1). Even if additional measures are taken at the superior-most part of the posterior edge, where the boundary of the cortical bone is clearly visible in both sections, the resulting index closely approaches the same value obtained for the locations previously used in the literature, those following the greatest superoinferior height of the femoral neck (Fig. 4).In the case of IPS18800.29, both sections displayed a more homogeneous FNCB distribution, and the SUP values resemble INF for both the midneck (SUP = 2.93 mm and INF = 2.73 mm; Pina et al., 2012) and the base of the neck (SUP = 3.96 mm and INF = 3.16 mm; this study) sections (Table 1). The obtained SUP/INF ratios for this femur are closer to unity than in the case of *D. fontani* (1.08 and 1.25, respectively; Table 1).

In terms of locomotor types, results for IPS41724(RES = -0.074, SUP/INF = 0.443; Fig. 6a, b) fall in the range of generalized quadrupeds, also overlapping with bipeds, slow-climbers, and vertical-clingers-and-leapers (Table 3). In contrast, IPS18800.29 (RES = 0.771 and SUP/INF = 1.020) shows an even more extreme condition than both specialized suspensory and knuckle-walking taxa (that is, taxa with enhanced abduction and external rotation of the hind limb; Table 3). Results obtained for proportions relative to body size show that IPS41724 (RESBM = 0.708) and IPS18800.29 (RESBM = 0.950) most closely resemble knuckle-walkers (Table 3; Fig. 6c). However, both *D. fontani* and *H. laietanus* further fall within the range of suspensory taxa (Fig. 6c). Uncertainties in BM estimation of fossil specimensdo not affect such conclusions (Fig. 6c).

When the FNCB distribution was inspected by means of the SUP/INF ratio among a more restricted sample of extant apes and early hominins (Fig. 7; Table 1) at both the midneck and the base of the neck, the results reported above were corroborated for both IPS41724 and IPS18800.29. The midneck ratio of IPS41724 falls in the range of modern humans and below that of the apes and early hominins, whereas in the case of IPS18800.29 the midneck ratio overlaps with those of orangutans and chimpanzees, and with the uppermost ranges of bonobos and siamangs (Fig. 7a). Differences between IPS41724 and IPS18800.29 are higher at the base of the neck section (Fig. 7b), since IPS18800.29clearly overlaps with the ranges of African apes, whereas IPS41724 falls close to the upper range of modern humans and is similar to early hominins.

**4. Discussion**

*4.1. Functional inferences*

Although the assignment of the ACM femur to *D. fontani* remains tentative (Moyà-Solà et al., 2009a), as in the case of the Castell de Barberà humerus and phalanges, results of the analyses presented here provide important information regarding locomotor diversity of middle Miocene dryopithecins, even if the taxonomic attribution of the ACM femur is wrong. The femoral external morphology of IPS41724 (Moyà-Solà et al., 2009a; Pina et al., 2015; Pina, 2016; this paper) displays features—such as small head related to the neck and notable proximal projection of the greater trochanter—that have been functionally related to generalized arboreal quadrupedalism (Ruff, 1988; Ward et al., 1993), as well as other characteristics (e.g., rounded femoral head with deep articular surface) associated with enhanced hind limb abduction (Ward et al., 1993; MacLatchy and Bossert, 1996).

Our results for the FNCB of IPS41724 reveal an asymmetric distribution of the cortical bone, implying that its femoral neck was loaded in a more stereotyped fashion than in *H. laietanus* (IPS18800.29; see also Pina et al., 2012). This fact also suggests, assuming our taxonomic assignment is correct, that *D. fontani* would be less specialized for enhanced hip abduction and external rotation than *H. laietanus*, whose femur more closely resembles that of extant apes, both externally and internally. An asymmetrical pattern is typical of modern humans, but also of quadrupedal monkeys (Rafferty, 1998; Lovejoy et al., 2002; Pina et al., 2012). Thus, the stereotyped loading pattern inferred from the obtained FNCB asymmetric pattern fits well with the quadrupedal component inferred for the positional behavior repertoire of *D. fontani* on the basis of other postcranial remains (Pilbeam and Simons, 1971; Alba et al., 2011; Almécija et al., 2012). This also fits with the so-called “Miocene ape-like” generalized quadrupedalism of early Miocene African apes such as *Ekembo*, *Proconsul*, or *Nacholapithecus* (Rose, 1983, 1994; Ward et al., 1993; Nakatsukasa et el., 2012; Ward, 2015), among others, and the persistence of a significant quadrupedal component in roughly coeval taxa from Eurasia such as *Pierolapithecus* (Almécija et al., 2009, 2013; Alba et al., 2010; Pina, 2016) and *Sivapithecus* (Madar et al., 2002; Morgan et al., 2015).

