Interpretation of variant morphological patterns in the hallucal cuneometatarsal joint

Scott E. BURNETT^{1*}, D. Troy CASE²

¹*Comparative Cultures Collegium, Eckerd College, 4200 54th Avenue South, St. Petersburg, FL 33711, USA*

²*Department of Sociology and Anthropology, North Carolina State University, Campus Box 8107, Raleigh, NC 27695-8107, USA*

Received 25 February 2014; accepted 30 June 2014

Abstract First cuneometatarsal joints are normally characterized by a single articulating facet. In some cases, however, they may bear some degree of division into two, or even three, distinct facets. Typically, double facets at this joint are interpreted as evidence of partial or complete division of the medial cuneiform earlier in development, though evidence to support this interpretation is limited. The purpose of this study was to examine the relationship between double facets and bipartition by comparing the sex ratio in double-faceted medial cuneiforms from two Euro-American skeletal samples, with the unbalanced sex ratio found in cases of complete bipartition of the medial cuneiform. Upon examination, no statistically significant differences were found in double-facet frequency between females and males, and the sex ratio differed significantly from that seen in known cases of bipartite medial cuneiform. These results suggest that the existence of double facets distally on the medial cuneiform is likely not exclusively indicative of developmental bipartition, a conclusion also supported by reports of divided distal surfaces in non-bipartite medial cuneiforms in some prenatal specimens. Furthermore, medial cuneiforms bearing three facets distally to the first metatarsal sometimes occur, possibly more frequently in individuals of advanced age. Ultimately, understanding distal facet patterns on the medial cuneiform may hold significance for understanding joint mobility and susceptibility to hallux valgus deformity in hominins from both bioarchaeological and paleoanthropological perspectives.

Key words: double facets, medial cuneiform, bipartition, tarsometatarsal joint

Introduction

Anatomists, bioarchaeologists, and paleoanthropologists have often interpreted double-faceted first cuneometatarsal joints as evidence of partial bipartition of the medial cuneiform earlier in development, or as indicative of synostosis of an originally bipartite medial cuneiform (Holtby, 1916; Jeyasingh et al., 1981; Ajmani et al., 1984; Anderson, 1998; Jashashvili et al., 2010). However, little support has been presented for the contention that double-faceted medial cuneiforms are closely linked to bipartition in this way. The purpose of this paper is to evaluate the assumption that double-faceted medial cuneiforms are indicative of bipartition. Specifically, we test for a sex bias in the occurrence of double-faceted medial cuneiforms to see if it matches the pattern recently documented in cases of complete bipartition (Burnett and Case, 2011). In addition, we examine sample frequencies and novel patterns of medial cuneiform facet variation that bear on the purported relationship between first cuneometatarsal joint facet pattern and development.

Background

The morphology and orientation of the first cuneometatarsal joint has received much recent attention from anthropologists due to its role in hallucal mobility and the implications for understanding habitual positional and locomotor patterns in hominoids, including the origins of bipedality in fossil hominins (e.g. Gomberg, 1981; Latimer and Lovejoy, 1990; Deloison, 1992; Berillon, 1999; Harcourt-Smith, 2002; Zipfel, 2004; McHenry and Jones, 2006; Proctor, 2010; Tocheri et al., 2011). Relative to other extant African hominoids, humans tend to have less joint curvature between the medial cuneiform and first metatarsal (Gomberg, 1981; Harcourt-Smith, 2002; Proctor, 2010) and a dorsoplantar elongation of a more anteroposterior facing joint (Volkov, 1904; Gomberg, 1981; Berillon, 1999; Harcourt-Smith, 2002). These characteristics, among others, are associated with the adducted hallux in humans and the concomitant loss of opposability of this digit (Gomberg, 1981; Aiello and Dean, 1990; Latimer and Lovejoy, 1990).

The actual outline of the facet between the human first metatarsal and medial cuneiform is variable but frequently reniform, or kidney-shaped (Figure 1A), with a concave lateral border and a convex medial border (Zipfel, 2004; Sarrafian and Kelikian, 2011). In some individuals, possibly even most, the facet is constricted both medially and laterally resulting in partially separate dorsal and plantar facet

* Correspondence to: Scott E. Burnett, Eckerd College, 4200 54th Avenue South, St. Petersburg, FL 33711, USA.
E-mail: burnetse@eckerd.edu

Published online 11 October 2014
in J-STAGE (www.jstage.jst.go.jp) DOI: 10.1537/ase.140630

