Trabecular Analysis of the Distal Radial Metaphysis during the Acquisition of Crawling and Bipedal Walking in Childhood: A Preliminary Study

A. Colombo · N. B. Stephens · Z. J. Tsegai · M. Bettuzzi · M. P. Morigi · M. G. Belcastro · J.-J. Hublin

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Abstract In modern day populations, children following a normal pattern of development acquire independent bipedal locomotion between the ages of 9 and 18 months. Variability in the timing of this psychomotor developmental milestone depends on various factors, including cultural influences. It is well known that trabecular bone adapts to changes in biomechanical loading and that this can be influenced by alternative locomotor modes, such as crawling, which may be adopted before the acquisition of bipedal locomotion. With the onset of crawling, increased loading of the distal metaphysis of the radius, a component of the wrist, may lead to changes in trabecular bone architecture. To test this hypothesis, eight distal metaphyses of the radius of non-pathological children aged 0 to 3 years from the Bologna collection of identified skeletons were µCT-scanned at a resolution of 10.7 μm. The microarchitectural parameters of the trabecular bone (trabecular bone volume fraction, trabecular thickness, trabecular spacing, and trabecular ellipsoid factor) were quantified for the entire metaphysis and 3D morphometric maps of the distribution of the bone volume fraction were generated. Analysis of these microarchitectural parameters and the 3D morphometric maps show changes in the trabecular bone structure between 6 and 15 months, the period during which both crawling and bipedalism are acquired. This preliminary study analyzed the trabecular structure of the growing radius in three dimensions for the first time, and suggests that ontogenetic changes in the trabecular structure of the radial metaphysis may be related to changes in the biomechanical loading of the wrist during early locomotor transitions, i.e. the onset of crawling. Moreover, microarchitectural analysis could supply important information on the developmental timing of locomotor transitions, which would facilitate interpretations of locomotor development in past populations.

Keywords Trabecular bone microarchitecture · Ontogeny · Bipedal walking · Biomechanics · Cancellous bone

Résumé Dans les populations actuelles, les enfants présentant un développement normal acquièrent une marche bipède autonome entre les âges de 9 et 18 mois. La variabilité dans le rythme de l’acquisition de cette étape clé du développement psychomoteur dépend aussi de divers facteurs culturels. Il est bien connu que l’os trabéculaire réagit aux changements bio-mécaniques et que les modes de locomotion alternatifs adoptés avant l’acquisition de la bipédie (e.g. marche à quatre pattes) peuvent influencer la structure de l’os trabéculaire.
Une augmentation de la charge sur la métaphyse distale du radius, l’une des composantes de l’articulation du poignet, très sollicitée pendant la marche à quatre pattes, pourrait entraîner des changements micro-architecturaux trabéculaires associés. Pour tester cette hypothèse, huit métaphyses de radius d’enfants ne présentant aucun signe pathologique, d’âges compris entre 0 et 3 ans, provenant de la collection ostéologique de référence de Bologne, ont été microscannés à une résolution de 10,7 μm. Les paramètres microarchitecturaux de l’os trabéculaire (la fraction volumique d’os trabéculaire, l’épaisseur trabéculaire, le facteur ellipsoidal trabéculaire) ont été quantifiés sur l’ensemble de la métaphyse et des cartographies morphométriques 3D de la distribution de la fraction volumique d’os trabéculaire ont été générées. L’analyse de paramètre microarchitecturaux et des cartes morphométriques 3D a montré des changements importants dans la structure osseuse trabéculaire entre 6 et 15 mois, période pendant laquelle locomotion alternative et marche bipède sont acquises. Cette étude préliminaire a analysé pour la première fois la structure trabéculaire tridimensionnelle de radius en croissance et suggère que les changements ontogéniques de la structure trabéculaire de la métaphyse radiale pourraient être reliés aux changements biomécaniques spécifiques à l’utilisation du poignet pendant les transitions locomotrices précoces. De plus, l’analyse micro-architecturale pourrait fournir des informations importantes sur les rythmes de développement de l’acquisition locomotrice de l’enfant, ce qui permettrait d’interpréter leur développement psychomoteur dans les populations du passé.