Nonetheless, fossil remains attributed to *D. fontani*, including the IPS41724 partial femur, also display some traits related to antipronograde behaviors and enhanced joint mobility (e.g., rounded femoral head and rounded humeral diaphyseal cross-section; Moyà-Solà et al., 2009a; Alba et al., 2011; Pina et al., 2015). However, these features are not reflected in the FNCB distribution of *D. fontani*, which suggests instead that this taxon would have engaged in locomotor patterns involving a stereotyped loading of the hip joint (namely, quadrupedalism and/or bipedalism; Rafferty, 1998; Lovejoy et a., 2002; Pina et al., 2012). Given that the morphology of IPS41724 allows us to discount habitual bipedalism (e.g., moderate femoral neck-shaft angle and proximal projection of the greater trochanter), the stereotyped loading pattern present in *D. fontani* would probably relate to some form of quadrupedalism unknown among extant apes, but inferred for a large number of fossil ape taxa (e.g., Rose 1994). For example, this would be the case of older proconsulids (e.g., Ward, 2015) and *N. kerioi* (e.g., Nakatsukasa and Kunimatsu, 2009), although the latter already shows clearer adaptations for forelimb-dominated behaviors, mainly at the humero-ulnar joint when compared with *D. fontani* remains (Ishida et al., 2004; Takano et al., 2018). In addition, given that the possession of SUP values thinner than INF is shared by living pronograde quadrupeds and bipedal hominins, these results cannot clarify if *D. fontani* had a pronograde or an orthograde body plan (just based on the femur). As stated above for other Miocene taxa, *D. fontani* displays a combination of primitive and derived traits that emphasizes the challenging work of inferring the positional behavior of extinct apes and, in particular, putative stem great apes. Given the mosaic evolution of the locomotor apparatus in hominoids, these taxa show combinations of morphological and biomechanical features that are currently unknown in their surviving counterparts (Almécija et al., 2007, 2009; Alba, 2012; Alba et al., 2012; Pina et al., 2014b; Ward, 2015).

It is also important take into account that the BM estimates available for *D. fontani* (40–50 kg on the basis of the femoral head and 46–55 kg based on the humeral shaft; Moyà-Solà et al., 2009a; Alba et al., 2011) are slightly above the maximum theoretical value of 40 kg for efficient arboreal quadrupedalism—i.e., for maintaining the center of mass above the base support without generating an additional torque force or using specialized adaptations for powerful grasping during displacement; Cartmill, 1985; Demes et al., 1994; Larson, 1998). *Dryopithecus fontani* might have overcome such a biomechanical constraint in different ways. First, the morphology and relatively large size of the pollical phalanx from Castell de Barberà suggest powerful grasping capabilities during above-branch quadrupedalism, as shown in other Miocene apes (contrary to that of extant great apes in which the pollical phalanx is relatively small and has faint muscular attachments; Almécija et al., 2012). The habitual engagement in antipronograde behaviors such as vertical climbing or below-branch suspension could have similarly ameliorated the problem (Cartmill, 1985). Vertical climbing in this taxon would be supported by the presence of some external traits associated with a wider range of excursion at the hip (e.g., rounded femoral head; Moyà-Solà et al., 2009a; Almécija et al., 2013; Pina et al., 2014a, 2015) and elbow (e.g., rounded humeral diaphyseal shaft and deep coronoid fossae; Alba et al., 2011) joints. In addition, the morphology of the Castell de Barberà phalanges does not support the possession of adaptations to suspensory behaviors (Almécija et al., 2012), as further argued for other middle Miocene putative stem hominids such as *Pierolapithecus* (Almécija et al., 2009; Alba et al., 2010a; contra Deane and Begun, 2008) as well as for the *D. fontani* humerus from Saint-Gaudens (e.g., Richmond and Whalen, 2001; contra Begun, 1992). Nevertheless, given the mosaic nature of locomotor evolution in hominoids, additional remains, representing other anatomical regions, would be necessary to test further such locomotor inferences, particularly for *D. fontani*.

