Journal of Human Evolution 67 (2014) 60–75

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Micro-finite element (μFE) modeling of the siamang (*Symphalangus syndactylus*) third proximal phalanx: The functional role of curvature and the flexor sheath ridge

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A R T I C L E I N F O

Article history:
Received 21 January 2013
Accepted 10 December 2013
Available online 2 February 2014

Keywords:
Cortical bone
Trabecular bone
Cancellous bone
Phalangeal curvature
Locomotor
Hominoid

A B S T R A C T

Phalangeal curvature is a commonly used morphological feature for the interpretation of extant and fossil primate locomotor behaviour. Here, we build on a recent biomechanical study (Richmond, 2007) in two ways: first, we use a 3D micro-FE model, which models the real internal microstructure (i.e., cortical thickness and trabecular bone structure) and, second, we model four siamang third proximal phalanges. We test identical 2D homogenized FE models and two 3D micro-FE phalanx models that are mathematically straightened to isolate the biomechanical significance of curvature. We further investigate how varying the loading configuration (e.g., boundary constraints) and modeling (e.g., 2D versus 3D) affects the biomechanical behaviour of the phalanx. Finally, we examine how intraspecific variation in external and internal bony morphology affects the biomechanical behaviour of the phalanx.

Simulation results demonstrate that the general pattern of strain and displacement is similar between the 3D micro-FE and 2D homogenized FE models but the absolute values differ substantially. The biomechanical behaviour of the 3D FE models more closely match the relative strain patterns from the validation experiment than the 2D homogenized FE models, indicating the 3D microstructure model is preferable. Varying the loading configuration can have dramatic effects on the biomechanical behaviour of the phalanx depending on individual morphology, but overall a cantilevered beam model is an equally valid, if not better, configuration for modeling the phalanx as other previously-proposed models. Variation in flexor ridge morphology has a substantial effect on phalanx strain; the taller the ridge, the less strain incurred by other regions of the palmar shaft. Finally, phalangeal curvature reduces overall strain experienced by the phalanx, but does not necessarily reduce bending or increase the compression-to-tension ratio. These results confirm the adaptive role of phalangeal curvature during flexed-finger grasping postures and demonstrate that modeling variation in cortical thickness and flexor ridge morphology improves the behaviour of the FE model, which has important implications for the functional interpretation of phalanx form.

Introduction

Phalangeal curvature is a morphological feature commonly considered to be a good indicator of function and locomotion in the primate hand and foot (e.g., Napier and Davis, 1959; Oxnard, 1963; Tuttle, 1969; Marzke, 1971; Stern et al., 1995; Jungers et al., 1997; Richmond, 1998). Arboreal primates, especially those that often engage in suspension or brachiation, have strong longitudinal curvature of the phalanges compared with more terrestrial primates (e.g., Tuttle, 1969; Preuschoft, 1973; Susman, 1979; Rose, 1988; Stern et al., 1995; Richmond, 1998; Deane and Begun, 2008). The degree of phalangeal curvature has been shown to respond to mechanical stimuli throughout ontogeny; primates that are more arboreal as juveniles than as adults show less curvature in

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0047-2484/$ – see front matter
http://dx.doi.org/10.1016/j.jhevol.2013.12.008

adulthood (Richmond, 1998). Thus, curvature of the phalanges is often used for reconstructing fossil primate locomotor behaviours (e.g., Napier and Davis, 1959; Marzke, 1983; Begun, 1993; Hamrick et al., 1995; Jungers et al., 1997; Moyà-Solà et al., 2004; Almécija et al., 2007, 2009).

Richmond (2007) tested the biomechanical role of phalangeal curvature using finite element (FE) modeling of the strongly-curved manual third proximal phalanx of a siamang (*Symphalangus syndactylus*). Richmond demonstrated that in a suspensory, flexed-finger hand posture, curvature lowered overall bone strain, reduced bending, but increased the compression-to-tension ratio. These results offer a clear biomechanical explanation for the link between phalangeal curvature and degree of arboreality in primates (Richmond, 2007). Richmond's study provided the first in vivo test of previous theoretical models (Preuschoft, 1970, 1973) as to why strong phalangeal curvature would be "more efficient" (Oxnard, 1973: 129) and reduces stress experienced by the fingers (Preuschoft, 1970, 1973). As such, Richmond's analysis contributes greatly to our understanding of the functional significance of phalangeal curvature and to our confidence in using this feature to reconstruct behaviour in fossil primates.