Figure 1. (A) Single facet on the distal surface of a medial cuneiform, (B) a double facet on the distal surface of a medial cuneiform, (C) a cleft dividing the proximal facet of a medial cuneiform, (D) a distal view of two medial cuneiforms with the three-facet pattern exhibiting variation in facet size and orientation.

portions (Singh, 1960; Ajmani et al., 1984). Occasionally, a double facet occurs when the dorsal and plantar facets are completely divided by the presence of a distinct ridge or a non-articular strip or cleft (Figure 1B), which may occur with or without constriction of the medial border (Singh, 1960). In cases with a transverse ridge dividing the proximal articular facet of the first metatarsal, the resulting dorsal and plantar surfaces form two separate concavities (Singh, 1960), which are not oriented parallel to each other (ElSaid et al., 2006).

Double facets at the hallucal cuneometatarsal joint may be noted in skeletal remains studied in both bioarchaeological (e.g. Anderson, 1998) and paleoanthropological contexts (e.g. Jashashvili et al., 2010), though their presence is variable. For example, within the hominin fossil record clear double facets occur in the *Australopithecus afarensis* specimen AL 333-54 from Hadar (Latimer and Lovejoy, 1990), but not in the nearby and contemporaneous BRT-VP-2/73c remains from Burtele locality 2 in the Woranso-Mille study area (Haile-Selassie et al., 2012). Double facets are also present on the recently described first metatarsal base from Drimolen, provisionally assigned to *Paranthropus robustus* (Vernon, 2013), and in a *Homo erectus* first metatarsal (D3442) from Dmanisi. In the latter case, the cause appears

to be a bipartite medial cuneiform (D4111a/b) attributed to the same individual (Jashashvili et al., 2010), though it is still unclear whether development of the medial cuneiform, or other factors, are responsible for the hallucal cuneometatarsal joint morphology in other hominin remains.

While difficult to distinguish solely from photographs, a side-by-side comparison of proximal MT1 facets across hominoids, including extant and fossil hominin specimens (Figures 6.1 and 6.2 in Proctor, 2010) suggests that great variation exists in peripheral invagination of the hallucal cuneometatarsal joint facet, its location, and the degree to which the articular surface is divided into two clear facets. Potential intra- and inter-specific variation in first tarsometatarsal facet patterns hold possible implications for understanding the development of the foot in fossil hominins (Jashashvili et al., 2010), the reconstruction of habitual behavior in hominoids (e.g., Tocheri et al., 2011) and even the predisposition to foot pathology in modern humans (Mason and Tanaka, 2012).

Bipartite medial cuneiform

Bipartition of the medial cuneiform is a congenital variant of the foot typified by separation of the medial cuneiform into both plantar and dorsal segments. Division of the

cartilaginous anlage for the medial cuneiform has been documented in human embryos and fetuses (Trolle, 1948; Gardner et al., 1959; Čihák, 1972), though in varying frequency. In a sample of 184 embryos and fetuses, Gardner et al. (1959) uncovered a single case of bipartition. Most other studies find similarly low rates (Barlow, 1942; Trolle, 1948), while some suggest the presence of non-chondrified tissue dividing the cuneiform is more frequent during prenatal development (Čihák, 1972).

Jashashvili et al. recently depicted the two suggested developmental pathways that may result in bipartition (Figure 8 in Jashashvili et al., 2010). The first involves separation of the mesenchymal primordium of the medial cuneiform into plantar and dorsal parts, a division that then persists through chondrification and ossification. The second developmental pathway involves a single undivided mesenchymal primordium and subsequent cartilaginous anlage for the medial cuneiform, followed by either a single or double ossification center. The cartilaginous anlage bearing a single ossification center becomes a normal medial cuneiform, while those with two ossification centers either result in a bipartite medial cuneiform, or a normal medial cuneiform if the two centers united during ossification (Jashashvili et al., 2010). These alternate pathways may help explain why the two medial cuneiform segments are joined together by a bridge of cartilage, fibrous tissue, or fibrocartilage (O'Neal et al., 1995; Azura and Sakellariou, 2001; Chiodo et al., 2002), in most cases, but not all. In the skeleton, the union is evident by roughening and/or pitting located in the center or distal half of the interarticular facet, often slightly lateral to the midline (Burnett and Case, 2011).

Our recent meta-analysis of all known cases of bipartite medial cuneiform reveals frequencies of less than 1% in large anatomical and archaeological samples (Gruber, 1877; Pfizner, 1896; Burnett and Case, 2011), and slightly higher rates of up to 2.4% documented in embryological/fetal samples (Trolle, 1948). Bipartite medial cuneiforms exhibit a moderate to high rate of bilateral occurrence (65.2–81.8%) and most known cases (82.5%) occur in males (Burnett and Case, 2011).