Alternatively, *D. fontani* might have relied to some extent on terrestrial quadrupedalism. However, no specific adaptations for terrestriality are found in IPS41724, which lacks, for example, the strong proximal projection of the greater trochanter displayed by large papionins. Among fossil hominoids, only *Equatorius africanus* displays postcranial adaptations that have been clearly associated with terrestriality (McCrossin et al., 1998; Sherwood et al., 2002). In the case of the femur, Ward (1997) suggested that the short femoral neck of *E. africanus* could be indicative of the habitual use of a terrestrial substrate. In this regard, Almécija et al. (2013) demonstrated that the relative biomechanical neck length of *D. fontani* is slightly longer than that of *E. africanus* (BMNH-M-16331), although in both cases their relative biomechanical length is longer than that of extant cercopithecoids, including the most terrestrial large-bodied baboons and mandrills. Terrestrial adaptations found in other anatomical regions of *E. africanus* (e.g., retroflexed medial epicondyle of the humerus and semiterrestrial hand proportions; Sherwood et al, 2002; Patel et al., 2009) are not found in *D. fontani* either (Alba et al., 2011; Almécija et al., 2012).

*4.2. Evolutionary implications*

Overall, above-branch quadrupedalism with powerful grasping capabilities and some degree of vertical climbing and/or cautious climbing could have characterized the locomotor repertoire for *D. fontani* based on the IPS41724 femur and the other few postcranial remains assigned to this taxon. Such inferences are not surprising when *D. fontani* is considered within the framework of Miocene apes, most of which (*Proconsul major*, *Ekembo* spp., *Nacholapithecus kerioi*, and *Sivapithecus* spp., among others) share a mosaic combination of morphological features which allows inferring locomotor repertoires that probably combined generalized arboreal quadrupedalism with a varying amount of antipronograde behaviors other than suspension (e.g., Rose, 1983; Nakatsukasa and Kunimatsu, 2009; Morgan et al., 2015; Ward, 2015). In any case, our results support previous inferences that the positional behavior of *D. fontani* included an important quadrupedal component, which has relevant evolutionary implications. IPS41724 shows interesting similarities with australopiths and modern humans in terms of FCNB distribution. Such similarities are in further agreement with previous works that highlighted closer morphological affinities (due to functional reasons) between early hominins and Miocene apes than between the former and modern apes (e.g., Lovejoy et al., 2009a; Almécija et al., 2013).

Previous studies have claimed that the symmetrical FNCB distribution associated with non-stereotyped loads at the hip joint in modern great apes could represent the plesiomorphic condition for crown hominoids (Ohman et al., 1997; Lovejoy et al., 2002). Under this viewpoint, the human asymmetric pattern, especially a relatively thin SUP (associated with more stereotyped loadings), would be derived in hominins and should be considered a diagnostic trait for inferring bipedal behaviors mainly in fossil hominines (e.g., Ohman et al., 1997; Lovejoy et al., 2002; Galik et al., 2004). However, subsequent works (Rafferty, 1998; Pina et al., 2012) based on a broader phylogenetic and functional sample including platyrrhines, catarrhines (cercopithecoids and hominoids), and strepsirrhines demonstrated evident similarities in the asymmetric pattern between quadrupeds and bipeds. Similarities in the mechanical environment of these two groups might reflect a more stereotyped loading regimes around their hip. A potential caveat for the latter interpretation is that monkeys and humans differ in the ossification pattern at the proximal femur (Serrat et al., 2007) —coalesced in the former (i.e., the femoral head and the greater trochanter develop together into a single epiphysis during ontogeny) and non-coalesced in humans (separate development of the femoral head and the greater trochanter). Even though Serrat et al. (2007) concluded that the type of ossification pattern is unrelated to locomotion, body size, and phylogeny, these differences raise the issue of whether FNCB configurations are comparable between monkeys and humans. The sample investigated by Serrat et al. (2007) included a large representation of mammals with highly divergence body masses and locomotor types, so that more specific analyses restricted to primates would be required to more conclusively discount the influence of proximal femur ossification patterns on FNCB. In any case, Serrat et al. (2007) argued that the development of a separate epiphyseal pattern might be related to increased hip mobility, whereas the coalesced epiphyseal pattern would be found among mammals with more stereotyped limb movements. This assertion agrees well with the fact that quadrupedal monkeys preferentially move the limbs along the parasagittal plane and display an asymmetric FNCB, while apes have a higher range of movement of the hip joint together with a symmetrical FNCB pattern, so that only humans would be an exception. Therefore, the current evidence on the proximal femur epiphyseal pattern (Serrat et al. 2007), the FNCB distribution on captive vs. wild individuals (Matsumara et al., 2010), and the ontogenetic development of the FNCB distribution (Claxton, 2015) reveals that the internal structure of the femoral neck in terms of cortical bone is not genetically determined or associated to phylogenic relationships. Determining whether this trait is ecophenotypic (Matsumara et al., 2010) and/or functionally related (Serrat et al. 2007) requires further investigation, but it seems clear that the surrounding mechanical environment around the hip joint has some relevance on modeling the structural shape of the proximal femur.