There are different ways to model bone in FE analysis. Many studies, including Richmond (2007), employ a two-dimensional (2D), homogenized, isotropic FE model, in which the entire bone is modeled as a homogeneous matter, with the same material properties and same structural orientation (e.g., Weinans et al., 1992; Richmond, 2007; Gíslason et al., 2010). In these FE models, variation in cortical thickness and trabecular structure is not considered. However, cortical bone and trabecular bone behave differently at the macroscopic level due to their differences in porosity and architecture (Martin et al., 1998; Curry, 2002) and thus it is ideal to include this mechanical variation within an FE model. With increased availability to high-resolution microtomography (microCT), powerful computers and modeling software, 3D FE analyses incorporating variation in internal bony structures are now becoming more common (e.g., Müller and Rüegsegger, 1995; van Rietbergen, 2001; Strait et al., 2005; MacNeil and Boyd, 2008; Pahr and Zysset, 2009). Such models can represent the entire bone in detail, thus providing the data needed for better understanding the functional roles of cortical bone versus trabecular bone, and the variation in these structures throughout the bone (van Rietbergen, 2001; Strait et al., 2005). Understanding the biomechanics of bone structure at this level can be particularly informative in intraspecific or interspecific comparisons when the external morphology may be broadly similar.

Here, we create 2D homogenized and 3D isosurface-based, micro-FE models of four siamang (*S. syndactylus*) third proximal phalanges. The 3D micro-FE models directly incorporate variation in the cortical and trabecular bone structure. To our knowledge, this is the first time a primate phalanx has been modeled to this level of structural detail. We conduct three different sets of analyses, varying how the phalanx is modeled (i.e., 2D versus 3D FE models and curved versus straight) and the loading configuration (i.e., using different loading conditions and boundary constraints) to both compare our study directly with the results of Richmond (2007) and to further build upon this work.

In the first analysis, we make direct comparisons to Richmond's (2007) study by creating 2D homogenized FE models of two siamang phalanges using an identical loading regime to that used by Richmond (2007). With this comparative analysis, we investigate the effects of individual variation of external morphology on the biomechanical behaviour of a 2D FE phalanx model.

In the second analysis, we test how variation in the loading configuration, the type of modeling (i.e., 2D versus 3D) and the phalanx morphology affects the biomechanical behaviour of the phalanx. There are multiple ways in which the proximal phalanx can be modeled and loaded, balancing the constraints of FE modeling with the actual biology in different ways. Therefore, we create 2D homogenized FE and 3D micro-FE models to test the effects of (Analysis 2a) different loading configurations and (Analysis 2b) modeling of the internal microstructure. We also create 3D micro-FE models of all four siamang proximal phalanges using the same loading configuration to further investigate (Analysis 2c) how individual variation in the external and internal morphology affects the biomechanical behaviour of the phalanx.

Finally, in the third analysis, we create a mathematically-straightened 3D micro-FE model of two siamang phalanges (using the same loading configuration as in Analysis 2c) to investigate how curvature affects the biomechanical behaviour of the phalanx when both variation in cortical and trabecular bone structure are considered.

Through these analyses, we test the hypothesis that modeling the internal microstructure in 3D will provide a more accurate model of the biological behaviour by yielding relative strain patterns that are more similar to the results of Richmond's (2007) validation experiment than the 2D homogenized FE models. Using the 3D micro-FE models of curved versus mathematically-straightened phalanges, we test the same hypotheses outlined and supported by Richmond (2007) regarding the biomechanical role of phalangeal curvature: (1) bone strain will be lower in the curved phalanx relative to the straight phalanx, and (2) phalanx curvature will reduce bending but increase the compression-to-tension strain ratio. We further investigate the biomechanical consequences of variation in external and internal phalanx morphology.

Material and methods

Sample

Four naturally-articulated *S. syndactylus* hands from the Berlin Museum für Naturkunde were used for this analysis (Table 1, Fig. 1). The hands had dried naturally, preserving some soft tissue and a complete or almost complete third ray (Table 1). All specimens were obtained from wild-shot individuals and exhibited no external signs of pathology or trauma. All specimens were considered adult based on complete epiphyseal fusion of the external morphology throughout the hand and associated skeleton. CT scanning revealed, however, that two specimens (ZMB 38573 and ZMB 38587) preserved a faint epiphyseal line in the trabecular structure of the proximal base of the phalanx (Table 1, Fig. 1).

The articulated hands were scanned with a high-resolution industrial BIR ACTIS 225/300 microCT scanner at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. All specimens were scanned with an acceleration voltage of 130 kV and 100 μA using a 0.25 mm brass filter. Because scan resolution is dependent on the geometry of the object and the hands varied in their dried, articulated position, voxel size ranged from 38.15 to 55.49 μm (Table 1). Each image was reconstructed as a 2048 × 2048 16-bit TIFF image stack from 1250 projections with two-frame averaging. Each bone of the third ray (third metacarpal through to the third distal phalanx) was cropped from the image stack using AVIZO 6.3® (Visualization Sciences Group, SAS) and further processed separately. The Ray Casting Algorithm (Scherf and Tilgner, 2009) was used to segment the bone from each image stack. Following segmentation, data were converted into 8-bit binarized image stacks in RAW format.