Medial cuneiforms may also exhibit partial bipartition, a term preferable to incomplete bipartition since the absence of serial radiographs prevents distinguishing between bipartition that is never completed and complete bipartition that later forms a partial synostosis (Burnett and Case, 2011). Medial cuneiforms with double facets, particularly in the presence of a crease or cleft between the two facets, are frequently interpreted as partial bipartition or fusion of an originally bipartite medial cuneiform (Smith, 1866; Banchi, 1906; Holtby, 1916; Barclay, 1932; Böker, 1935; Böker and Müller, 1936; Barlow, 1942; Anderson, 1987; Dastugue and Gervais, 1992; Anderson, 1998; Jashashvili et al., 2010). This contention is supported by several published cases (e.g. Gruber, 1877; Banchi, 1906) with complete bipartition on one side and partial bipartition on the other.

Two different types of non-bipartite medial cuneiforms are thought to be related to bipartition (Jashashvili et al., 2010). The first is characterized by the existence of clefts or creases along the medial and lateral surfaces where the division between plantar and dorsal parts occurs in complete

bipartition. Partial bipartition has also been suggested as an explanation for the presence of double facets on each face of the medial cuneiform-first metatarsal joint (e.g. Holtby, 1916; Jeyasingh et al., 1981; Ajmani et al., 1984), either with or without the existence of joint surface clefts/creases, or other hints of bipartition. To date, little support has been presented for the contention that double-faceted first cuneometatarsal joints without evidence of clefts or creases are closely linked to bipartition.

Materials and Methods

Visual examination for double facets was restricted to the distal facet of medial cuneiforms. The distinction between partially separate and distinctly double facets is somewhat subjective (Zipfel, 2004). For our analysis, double facets were only noted as minimally present when peripheral invagination resulted in two facets with a complete ridge, ring, or cleft between them. It is conceivable that complete synostosis of a previously bipartite medial cuneiform could be scored, using these criteria, as a double facet. However, bipartite medial cuneiform frequencies in large studies are low (typically under 1%), and complete synostosis is likely to only occur in a small fraction of cases. As a result, we feel that any such occurrences would have a negligible effect on our results.

Data were collected on two skeletal samples (Table 1). The first consisted of 502 individuals (229 females, 273 males) from medieval Danish church cemeteries from the main peninsula of Jutland and the adjacent island of Funen to the east. Detailed information about the individual samples and their composition can be found in Case (2003). A sample of 401 Euro-American skeletons (201 female, 200 male) was also analyzed from the Robert J. Terry Collection, a large series of skeletons from individuals who died in the St Louis area during the first half of the 20th century (Hunt and Albanese, 2005).

Statistical examination was conducted on the sex distribution of medial cuneiforms with a distal double facet for the first metatarsal. For each sample, a two-tailed Fisher's exact test ($\alpha = 0.05$) was used to test for sex-related frequency differences between males and females. In addition, the sex ratios of those exhibiting double facets were statistically

Table 1. Medial cuneiform bipartition and facet patterns

		Single facets	Double facet	Complete bipartition	Total sample
Terry Collection	Females	191	10 ^a	0	201
	Males	187	13 ^a	0	200
					401 ^b
Medieval Danish	Females	212	17	0	229
	Males	259	12	2	273
					502 ^c

^a Includes an individual counted as partial bipartition in Burnett and Case (2011).

^b Excludes two non-Euroamericans from sample in Burnett and Case (2011).

^c Excludes four individuals with less reliable sex information from Burnett and Case (2011).

compared with the sex ratio previously documented in cases of complete bipartition of the medial cuneiform (Burnett and Case, 2011).

Results and Discussion

Double facets were identified in 7.4% (17/229) of females and 4.4% (12/273) of males from Denmark, for a total sample frequency of 5.8%. In the Terry Collection, 23 (5.7%) out of 401 individuals exhibited a double facet at the medial cuneiform-first metatarsal joint, with 6.5% (13/200) of males and 5.0% (10/201) of females affected. Two-tailed Fisher's exact tests indicate no statistically significant frequency differences ($\alpha = 0.05$) between females and males (Danish sample: $P = 0.18$; $1 - \beta = 0.31$; Terry Collection $P = 0.53$; $1 - \beta = 0.10$). Accordingly, the null hypothesis is accepted for both the Terry Collection and Danish samples—males and females exhibit the same frequencies of double-faceted medial cuneiforms. The same is not true for the sex ratio of bipartite medial cuneiforms (82.5% male; 17.5% female) (Burnett and Case, 2011), which differs significantly from the sex ratio found in double-faceted medial cuneiforms from both the Danish ($P < 0.001$; $1 - \beta = 0.97$) and Terry ($P = 0.023$; $1 - \beta = 0.67$) samples.