To further interpret the evolutionary implications of the symmetrical FNCB displayed by the femur assigned to *D. fontani* is it necessary to take into account the phylogenetic relationships of Miocene dryopithecines as a whole. This is complicated by the fact that, until a decade ago, middle and late Miocene dryopithecines were lumped into a single genus (*Dryopithecus* s.l.), and it was not until Moyà-Solà et al. (2009a) and Begun (2009) that *Hispanopithecus* and *Rudapithecus* were resurrected to distinguish the late Miocene taxa. Here we follow Alba (2012) in recognizing two distinct tribes (Dryopithecini and Hispanopithecini) within the subfamily Dryopithecinae. Nonetheless, other authors (Begun, 2009; Begun et al., 2012) classify these taxa as a single tribe (Dryopithecini) within the subfamily Homininae (i.e., African apes and humans). Such disagreements reflect current uncertainties about the phylogenetic relationships of dryopithecines, which as a group have not been subjected to formal cladistic analysis since the description of *Pierolapithecus* and *Anoiapithecus* (Moyà-Solà et al., 2004, 2009b) or the distinction between dryopithecins and hispanopithecins (Begun, 2009; Moyà-Solà et al., 2009a; Alba, 2012). Thus far, only *Hispanopithecus* and *Pierolapithecus* have been included in formal cladistic analyses, which recovered them as successive stem hominoids (Alba et al., 2015)—thereby substantiating previous inferences that dryopithecines as a whole are likely stem hominids (Moyà-Solà et al., 2004, 2009a,b; Alba, 2012)—or left them unresolved in a trichotomy with pongines and hominines (Nengo et al., 2017). On the other hand, other authors (e.g., Begun, 2015) still adhere to the view that dryopithecines as a whole are stem hominines—as supported by some cladistic analyses performed when driopithecins and hispanopithecins were lumped into a single genus *Dryopithecus* (Begun and Kordos, 1997; Begun et al., 1997), although other analyses supported a stem hominid status for *Dryopithecus* s.l. (Finarelli and Clyde, 2004). In either case, the internal phylogeny of dryopithecines is currently uncertain (Alba, 2012), so that more comprehensive analyses would be required to test whether they constitute a monophyletic clade or a paraphyletic assemblage.

In a strict sense, the fact that the FNCB distribution is probably a largely ecophenotypic trait would advise against using this character in a formal cladistic analysis. On the other hand, if this is the case then the FNCB distribution must be tightly linked to positional behaviors—which, in turn, are arguably related to genetically determined morphological features selected as adaptations because of functional reasons. Therefore, it makes sense to investigate the evolution of FNCB distribution patterns within crown hominoids in the light of the two aforementioned main alternative phylogenetic interpretations of dryopithecines (Fig. 8). Based on extant taxa alone, it would be most parsimonious to assume that the symmetric pattern is a shared-derive feature of at least crown hominoids that was secondarily reversed during the evolution of the hominin lineage. However, the asymmetric pattern displayed by IPS41724 indicates a more complex evolutionary history for FNCB distribution—irrespective of whether *D. fontani* is considered a stem hominid (Fig. 8a) or a stem hominine (Fig. 8b). Indeed, the overall picture would still remain if IPS41724 belonged to a dryopithecine genus other than *Dryopithecus*.