Mots clés Micro-architecture osseuse trabéculaire · Ontogénie · Bipédie · Biomécanique

Introduction

The acquisition of bipedal locomotion is a complex psychomotor process, requiring development of both postural (e.g. standing) and dynamic (e.g. walking) motor skills. The timing of this process is influenced by both biological and cultural factors. The development of bipedal locomotion is dependent on the maturation of the central nervous system [1,2], since it relies on improved motor coordination in response to stimuli from the vestibular and proprioceptive systems and, especially, the visual system. Visual information is essential for the development of postural control [3,4], and its absence causes substantial delays in locomotor development [5]. In addition to maturation of the nervous system, motor skills improve as both muscular tone and strength increase, which, along with changes in the distribution of muscle mass, facilitate independent postural and locomotor coordination [3].

Locomotor development can be divided into a sequence of steps observed in all children [6]. An innate reflex stepping phase is the first stage in locomotor development. The subsequent stages are: head support; chest raising; sitting with and then without support; acquisition of an alternative autonomous locomotor mode (i.e. crawling); standing independently; moving with support; and, finally, independent bipedalism [6]. Provided their development is normal, children in present-day populations are able to walk independently between the age of 9 and 18 months [3,6]. A mature, adult-like gait usually develops around the age of 6 [3], although there is a great deal of both intra- and inter-individual variability in the developmental timing of locomotor transitions [7], in part due to differences among socio-cultural groups [2,5,8-10]. Child-rearing strategies differ between socio-cultural contexts, with the acquisition of independent bipedal locomotion representing the beginning of an individual’s autonomy [2]. Thus, interactions with family and friends, especially with the mother [11], the quality of emotional exchanges, the degree of encouragement to walk [3], and the learning provided [2,9] are all important factors contributing to variability in the developmental timing of locomotor acquisition.

It has been well established that trabecular bone responds to changes in biomechanical loading by modifying its structure to optimize stress resistance [12,13]. Signals of locomotor behaviour can thus be identified from the variability of the trabecular microarchitecture [14-16]. Differences between individuals at different ages, and most likely at different stages of locomotor development, could therefore lead to a more complete understanding of the impact of loading on bone development.

During foetal development, the femur and humerus have a similar trabecular structure [17], most likely because prenatal bone morphology is under stricter genetic regulation. Subsequently, during ontogeny, the trabecular structure of the humerus and femur begins to diverge as they adopt different functional roles and experience a very different biomechanical environment. This partly accounts for the wide microarchitectural variations observed between different anatomical locations in adulthood [17-21]: remodelling of the trabecular structure occurs at a rapid rate during development, and especially during the first few years of life [22]. During growth, locomotor changes lead to morphological adaptations of the bone tissue of the lower limb, with especially pronounced changes in the bony morphology of the proximal femur [23]. In contrast, the rate of change of the trabecular structure of the proximal humerus is slower than in the proximal femur and, once bipedal locomotion is acquired, the upper limb switches from assistance during locomotion to working in conjunction with the hand during complex manipulation [21,24]. However, during the developmental stages preceding independent bipedalism, especially during crawling and
standing, the distribution of loads between the limbs changes. This is especially the case for the wrist, a joint predominantly used when a child crawls [3]. The wrist is likely to experience relatively large biomechanical loads during crawling, which are lessened with the acquisition of bipedal locomotion as the upper limb is no longer used to support the weight of the body.

Considering these different factors, this preliminary study investigates the trabecular structure of the wrist, specifically that of the distal radius, to test whether its trabecular micro-architecture could reflect this biomechanical shift from crawling to independent bipedal locomotion. We hypothesize that the trabecular structure of the distal radius will be more robust as crawling begins and loading increases, while a reduction in bone robustness will be observed after the transition to bipedal locomotion, due to the subsequent decrease in locomotor loading of the upper limb.

**Materials and Methods**

This preliminary study analyzed the distal metaphysis of the radius, as a component of the wrist. Its growth cartilage contributes to 75% of the total bone length [25], and it is therefore likely to retain a record of osteological changes to the trabecular structure during the locomotor transition from crawling to independent bipedalism.