If a close relationship exists between double-faceted medial cuneiforms and bipartition, then a similar sex ratio would be expected, particularly since some completely bipartite cuneiforms may undergo synostosis later. However, our data on double-faceted medial cuneiforms did not uncover a male bias. Accordingly, at least some double facet cases are unlikely to be minor forms of bipartition. An alternative way to interpret the statistically insignificant preponderance of females with double facets in Denmark is that females are more likely to exhibit one end of a continuum, double facets, while males are more likely to actually exhibit bipartition at the other end of the continuum. Although possible, additional support for such a continuum is currently lacking.

Further evidence that double facets alone are not sufficient to diagnose bipartition is the dearth of double facets on the medial cuneiform facet for the navicular in the absence of true bipartition. When the medial cuneiform is bipartite, both the navicular and first metatarsal regularly show doubled facets. However, Holtby (1916) found no double facets on the proximal articular surface of the medial cuneiform or on the corresponding navicular facet, even though he identified double facets on 7% of first metatarsals ($n = 84$) and the distal surface of the medial cuneiform (Holtby, 1916). All subsequent studies have confirmed the paucity of double facets at the naviculo-cuneiform I joint relative to the first cuneometatarsal joint (Barlow, 1942; Jeyasingh et al., 1981; Ajmani et al., 1984), indicating that double facets are frequently absent on the proximal surface of the medial cuneiform, even in individuals with double facets distally. The greater propensity for double facets on the distal end of the medial cuneiform could indicate that bipartition begins distally rather than at the proximal surface, though medial cuneiforms with proximal clefts (Figure 1C) and single facets distally do occur. This proposal is also difficult to reconcile with the distal location of non-osseous bridging that

occurs between the plantar and dorsal portions in bipartite medial cuneiforms (Burnett and Case, 2011). The consistent location of these lesions, evident in all but a few cases, suggests that the distal half of the medial cuneiform may be less prone to segmentation embryologically.

Aside from the low frequency (<1.0%) found in a combined sample of native South Africans (Zipfel, 2004), double-faceted first cuneometatarsal joints comprise between 4 and 7% of most samples, well above the frequencies of bipartition seen in studies of prenatal development. The largest prenatal study of pedal defects is that on Danish embryos and fetuses by Trolle (1948). Twelve bipartite cuneiforms were included in his final sample of 500 feet (2.4%), the highest sample frequency known (Burnett and Case, 2011). Prenatal samples such as that studied by Trolle are likely to contain a higher proportion of individuals with congenital anomalies since many were unviable and were spontaneously miscarried. Indeed, in addition to the highest known rate of bipartite medial cuneiforms, Trolle's sample also contains significantly higher rates of infrequent forms of tarsal coalition (Burnett and Case, 2005) when compared to Euro-American samples of anatomical or archaeological specimens (Burnett and Wilczak, 2012; Case and Burnett, 2012). Since bipartition does not develop after the embryonic/fetal transition, the frequency of complete bipartition of the medial cuneiform in adults is very unlikely to exceed the high frequency seen in Trolle's fetal samples. As a result, many, and probably most, medial cuneiforms with a double facet distally cannot represent complete bipartition that has undergone synostosis, since the frequencies are already higher than the upper limit set by prenatal analysis, and they lack a double facet proximally.

It has already been established that medial cuneiforms displaying distal facets for the first metatarsal separated by a groove do not necessarily indicate bipartition earlier during development. Barlow (1942) inspected the distal facet morphology in the medial cuneiforms of 26 fetuses and embryos between 2 and 7 months of developmental age. Two exhibited grooves in the anterior facet identical to that found in an adult skeleton (Barlow, 1942), which would be interpreted by many authors as evidence of incomplete fusion between the halves of an originally bipartite cuneiform, or an absence of total union between two distinct ossification centers in a single cartilaginous template. Neither need be true, as Barlow correctly notes "If this were true, such a groove would not be found in the cartilaginous stage but instead there should be bipartition" (Barlow, 1942: 110). In other words, distinct double facets can occur distally without bipartition in either the cartilaginous or ossified medial cuneiform, or in the presence of double ossification centers.