The asymmetric pattern of FNCB distribution of IPS41724 could merely represent an autapomorphy of *D. fontani* convergent with the hominin condition. However, given the presence of such a pattern in the sister taxon of hominoids and the mosaic evolution of the hominoid locomotor apparatus throughout the Miocene (e.g., see discussion in Alba et al., 2012), it appears equally (if not more) likely that this represents the ancestral hominoid condition. Hence, the symmetrical FNCB pattern might evolve in parallel along various hominoid lineages as a result of the independent adoption of forelimb-dominated antipronograde positional behaviors with large suspensory components, as concluded based on evolutionary modeling of the femoral external morphology (Almécija et al., 2013). If dryopithecines are considered stem hominids (Fig. 8a), the symmetrical pattern must have independently evolved at least in hylobatids and crown hominids (if not also *Hispanopithecus*, assuming it is more closely related to *Dryopithecus* than extant hominids). If dryopithecines are considered stem hominines (Fig. 8b), then the symmetrical pattern must have additionally evolved independently in orangutans. While this might seem counterintuitive on parsimony grounds, the mosaic of plesiomorphic and derived (modern hominoid-like) locomotor-related features displayed by putative stem hominids such as *Pierolapithecus* (Moyà-Solà et al., 2004; Almécija et al., 2009) and, especially, the putative pongine *Sivapithecus* (Madar et al., 2002) supports the view that suspensory adaptations evolved independently not only between hylobatids and hominids, but also between pongines and hominines (and probably *Hispanopithecus*)among the latter clade (Almécija et al., 2009; Alba et al., 2010a; Alba, 2012). This view is further reinforced by the possession of a symmetric FNCB pattern in atelids, which are the most suspensory platyrrhines (Rafferty, 1998).

Under the two slightly different scenarios discussed above, the hominin condition would have evolved from an ancestor characterized by a symmetrical pattern and would represent a secondary reversal to the more primitive condition displayed by *D. fontani*—probably as a result of the more stereotyped loadings at the hip associated with habitual bipedalism. Alternatively, given the multiple acquisitions of a symmetrical pattern implied by IPS41724 (particularly when dryopithecines are interpreted as stem hominines; Fig. 8b), the possibility that the asymmetric pattern of FNCB distribution was still present in the last common ancestor of hominines cannot be currently ruled out. If that were the case, the homogeneous FNCB distribution related to a non-stereotyped loading at the proximal femur would have evolved independently along the various lineages of extant great apes, with hominins (including modern humans) merely retaining the plesiomorphic condition for this feature. Under this scenario, the possession of an asymmetric FNCB distribution would not be a reliable anatomical proxy for inferring bipedalism in early hominins (e.g., the long saga on *Orrorin tugenensis*; Galik et al, 2004; Kuperavage et al., 2010, among others), particularly if they evolved from non-suspensory ancestors as argued by some on the basis of *Ardipithecus* (Lovejoy et al., 2009b). Hence, further analyses of FNCB distribution, based on a greater sample (including more fossil apes and extant cercopithecoid and platyrrhine monkeys) and using evolutionary modeling and phylogenetic comparative methods, would be necessary to provide a broader and more informed perspective on this question.

**5. Summary and conclusions**

This study focuses on the internal structure of the femoral neck of IPS41724, a partial proximal femur tentatively attributed to the middle Miocene dryopithecine *D. fontani*. Our results show that this femur displays a FNCB asymmetric pattern, with SUP being thinner than INF (shared with living quadrupedal primates and bipedal hominins). This pattern contrasts with that found in the younger dryopithecine *H. laietanus*, which shows a symmetric (SUP similar to INF) FNCB distribution (shared with living primates with enhanced antipronograde behaviors, namely vertical climbing and/or below-branch suspension). The FNCB pattern displayed by IPS41724 has been previously associated with stereotyped loadings at the hip joint, which are linked with either quadrupedal or bipedal behaviors. Given that the external femoral morphology of IPS41724 clearly departs from that of humans, the internal structure of its femoral neck well supports an important above-branch quadrupedal component for the positional behavior repertoire of this taxon, as previously inferred based on this partial femur, a partial humerus, and some phalanges (Moyà-Solà et al., 2009a; Alba et al., 2011; Almécija et al., 2012). Such inferences should be taken with caution until additional postcranial remains attributable to *D. fontani* become available, since with the exception of the Saint-Gaudens humerus most of the currently available postcranial evidence is only tentatively assigned to this taxon.

In evolutionary terms, two different hypotheses are plausible irrespective of the controversial systematic status of dryopithecines (either stem hominids or stem hominins). One possibility is that the asymmetric pattern observed in *D. fontani* and humans is convergent, with the symmetric pattern displayed by *Hispanopithecus* and extant apes reflecting the plesiomorphic condition for crown hominoids. Alternatively, the asymmetric pattern shared by *D. fontani* and humans might be a simplesiomorphy retained from the last common ancestor of crown hominoids, with the symmetrical pattern of living apes having independently evolved several times along various hominoid lineages. The latter hypothesis is reasonable in the light of other lines of evidence indicating pervasive homoplasy in the evolution of the hominoid locomotor apparatus. Additional data from other Miocene apes would be required in order to better reconstruct the ancestral condition for the last common ancestor of various hominoid subclades, including that of chimpanzees and humans from which the earlies hominins evolved. Given current uncertainties in the ancestral condition, and the functional relationship between an asymmetrical pattern (which is probably largely ecophenotypical) and both quadrupedalism and bipedalism, caution would be required when making locomotor inferences in earliest hominins based on FNCB distribution alone.