The sample included in this preliminary study includes the distal radial metaphysis of 8 children of known age and sex, aged between 0 and 3 years (Table 1), from the Bologna collection of identified skeletons [26]. The age of the individuals was chosen to encompass the period which, in European populations, spans the developmental milestones that lead to independent bipedalism. This skeletal collection is unique in that the occupation of 94% of the individuals more than 15 years of age is known, so that the socio-economic group to which they belonged can be inferred. The majority of the women were housewives, domestic workers or farmers, while most of the men were farmers, labourers, masons, woodworkers or soldiers [26]. Accordingly, the individuals selected are considered to be from a homogeneous low-to-middle socio-economic group. The left radii were analyzed for this study. However, although absolute bilateral asymmetry has been identified for the human proximal humerus during ontogeny, the asymmetry is not directional [27]. Moreover, during this period of development, it is likely that the left and right wrist joints are equally loaded. The skeletons of the individuals selected did not show any macroscopic pathological signs.

Microcomputed tomography (μCT), a non-destructive X-ray imaging technique, was used to analyze the radii; all were positioned and oriented in a uniform manner inside the μCT-scanner, with the Z-axis of acquisition parallel to the long axis of the bone. As bone is initially deposited in a grid-like structure, the most recently formed trabecular bone, located directly below the metaphyseal surface, is the least influenced by biomechanical stresses; this region was therefore excluded from scanning. The μCT-scanned area began at 5% of the bone length and stopped at 15% of its maximum length, representing a section 5 to 10 mm in thickness depending on the length of the bone. Acquisitions were performed with a laboratory system1 (Figure 1a) at the Department of Physics and Astronomy of Bologna University (Table 1) at an isometric voxel size of 10.7 μm. Tomographic reconstruction was performed with IMAGEREC research software, implementing the Filtered Back Projection algorithm in cone-beam geometry [28].

**Table 1** Sample composition and μCT acquisition parameters / Composition de l'échantillon étudié et paramètres d’acquisition microtomodensitométrique

<table>
<thead>
<tr>
<th>Sex</th>
<th>n</th>
<th>Ages (in months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>4</td>
<td>0, 15, 17, 36</td>
</tr>
<tr>
<td>F</td>
<td>4</td>
<td>6, 8, 11, 24</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>μCT acquisition parameters</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Voltage (V)</td>
<td>130 kV</td>
</tr>
<tr>
<td>Current (μA)</td>
<td>32</td>
</tr>
<tr>
<td>Filter (mmAl)</td>
<td>0.5</td>
</tr>
<tr>
<td>Exposure time (ms)</td>
<td>2250</td>
</tr>
<tr>
<td>Frames averaged</td>
<td>32</td>
</tr>
<tr>
<td>Projections</td>
<td>1200</td>
</tr>
<tr>
<td>Angle</td>
<td>360°</td>
</tr>
<tr>
<td>Pixel size (μm)</td>
<td>18</td>
</tr>
<tr>
<td>Source-detector distance (mm)</td>
<td>228.5</td>
</tr>
<tr>
<td>Source-object distance (mm)</td>
<td>135.5</td>
</tr>
<tr>
<td>Magnification</td>
<td>1.69</td>
</tr>
<tr>
<td>Scanning time (hours)</td>
<td>20</td>
</tr>
<tr>
<td>Voxel size (μm)</td>
<td>10.7</td>
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</table>

1. The μCT protocol was set to obtain the best quality from the 3D reconstruction of the volume. Thus, the Kevex microfocus X-ray tube (PSX-10 65W) was operated at its lowest power (4 W) to reduce the focal spot size to the minimum (6 μm). The X-ray detector was a CCD camera produced by Photonic Science. The CCD sensor (Kodak KAI 1100) counts 4000 x 2600 square pixels with a pixel size of 9 μm. This was coupled to a scintillator layer by means of a fibre optic plate. The CCD camera was double-cooled with a Peltier cell and liquid circulation for maximum efficiency and stability in long-term measurements. To reduce the fairly high noise, due to CCD and electronics construction at full resolution, a 2x2 binning mode (actual pixel size of 18 μm) was used. Furthermore, 32-frame averaging was used to increase the signal-to-noise ratio and obtain the best image contrast. The magnification factor in cone beam geometry was 1.69.
The reconstructed scans of the distal radius were segmented into bone and non-bone components with the Ray Casting Algorithm [29]. From the segmented scans, the trabecular and cortical tissues were separated using an in-house script for medtool v4.0 (http://www.dr-pahr.at) [30]. Here, the voxels are defined by four grey values (i.e. 0-3), corresponding to external non-bone, cortical bone, trabecular bone, and internal non-bone (Figure 1d-). Segmentation of these regions enabled analysis of trabecular bone throughout the entire metaphysis (Figure 1).