In addition, during larger-scale research on congenital variation in the skeletons of 20th century indigenous South Africans in the Raymond Dart Collection (Burnett, 2005), three individuals (A1239, A1383, A2318) were found to bear three facets on the distal aspect of the medial cuneiform for articulation with the corresponding first metatarsal (Figure 1D). In each case, the three facets consist of a large dorsal facet and two facets on the plantar half of the joint. The third (lateroplantar) facet is the smallest of the three and exhibits variation in shape (round to oval). All three cases

were bilateral and only one individual exhibited a cleft dividing the proximal facet of the medial cuneiform. None exhibited any evidence of clefting that could be interpreted as tripartition of the medial cuneiform. Indeed, we are unaware of any published examples of tripartite medial cuneiforms embryologically or otherwise. The three faceted pattern at the hallual cuneometatarsal joint has not been described in the literature until recently noted in a study on facet forms and hallux valgus (Mason and Tanaka, 2012).

In research on hallux valgus deformity, a disorder characterized by lateral deviation of the hallux, Mason and Tanaka (2012) identified a correlation with facet patterning at the hallual tarsometatarsal joint. They classified the joint as unifacet, bifacet, or trifacet in 41 dissected feet. Surprisingly, the bifacet pattern, defined and depicted by the authors as a distinct double facet, was most frequently encountered with 18 instances (43.9%), followed by the trifacet pattern in 16 feet (39.0%). Unifacets were only identified in 7 of 41 feet (17.1%). Interestingly, hallux valgus deformity decreased in frequency as facet number increased, with the condition identified in all seven feet (100%) with a unifacet and 12 (66.7%) of 18 feet with bifacets. Hallux valgus was not encountered in any of the 16 feet with the trifacet pattern, leading the authors to conclude that it restricts the joint hypermobility that some believe to be a precipitating factor (Carl et al., 1988; Klaue et al., 1994). The rarity of the unifacet pattern, often noted as one of the most frequently occurring patterns at the hallual tarsometatarsal joint (Singh, 1960; Jeyasingh et al., 1981; Ajmani et al., 1984; Zipfel, 2004) is surprising, as is the high rate of trifacets. The cadaver sample studied by Mason and Tanaka (2012) consists exclusively of elderly individuals with a range of 66–104 years of age (mean = 86 years), an age profile that is likely to differ from many, if not most, archaeological and anatomical samples. The association of hallux valgus, an age-progressive deformity (Nix et al., 2010), with facet number at the first cuneometatarsal joint and alongside the high frequencies of double and triple facets at the joint in the elderly sample studied by Mason and Tanaka (2012), warrants further investigation. These results may imply remodeling of the joint during adulthood.

Collectively, the data suggest that facet patterns on the medial cuneiform may be partly related to other factors aside from bipartition, including joint mechanics. A parallel may be found in the double facet at the atlanto-occipital joint, an infrequent variant in humans (Berry and Berry, 1967). The occipital condyle develops from the exoccipital and, to a lesser extent, the basioccipital (O’Rahilly et al., 1983). Though the condyle forms from two separate units during development, a single facet is most common at the atlanto-occipital joint and the location of the non-articular strip between the facets in bipartite condyles does not correspond well with the unbalanced contribution of the exoccipital and basioccipital.

Similar to the first cuneometatarsal joint facets, superior facets of the atlas are variable but often elongated oval-shaped or reniform surfaces, frequently including peripheral invaginations and/or transverse grooves partitioning the joint surface either partially or completely (Paraskevas et al., 2008). A recent study of the superior atlas facets revealed

that partial and complete partitioning occurs much more commonly in individuals 60–79 years of age (33.3% and 25.0% respectively) relative to individuals 20–39 years of age (8.3%, 4.1%; Paraskevas et al., 2008). The difference in morphology by age is statistically significant (Paraskevas et al., 2008), and likely caused by long-term conversion of less biomechanically stressed areas of the joint into non-articular surfaces over time (Billmann et al., 2007; Paraskevas et al., 2008). Instead of envisioning bipartite occipital condyles or superior atlas facets as necessary sequelae of development, postnatal mechanical factors have also been proposed to explain this division, either in whole or part (Tillmann and Lorenz, 1978; Billmann et al., 2007). Similarly, double (or triple) facet patterns on the medial cuneiform may not be indicative of bipartition (or tripartition) during development. If true, hallual cuneometatarsal joint patterns may not accurately reflect developmental differences in the medial cuneiform among modern humans. This may also be true in fossil hominins if new discoveries of medial cuneiforms document double-faceted medial cuneiforms without strong evidence of developmental bipartition. Instead, the different joint patterns in both fossil hominins and modern humans could reflect, in part, varying biomechanical factors as part of a complex suite of bipedal adaptations within individual species. It is worth noting, however, that the mean age of individuals with double facets (55.0 years) in the Terry Collection sample—the only one for which we have precise data on the age at death—is indistinguishable from those bearing a single facet (55.1 years). Accordingly, if biomechanical remodeling of the hallual cuneometatarsal joint is, in some way, related to joint facet patterns, it likely occurs at greater ages than those studied here.