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**Figure captions**

**Figure 1.** X-ray image of the IPS41724 proximal femur fragment. Black arrowheads point the densest (black) regions found at the femoral head and greater trochanter of the femur. These regions are associated with high mineralization that results in extremely bright (white) areas in the final CT images.

**Figure 2.** Midcoronal computed tomography (CT) sections of the IPS41724 femur obtained at: a) the industrial CT scanner of the Universidad de Burgos, Spain; b) the µCT scanner of the American Museum of Natural History, New York, USA; c) the µCT scanner of the “Abdus Salam” International Centre for Theoretical Physics, Italy; d**)** the industrial CT scanner of the Institut Català de Paleontologia Miquel Crusafont, Spain. See Table 1 for the CT settings of every scan. Vertical white lines point the location of the selected slices for this study: midneck (right) and base of the neck (left).

**Figure 3.** Midcoronal CT section showing the location of the base of neck (left vertical white line) and midneck (right vertical white line) slices used to measure the cortical bone thicknesses at the superior (SUP) and inferior (INF) cortices of the femoral neck in: a) IPS41724 (*Dryopithecus fontani*); b) IPS18800.29 (*Hispanopithecus laietanus*).

**Figure 4.** Cross-sections (top) and drawn FNCB distribution (bottom) of the femoral neck of *Hispanopithecus laietanus* (IPS18800.29; a, b) and *Dryopithecus fontani* (IPS41724; c, d), including the base of the neck (a, c) and the midneck (b, d) sections. Scale = 10 mm. Abbreviations: S = superior; I = inferior; A = anterior; P = posterior.

**Figure 5.** Different views of IPS41724, a partial proximal femur from ACM/C3-Az tentatively assigned to *Dryopithecus fontani*: a) medial; b) posterior; c) lateral; d) anterior; e) proximal; f) distal views. Abbreviations: M = medial; P = posterior. Modified from Moyà-Solà et al. (2009a).

**Figure 6.** Box-and-whisker plots comparing proportions of femoral neck cortical thickness in extant non-human primates (grouped according the locomotor groups reported in Pina et al., 2012), humans (male and female means), and the proximal femora IPS41724 (black star) and IPS18800.29 (open star). a) SUP/ INF index. b) Allometric residuals of SUP vs.INF (RES). c) Allometric residuals of SUP vs.BM (RESBM), in the case of IPS41724 and IPS18800.29 depicting the ±50% uncertainty range of BM estimates (black circles). Vertical lines represent the median, boxes the interquartile range (IQR; between the 25th and the 75th percentiles), whiskers the 1.5\*IQR for a) and b) and the extreme values for c), circles are outliers, and asterisks represent the extreme outliers. Abbreviations: VCL = vertical clingers and leapers.

**Figure 7.** Box plots comparing proportions of femoral neck cortical thickness in a selected sample of hominoids, early hominins (data from Ruff and Higgins, 2013), IPS41724 (black star), and IPS18800.29 (open star). Indices between superior and inferior cortical thickness (SUP/INF) at the mid-neck (a) and the base of neck (b) sections. Vertical lines represent the median, boxes the interquartile range (IQR; between the 25th and the 75th percentiles), whiskers the 1.5\*IQR for a) and the extreme values for b), and circles the outliers. Color codes: light brown = *Australopithecus*; dark brown = *Paranthropus*.

**Figure 8.** Schematic cladogram depicting the two phylogenetic positions for dryopithecines (including *Dryopithecus fontani* and *Hispanopithecus laietanus*) relative to extant hominoids that are more widely accepted based on the recent literature: a) stem hominids (e.g., Alba, 2012); b) stem hominines (e.g., Begun et al., 2012). The FNCB distribution pattern (symmetrical or asymmetrical) has been plotted onto the cladogram to better visualize the possible evolutionary interpretations. It is currently uncertain whether dryopithecines represent a monophyletic subclade or else a paraphyletic assemblage, so *Dryopithecus* and *Hispanopithecus* are nested in a polytomy under both hypotheses; see text for further details.

1. The term “great ape” is here applied to all non-hominin hominids (i.e., to both members of the stem lineage and members of the crown group), in agreement with a stem-based definition of this family (e.g., Alba, 2012). [↑](#footnote-ref-1)