Quantitative analyses were performed on the entire inner region of the metaphysis (i.e. only voxels representing the trabeculae and internal non-bone). The trabecular bone volume fraction (BV/TV: trabecular bone volume/total volume) was quantified by superimposing a 2.5 mm grid onto the voxel data (Figure 1e), then calculating BV/TV from within a 5 mm spherical volume of interest (VOI) at each node of the grid. To visualize BV/TV distribution, the VOI results were interpolated onto a 3D tetrahedral mesh of the inner region, which was generated from the voxel data using CGAL v4.11 [31]. Colour maps were then created and displayed in Paraview 4.3 [32] (Figure 1f).

Trabecular bone variables were quantified for the entire inner region of the metaphysis, and are described in Table 2. Mean trabecular thickness (Tb.Th) and mean trabecular spacing (Tb.Sp) were quantified using medtool v4.0, following the sphere fitting method [33]. The ellipsoid factor (Tb.EF) was quantified to characterize the mean shape of the trabecular struts (i.e. along a continuum: -1 = oblate (i.e. plate-like), 0 = sphere (i.e. intermediate trabecular strut shape), 1 = prolate (i.e. rod-like) [34, 35]), using the BoneJ 1.4.2 plugin [36] for Image J 1.50 [37].

Results and Discussion

This preliminary study quantified the trabecular structure of the distal radius in individuals from birth to 3 years of age. Although each age is represented by a single individual in this cross-sectional sample, some trends were identified that demonstrate the high potential of trabecular bone analysis for reconstructing locomotor transitions.

In general, the distal metaphysis of the radius shows differences between ages in its trabecular structure during the period from birth to 3 years of age, which includes the bipedal acquisition stage, and a general trend can be observed. Specifically, BV/TV decreases during this period from 26.5% to 11.1%, Tb.Th increases from 0.108mm to 0.118mm, and Tb.Sp increases from 0.261mm to 0.583mm. As a result of the increased Tb.Sp, the trabecular network becomes less dense with increasing age, despite the increase in trabecular thickness. This pattern of change during ontogeny suggests that the trabecular structure reflects biomechanical changes. Of particular interest is the reversal of this trend for all parameters between 6 and 15 months of age (Figure 2). In present-day European populations, this age range encompasses the period during which infants begin to sit both with and without support, at 5 and 9 months old respectively; stand with the help of the hands; enter the crawling phase, at around 11 months; and finally become independently bipedal, before 15 months of age [3].

The youngest individual, a neonate (0 months old), has a higher BV/TV than all the older individuals (Figure 2), with trabecular bone distributed homogeneously throughout the metaphysis (Figure 3). Tb.Sp is lower than in all the older individuals and Tb.EF is close to 0, reflecting an imperfectly
Table 2 Definition of trabecular variables quantified in the distal radial metaphysis / Définitions des paramètres micro-architecturaux trabéculaire mesurés au niveau de la métaphyse distale du radius.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bone volume fraction</td>
<td>BV/TV</td>
<td>-</td>
<td>Bone volume / total volume</td>
</tr>
<tr>
<td>Fraction volumique d’os trabéculaire</td>
<td>-</td>
<td></td>
<td>Volume osseux trabéculaire / Volume total</td>
</tr>
<tr>
<td>Trabecular thickness</td>
<td>Tb.Th</td>
<td>mm</td>
<td>Mean thickness of trabeculae</td>
</tr>
<tr>
<td>Espacement trabéculaire</td>
<td>Tb.Sp</td>
<td>mm</td>
<td>Mean spacing between trabeculae</td>
</tr>
<tr>
<td>Ellipsoid factor</td>
<td>Tb.EF</td>
<td>-</td>
<td>Mean trabecular shape where -1 is plate-like and 1 is rod-like</td>
</tr>
</tbody>
</table>

Fig. 2 Variations of TBMA parameters according to the age of individuals (Tb.EF - ellipsoid factor, Tb.Sp - trabecular spacing, Tb.Th - trabecular thickness, BV/TV-trabecular bone volume fraction, red dashed lines highlight an important period of variation) / Variations des paramètres micro-architecturaux en fonction de l’âge des individus (Tb.EF - facteur ellipsoïde, Tb.Sp – espacement trabéculaire, Tb.Th - épaisseur trabéculaire, BV/TV - fraction volumique d’os trabéculaire, les lignes pointillées rouges mettent en évidence une période importante de variation)
defined trabecular strut shape (Figure 2). At birth, individuals are growing rapidly and a high volume of unspecialized trabecular bone is produced [18].