Ultimately, true cases of partial bipartition are probably more conservatively defined as sharing two or more of the following characteristics: (1) distinct double facets on the distal surface of the medial cuneiform, particularly those divided by a strong ridge, crease, or cleft; (2) similar division of the proximal facet of the medial cuneiform; and/or (3) a demarcation line or furrow along the medial or lateral border of the bone (Burnett and Case, 2011). The latter feature has been noted in several partial bipartition cases including the partial case found at Poundbury (T. Molleson, personal communication), and those described by Pfitzner (1896).

Conclusion

The high rate of partially divided facets at the hallual cuneometatarsal joint suggests a propensity for double facets, and the frequency of both partially divided and completely divided ‘double facets’ greatly exceeds the frequency of medial cuneiform bipartition in embryonic and fetal samples. Furthermore, double facets do not conform to the skewed sex ratio identified in published bipartite medial cuneiform cases. As a result, caution is urged in interpreting both double facets, and potential differences in double-facet frequencies between populations or species, as indicative of developmental processes.

The triple-faceted first cuneometatarsal joint was only recently identified in clinical (Mason and Tanaka, 2012) and

skeletal analyses (this study) of humans, and has not been identified in other extant hominoids or fossil hominins to the best of our knowledge. In light of the differential orientation and curvature of multiple facets at the joint and clear association between facet number and hallux valgus (Mason and Tanaka, 2012), two- and three-faceted first cuneometatarsal joints are likely to be associated with an increasingly diminished mobility of the hallux. Currently, limited data exist on the frequency of the three-facet pattern. Due to the important grasping function of the hallux in other extant hominoids and the lack of cases in the hominin fossil record, the three-facet joint pattern may be hypothesized to be restricted to obligate bipeds, potentially exclusively in *Homo sapiens*.

Acknowledgments

We would like to thank Dr. David Hunt, Smithsonian Institution, for access and assistance with the Terry Collection and Dr. Jesper Boldsen, University of Southern Denmark, for access and assistance with the medieval Danish sample. Dr. Kevin Kuykendall and Elijah Mofokeng were instrumental in facilitating research on the Raymond Dart Collection at the University of Witwatersrand. This research was funded by grants from the US National Science Foundation (grant number 0083366); the Wenner-Gren Foundation (grant number 6670); 2000–2001 Fulbright Program; grants from the National and ASU Chapters of Sigma Xi; the Arizona State University Graduate Student Research Organization; and the ASU Department of Anthropology.

