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Cortical bone mapping: An application to hand and foot bones in hominoids

Distribution topographique de l'os cortical : une application aux os de la main et du pied chez les hominoïdes

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ABSTRACT

Bone form reflects both the genetic profile and behavioural history of an individual. As cortical bone is able to remodel in response to mechanical stimuli, interspecific differences in cortical bone thickness may relate to loading during locomotion or manual behaviours during object manipulation. Here, we test the application of a novel method of cortical bone mapping to the third metacarpal (Mc3) and talus of *Pan*, *Pongo*, and *Homo*. This method of analysis allows measurement of cortical thickness throughout the bone, and as such is applicable to elements with complex morphology. In addition, it allows for registration of each specimen to a canonical surface, and identifies regions where cortical thickness differs significantly between groups. Cortical bone mapping has potential for application to palaeoanthropological studies; however, due to the complexity of correctly registering homologous regions across varied morphology, further methodological development would be advantageous.

RÉSUMÉ

Mots clés :
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La forme d'un os reflète simultanément le profil génétique et l'histoire comportementale d'un individu. L'os cortical est capable de remodelage en réponse à des stimuli mécaniques. Les différences interspécifiques dans l'épaisseur de l'os cortical peuvent donc être corrélées avec la charge mécanique exercée durant la locomotion ou la manipulation d'objets. Ici, nous présentons l'application d'une méthode novatrice pour cartographier la distribution de l'os cortical du troisième métacarpien et du talus chez *Pan*, *Pongo* et *Homo*. Cette méthode permet d'analyser l'épaisseur corticale sur toute la longueur de l'os et est applicable à tous les éléments osseux ayant une morphologie complexe. En outre, cette méthode permet de recaler chaque spécimen sur une surface canonique et d'identifier les régions où l'épaisseur

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corticale diffère significativement entre les groupes. Ce procédé peut être appliqué à des études paléoanthropologiques. Cependant, du fait de la complexité du recalage correct des régions homologues, des progrès méthodologiques futurs sont envisagés.

1. Introduction

Identifying skeletal variables that relate to functional patterns is essential for reconstructing the behaviour of extinct species. However, it is often unclear which morphological features are most functionally relevant, as some researchers focus on novel, derived features, with the intention of understanding evolutionary change, while others are interested in the entire morphological complex of features, aiming to reconstruct the way in which a species lived (Ward, 2002). This is a common problem in palaeoanthropology, and has led to differing interpretations of skeletal morphology in fossil hominins (e.g., Latimer, 1991; Stern, 2000; Ward, 2002). In this debate, more plastic morphological features that can adapt in response to an individual's behaviour are of critical importance.

As cortical bone is able to remodel during life in response to mechanical load – a concept known as bone functional adaptation – it has the potential to hold a signal of an individual's behaviour (see Ruff et al., 2006, and references therein). Bone adapts to loading in several ways, for example by increasing/decreasing mineralisation to adapt its stiffness, changing shape to alter load transmission, or increasing thickness (Currey, 2003, 2010). However, this is a complex process that is likely to vary depending on skeletal location and systemic factors such as age, hormones and genes (e.g., Lovejoy et al., 2003; Pearson and Lieberman, 2004). Moreover, individual factors such as the magnitude and frequency of strain and the previous loading history of the bone cells can also affect cortical remodelling (e.g., Frost, 1987; Pearson and Lieberman, 2004; Ruff et al., 2006). Experimental studies are not always able to demonstrate that bone structure is well adapted to withstand strains (Demes et al., 1998, 2001; Lieberman et al., 2004) or that bone morphology changes in the expected way (Wallace et al., 2015a). However, in general, studies have shown that cortical bone is able to respond to behaviour during an individual's lifetime (Carlson and Judex, 2007; Christen et al., 2014; Robling et al., 2002; Ruff et al., 2006), and thus analysis of cortical bone thickness holds potential for reconstructing behaviour in extinct species.

Within palaeoanthropology, numerous studies have investigated how cortical bone properties relate to behaviour in both extant and fossil taxa. These can be broadly separated into three methodologies:

- analysis of cross-sectional geometric properties either at midshaft or at several points throughout the length of the shaft (e.g., Carlson, 2005; Carlson et al., 2006, 2008; Davies and Stock, 2014; Marchi, 2005; Ruff, 2002, 2008; Ruff et al., 2013, 2015; Sarringhaus et al., 2005; Shaw and Stock, 2013);
- generating 2D colour maps of cortical thickness throughout the diaphysis, with potential for application to non-cylindrical, irregularly shaped elements, although as yet this has only been tested on tooth roots, and not the epiphyses of long bones (e.g., Bondioli et al., 2010; Jashashvili et al., 2015; Puymerail, 2013; Puymerail et al., 2012a, 2012b);
- analysis of bone profiles at the articular surfaces, some of which include both cortical bone and also the underlying trabecular structure (Carlson et al., 2013; Mazurier et al., 2010; Patel and Carlson, 2007).

These analyses have been conducted using both clinical and micro-computed tomography (microCT) (e.g., Lillie et al., 2015). Several studies have focused specifically on cortical bone of the hands (e.g., Lazenby, 1998; Marchi, 2005) and feet (e.g., Griffin and Richmond, 2005; Jashashvili et al., 2015; Marchi, 2005). Recent studies that have analysed cortical bone thickness identified subtle differences both between African apes and modern humans, and between modern and fossil *Homo* species (Jashashvili et al., 2015; Puymerail, 2013; Puymerail et al., 2012a, 2012b).

Here, we investigate the potential applications of a novel method of cortical thickness analysis, developed for medical research, which allows for statistical comparison between groups (Poole et al., 2011, 2012; Treece et al., 2010, 2012). The main advantage of this method is that, unlike previous methods, it allows measurement of cortical bone thickness throughout the entire bone, i.e., including the diaphysis, metaphysis and epiphyses, and as such is applicable to both long bones and to more complex elements. Moreover, in contrast to existing methods, which require registration to a 2D map (e.g., Bondioli et al., 2010), it enables generation of 3D colour maps for each taxon/group, as well as quantification and visualization of regions whose difference in cortical thickness between groups can be assessed for statistical significance.

We test the application of this method on comparative samples of hand (third metacarpal) and foot (talus) bones of extant hominoids and, in order to test the applicability of this method in specimens with taxonomic alteration, one early Holocene human (Arene Candide 2, third metacarpal). As the hands and feet are the direct contact between an individual and the substrate, they are likely to experience the initial forces of both locomotion and object manipulation. As such, the skeletal elements in these regions are likely to reflect loading from these behaviours. However, many bones of the hands and feet, particularly carpals and tarsals, have irregular and complex shapes. As such, existing methods of analysis may not be applicable because complex bones cannot be modelled as simple beams and

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