For individuals aged from 6 to 8 months, the trabecular structure of the radial metaphyses still has a homogeneous BV/TV distribution (Figure 3) but, despite a higher Tb.Th from 0.101 to 0.120mm than in the youngest individual, their BV/TV values subsequently decrease with increasing age. This is likely to be attributable to a smaller trabecular number with a larger Tb.Sp and the proliferation of more rod-like structures, as shown by the increase in Tb.EF (Figure 2) with age. These observations could reflect significant remodelling of the trabecular structure to reduce a biomechanically unnecessary amount of bone. This suggests that the thicker - or more biomechanically useful - trabeculae are preserved and reinforced in response to the initial changes in the loading environment, the most notable change resulting from the need to distribute and transfer body mass [38].

In the 11-month-old individual, BV/TV distribution is fairly heterogeneous. The regions with the highest BV/TV are located close to the cortex and to the growth plate, and BV/TV is relatively lower towards the centre of the metaphysis (Figure 3). In this case, compared to younger individuals, there is an increase in BV/TV, a decrease in Tb.Sp, a higher Tb.Th (Figure 2), while Tb.EF decreases to nearly 0. At this age, children are usually very mobile but not yet able to walk independently [6]. The wrists are used in both static positions (i.e. sitting or standing) and dynamic movement (i.e. crawling). The concentric organization of BV/TV could potentially reflect a reinforcement of the metaphyseal trabecular structure through the production of trabeculae of undifferentiated shape. These structural changes could highlight the capacity of bone to adapt to both support and mechanical resistance functions, and would show adaptation to a changing pattern of loading, as has been previously demonstrated [38].

Compared to younger individuals, the 15-month-old shows more heterogeneously distributed BV/TV, with the region of highest BV/TV on the medial side (Figure 3). BV/TV decreases again and Tb.Sp reaches its highest values, while Tb.Th decreases and the values for Tb.EF indicate a larger number of rod-like trabeculae as age increases (Figure 2). The microarchitectural pattern observed at this age – when independent bipedalism usually begins – could mark the potential hyper-specialization of trabecular bone within the radial metaphysis, which may be an adaptation to the biomechanical demands of crawling.

Among the three older individuals (17, 24 and 36 months of age), the regions with the highest BV/TV are localized and the overall distribution is highly heterogeneous (Figure 3), while BV/TV remains relatively low in comparison with the younger individuals and stable among these three. Tb.Sp is lower than in younger individuals and becomes quite stable between these three (Figure 2). Reduced biomechanical

![Fig. 3 Distal view of 3D maps of BV/TV distribution inside the radial metaphysis of each individual](image)
loading of the wrist with the onset of bipedalism may be reflected in the BV/TV of these older individuals. The upper limb is increasingly free of locomotor constraints and becomes specialized for other functions [24], which are likely to exert smaller loads on the wrist compared to locomotion. However, the 36-month-old individual has a slightly higher Tb.Th and a Tb.EF close to 0 (Figure 2) compared to younger individuals. This may reflect a new phase of adaptation, with changes in the use of the wrist that may be linked to changes in hand use, such as improved hand dexterity and more precise manual manipulation.

Trabecular bone may reflect locomotor behaviour [15] by responding to changes in biomechanical loading [12,13,38], for example reflecting the refinement of bipedalism with ontogenetic changes in trabecular anisotropy within the distal tibial metaphysis [20]. Therefore, we suggest that the observed differences in trabecular structure of the distal radius between individuals of different ages could reflect an ontogenetic pattern resulting from biomechanical changes initiated by the acquisition and subsequent reduction of a transitional locomotor mode (i.e. crawling) that occurs between 6 and 15 months of age.

In anthropology, previous analyses of trabecular bone ontogeny in humans have focused on the lower limb, either on the proximal femur or the proximal and distal tibia [e.g. 20,21], and three studies have analyzed the proximal humerus [18,28,39]. These studies identified a common pattern of trabecular architectural change in both the forelimb and hindlimb during ontogeny, whereby the trabecular structure is very robust at birth, with robustness decreasing until around 1-2 years of age, then increasing to reach adult-like levels during adolescence. Biomedical studies have previously explored the trabecular ontogeny of the distal radius, but due to the methodologies applied and the period of development investigated, the results cannot be directly compared with those of the present study [e.g. 40-42]. The preliminary results of this study suggest that the pattern of trabecular ontogeny of the distal radius may differ from that of other skeletal sites. The robustness of the trabecular structure decreases after birth, but peaks again (i.e. high BV/TV and high Tb.Th) between the ages of 6 and 15 months. This distinct ontogenetic pattern suggests that this anatomical region may record a locomotor signal of crawling.