References

- Aiello L. and Dean C. (1990) *An Introduction to Human Evolutionary Anatomy*. Academic Press, New York.
- Ajmani M.L., Ajmani K., and Jain S.P. (1984) Variations in the articular facets of the adult cuneiform bones. *Anthropologischer Anzeiger*, 42: 121–126.
- Anderson T. (1987) Post-cranial Non-metric Variation: The Examination of a Neglected Subject. MA thesis, Department of Prehistory and Archaeology, Sheffield University, Sheffield.
- Anderson T. (1998) Two cases of hypoplastic hamulus from Iron Age and Roman Northamptonshire. *Journal of Paleopathology*, 10: 31–35.
- Azura K. and Sakellariou A. (2001) 'Osteosynthesis' of a symptomatic bipartite medial cuneiform. *Foot & Ankle International*, 22: 499–501.
- Banchi A. (1906) Cunéiforme I biparti: le cunéiforme comprend-il le tarsal distal du préallux. *Archives Italiennes de Biologie*, 45: 280.
- Barclay M. (1932) A case of duplication of the internal cuneiform bone of the foot (cuneiforme bipartitum). *Journal of Anatomy*, 67: 175–177.
- Barlow T.E. (1942) Os cuneiforme I bipartitum. *American Journal of Physical Anthropology*, 29: 95–111.
- Berillon G. (1999) Geometric pattern of the hominoid hallucal tarsometatarsal complex. Quantifying the degree of hallux abduction in early hominins. *Comptes Rendus de l'Académie des Sciences Series IIA*, 328: 627–633.
- Berry A.C. and Berry R.J. (1967) Epigenetic variation in the human cranium. *Journal of Anatomy*, 101: 361–379.
- Billmann F., Le Minor J-M., and Steinwachs M. (2007) Bipartition of the superior articular facets of the first cervical vertebra (atlas or C1): a human variant probably specific among primates. *Annals of Anatomy*, 189: 79–85.
- Böker H. (1935) Vergleichende biologische Anatomie der Wirbeltiere I. Gustav Fisher, Jena.
- Böker H. and Müller W. (1936) Das os cuneiforme I bipartitum, eine fortschreitende Umkonstruktion des Quergewölbes im menschlichen Fuss. *Anatomischer Anzeiger*, 83: 193–204.
- Burnett S.E. (2005) Developmental Variation in South African Bantu: Variant Co-occurrence and Skeletal Asymmetry. Ph.D. dissertation, School of Human Evolution and Social Change, Arizona State University, Tempe.
- Burnett S.E. and Case D.T. (2005) Naviculo-cuneiform I coalition: evidence of significant differences in tarsal coalition frequency. *Foot*, 15: 80–85.
- Burnett S.E. and Case D.T. (2011) Bipartite medial cuneiform: new frequencies from skeletal collections and a meta-analysis of previous cases. *Homo*, 62: 109–125.
- Burnett S.E. and Wilczak C. (2012) Tarsal and tarsometatarsal coalitions from Mound C (Ocumulgee Macon Plateau Site, Georgia): implications for understanding the pattern, origin, and antiquity of pedal coalitions in Native American populations. *Homo*, 63: 167–181.
- Carl A., Ross S., Evanski P., and Waugh T. (1988) Hypermobility in hallux valgus. *Foot & Ankle International*, 8: 264–270.
- Case D.T. (2003) Who's related to whom? Skeletal kinship analysis in medieval Danish cemeteries. Ph.D. dissertation, Department of Anthropology, Arizona State University, Tempe.
- Case D.T. and Burnett S.E. (2012) Identification of tarsal coalition and frequency estimates from skeletal samples. *International Journal of Osteoarchaeology*, 22: 667–684.
- Chiodo C.P., Parentis M.A., and Myerson M.S. (2002) Symptomatic bipartite medial cuneiform in an adult athlete: a case report. *Foot & Ankle International*, 23: 348–351.
- Čihák R. (1972) Ontogenesis of the skeleton and intrinsic muscles of the human hand and foot. *Ergebnisse der Anatomie und Entwicklungsgeschichte*, 46: 5–194.
- Dastugue J. and Gervais V. (1992) *Paleopathologie du Squelette Humain*. Société Nouvelle Des Éditions Boubée, Paris.
- Deloison Y. (1992) The anatomical study of the cuneometatarsal joint of the hallux regarded as a key element locomotion. Comparison between Australopithecus, and Homo Pan. *Comptes Rendus de l'Académie des Sciences Série 2*, 314: 1379–1385.
- ElSaid A.G., Tisdell C., Donley B., Sferra J., Neth D., and Davis B. (2006) First metatarsal bone: an anatomic study. *Foot & Ankle International*, 27: 1041–1048.
- Gardner E., Gray D.J., and O'Rahilly R. (1959) The prenatal development of the skeleton and joints of the human foot. *Journal of Bone and Joint Surgery*, 41A: 847–876.
- Gomberg D.N. (1981) Form and Function of the Hominoid Foot. Ph.D. dissertation, Department of Anthropology, University of Massachusetts, Amherst.
- Gruber W. (1877) Monographie über das Zweigtheilte erste Keilbein beim Menschen. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*, 24: 1–35.
- Haile-Selassie Y., Saylor B.Z., Deino A., Levin N.E., Alene M., and Latimer B.M. (2012) A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature*, 483: 565–569.
- Harcourt-Smith W. (2002) Form and Function in the Hominoid Tarsal Skeleton. Ph.D. dissertation, University College of London, London.
- Holtby J.R.D. (1916) Symmetrical division of the medial cuneiform bone of the foot. *Transactions of the Royal Academy of Medicine in Ireland*, 34: 185–187.
- Hunt D.R. and Albanese J. (2005) History and demographic composition of the Robert J. Terry Anatomical Collection. *American Journal of Physical Anthropology*, 127: 406–417.
- Jashashvili T., Ponce de León M.S., Lordkipanidze D., and Zollikofer C.P.E. (2010) First evidence of a bipartite medial cuneiform in the hominin fossil record: a case report from the Early Pleistocene site of Dmanisi. *Journal of Anatomy*, 216: 705–716.

- Jeyasingh P., Gupta S.C., Gupta C.D., Agarwal A.K., and Srivastava A.K. (1981) Variations in the articular facets of the adult cuneiform bones. *Indian Journal of Medical Research*, 73: 296–302.
- Klaue K., Hansen S.T., and Masquelet A.C. (1994) Clinical, quantitative assessment of first tarsometatarsal mobility in the sagittal plane and its relation to hallux valgus deformity. *Foot & Ankle International*, 15: 9–13.
- Latimer B. and Lovejoy C.O. (1990) Hallucal tarsometatarsal joint in *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 82: 125–133.
- Mason L.W. and Tanaka H. (2012) The first tarsometatarsal joint and its association with hallux valgus. *Bone & Joint Research*, 1: 99–103.
- McHenry H.M. and Jones A.L. (2006) Hallucial convergence in early hominids. *Journal of Human Evolution*, 50: 534–539.
- Nix S., Smith M., and Vicenzino B. (2010) Prevalence of hallux valgus in the general population: a systematic review and metaanalysis. *Journal of Foot and Ankle Research*, 3: 21.
- O’Neal M.L., Ganey T.M., and Ogden J.A. (1995) Fracture of a bipartite medial cuneiform synchondrosis. *Foot & Ankle International*, 16: 37–40.
- O’Rahilly R., Müller F., and Meyer D.B. (1983) The human vertebral column at the end of the embryonic period proper: 2. The occipitocervical region. *Journal of Anatomy*, 136: 181–195.
- Paraskevas G., Papaziogas B., Tzaveas A., Natsis K., Spanidou S., and Kitsoulis P. (2008) Morphological parameters of the superior articular facets of the atlas and potential clinical significance. *Surgical and Radiologic Anatomy*, 30: 611–617.
- Pfützner W. (1896) Beiträge zur Kenntnis des Menschlichen Extremitätenskelets. VII. Die Variationen in Aufbau des Fußskelets. In: Schwalbe G. (ed.), *Morphologische Arbeiten*. Gustav Fischer, Jena, pp. 245–527.
- Proctor D.J. (2010) Three-dimensional Morphometrics of the Proximal Metatarsal Articular Surfaces of Gorilla, Pan, Hylobates, and Shod and Unshod Humans. Ph.D. dissertation, Department of Anthropology, University of Iowa.
- Sarraffian S.K. and Kelikian A.S. (2011) Osteology. In: Kelikian A. (ed.), *Sarraffian’s Anatomy of the Foot and Ankle*, 3rd edn. Lippincott Williams & Wilkins, Philadelphia, pp. 40–119.
- Singh I. (1960) Variations in the metatarsal bones. *Journal of Anatomy*, 94: 345–350.
- Smith T. (1866) A foot having four cuneiform bones. *Transactions of the Pathological Society of London*, 17: 222–223.
- Tillmann B. and Lorenz R. (1978) The stress at the human atlanto-occipital joint. 1. The development of the occipital condyle. *Anatomy and Embryology*, 153: 269–277.
- Tocheri M.W., Solhan C.R., Orr C.M., Femiani J., Frohlich B., Groves C.P., Harcourt-Smith W.E., Richmond B.G., Shoelson B., and Jungers W.L. (2011) Ecological divergence and medial cuneiform morphology in gorillas. *Journal of Human Evolution*, 60: 171–184.
- Trolle D. (1948) Accessory Bones of the Human Foot: A Radiological, Histo-Embryological, Comparative Anatomical, and Genetic Study. Munksgaard, Copenhagen.
- Vernon D.S. (2013) A Morphometric Analysis of the Phalanges and a Fragmentary First Metatarsal from the Drimolen Hominin Site, South Africa. MA thesis, University of Johannesburg, Johannesburg.
- Volkov T. (1904) Variation squelettiques du pied chez les primates et dans les races humaines. *Bulletin et Mémoires de la Société Anthropologique de Paris*, Series 5, 5: 201–331.
- Zipfel B. (2004) Morphological Variation in the Metatarsal Bones of Selected Recent and Pre-pastoral Humans from South Africa. Ph.D. dissertation. University of Witwatersrand, Johannesburg.