It should be kept in mind that these are preliminary results and that additional research is needed to confirm these findings. In order to assess the degree of variability at each developmental stage, a larger sample would further clarify the signal identified here. Although skeletal collections including individuals of known age are relatively rare, these results would be further strengthened by including individuals from other populations. Because trabecular bone structure may be influenced by numerous factors other than direct biomechanical loading of a localized joint, this analysis would benefit from a comparison with a different anatomical site. For example, comparisons between parts of the forelimb and hindlimb, using comparable methodologies, could reflect the different loading regimes of the forelimb and hindlimb at this developmental stage. Moreover, trabecular bone analysis is often limited by the absence of a skeletal site that can be used as a control, because identifying a region of the skeleton that does not undergo biomechanical changes is a challenge. We suggest that including the cranial vault or a skeletal element from the axial skeleton, a rib or a vertebra for instance, may improve the identification of trabecular structural changes that are triggered by a changing biomechanical environment.

A few biomedical studies exist on the ontogeny of the trabecular bone microarchitecture of vertebrae [43,44] and ribs [45,46] but they cannot be used for comparison with our results because the methodologies applied and the period of development investigated are different. Comparisons of trabecular ontogeny between humans and extant apes may also reveal different ontogenetic trajectories that can be related to locomotor transitions.

We predicted that trabecular structure would reflect behavioural changes related to the acquisition of bipedal locomotion, and therefore selected individuals of known age from the transitional stage prior to crawling and independent bipedalism. Our results suggest that this approach could help to detect differences in trabecular bone microarchitecture between individuals, related to biomechanical changes caused by the locomotor transition. Although males and females differ slightly in the timing of these developmental stages [6], it is generally accepted that before adolescence, there are no significant differences in trabecular structure between the sexes [18,19]. The skeletons of the individuals analyzed here showed no pathological signs of abnormal growth or dietary deficiency (e.g. vitamin D, iron) that could have affected their physical and psychomotor development [47,48]. Furthermore, the provenance of the individuals in the study sample is constrained both chronologically (all died in 1901) and geographically (city of Bologna, Italy), so that the sample is from a single biologically and culturally homogeneous population [26].

Child care is socially and culturally defined, and the socio-cultural environment during childhood has a major effect on the timing of psychomotor development [6]. Daily stimulation and increased social interaction, with parents and other individuals, accelerates psychomotor development, as has been shown in Malian and Korean populations in which children are able to walk at the mean age of 9 months [10]. Moreover, the influence of this socio-cultural context is dominant whether in rural or urban areas, with consequences for early independent bipedalism across different African countries [49] even if the nutritional status is unfavorable [8].

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Conclusions

This preliminary study has quantified, for the first time, the trabecular structure of the human distal radius during the first years of development, a time during which there are notable changes in biomechanical loading. Morphometric maps of bone distribution were generated for the first time for an ontogenetic series of human individuals of known age. Although further investigations are necessary to confirm the findings presented here, the results suggest that the trabecular structure of the distal radial metaphysis holds potential for the identification of signals of locomotor transitions during growth. As the age of acquisition of bipedalism in a normal developmental context (i.e., good health status, adequate nutrition and absence of developmental stressors) is largely influenced by cultural factors, trabecular bone analysis may provide important insights into the developmental timing of locomotor changes during early locomotor transitions and support interpretations of psychomotor development in past populations. For example, Neolithization led to significant changes in lifestyle (from nomadism to sedentism, from hunter-gatherers to farmers), redefining human cultures and certainly affecting the timing of developmental changes. Trabecular analysis would thus make it possible to understand the impacts of cultural practices on the biology of the individual. Finally, the analysis of microarchitectural signals of locomotor changes in young extant primates, together with studies on brain evolution, could potentially inform cultural interpretations concerning modern humans and provide additional insights into ontogenetic processes and their patterns during hominid evolution.

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