Mathematical analysis of trabecular ‘trajectories’ in apparent trajectorial structures: The unfortunate historical emphasis on the human proximal femur

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Abstract

Wolff’s “law” of the functional adaptation of bone is rooted in the trajectorial hypothesis of cancellous bone architecture. Wolff often used the human proximal femur as an example of a trajectorial structure (i.e. arched trabecular patterns appear to be aligned along tension/compression stress trajectories). We examined two tenets of the trajectory hypothesis; namely, that the trabecular tracts from the tension- and compression-loaded sides of a bending environment will: (1) follow ‘lines’ (trajectories) of tension/compression stress that resemble an arch with its apex on a neutral axis, and (2) form orthogonal (90°) intersections. These predictions were analysed in proximal femora of chimpanzees and modern humans, and in calcanei of sheep and deer. Compared to complex loading of the human femoral neck, the chimpanzee femoral neck reputedly receives relatively simpler loading (i.e. temporally/spatially more consistent bending), and the artiodactyl calcaneus is even more simply loaded in bending. In order to directly consider Wolff’s observations, measurements were also made on two-dimensional, cantilevered beams and curved beams, each with intersecting compression/tension stress trajectories. Results in the calcanei showed: (1) the same nonlinear equation best described the dorsal (“compression”) and plantar (“tension”) trabecular tracts, (2) these tracts could be exactly superimposed on the corresponding compression/tension stress trajectories of the cantilevered beams, and (3) trabecular tracts typically formed orthogonal intersections. In contrast, trabecular tracts in human and chimpanzee femoral necks were non-orthogonal (mean ~70°), with shapes differing from trabecular tracts in calcanei and stress trajectories in the beams. Although often being described by the same equations, the trajectories in the curved beams had lower $r^2$ values than calcaneal tracts. These results suggest that the trabecular patterns in the calcanei and stress trajectories in short beams are consistent with basic tenets of the trajectory hypothesis while those in human and chimpanzee femoral necks are not. Compared to calcanei, the more complexly loaded human and chimpanzee femoral necks probably receive more prevalent/predominant shear, which is best accommodated by non-orthogonal, asymmetric trabecular tracts. The asymmetrical trabecular patterns in the proximal femora may also reflect the different developmental ‘fields’ (trochanteric vs. neck/head) that formed these regions, of which there is no parallel in the calcanei.

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1. Introduction and historical background

“By wondering about what mathematical rules bone architecture might be the answer to, we do not learn anything useful at all. The key to information is in the metabolic process of bone production and maintenance.” (Huiskes, 2000, p. 154)

Anisotropic patterns in the trabecular architecture of cancellous bone are commonly used to infer local loading history in extant and extinct animals (Black, 2004; Cheal et al., 1987; Fajardo and Muller, 2001; Herrera et al., 2001; Macchiarelli et al., 1999; Martínón-Torres, 2003; Oxnard
Numerous authors (e.g. Bertram and Swartz, 1991; Brand) form orthogonal (90°) intersections. The seeds of the trajectorial hypothesis were planted in 1866 when the notable engineer and mathematician Karl Culmann suggested to the anatomist G.H. von Meyer that arched trabecular patterns in a sagittally sectioned human first metatarsal and calcaneus appear to be aligned along principal stress directions engendered by functional loading (Rittmann, 1992; Thompson, 1917, 1943; von Meyer, 1867). Evidently, Culmann drew an analogy between these trabecular patterns and the stress trajectories of a short, cantilevered beam illustrated in his textbook “Die Graphische Statik” (“Graphical Statics”) (Culmann, 1866) (Figs. 1 and 2). Culmann and von Meyer also compared the trabecular architecture in a coronally (frontally) sectioned human proximal femur to the mathematically constructed stress trajectories of a curved crane-like beam that resembled a human femur (without trochanters) loaded in single-legged stance (see Appendix A for further discussion of the origins of Culmann’s ‘crane’). Notably, the arched trabecular patterns in the von Meyer femur do not form orthogonal intersections as they clearly do in the human proximal femur. The interpretation that the trabecular arches in this bone follow the ‘lines’ of tension and compression stresses is still common in contemporary literature (Bagi et al., 1997; Barbieri and Buoncristiani, 1975; Baumgaertner and Higgins, 2002; Beck et al., 1990; Berquist and Coventry, 1992; Brown and DiGioia, 1984; Bullough and Vigorita, 1984; Chapman and Zickel, 1988; Cowin, 1984; Elke et al., 1995; Fazzalari et al., 1989; Finlay et al., 1991; Fox, 2003; Ganev and Ogden, 1998; Gibson and Ashby, 1997; Greenspan, 1988; Herrera et al., 2001; Kapandji, 1987; Kawashima and Uthoff, 1991; Kerr et al., 1986; Kerr and Bishop, 1986; Knote Tate, 2003; Koval and Zuckerman, 2002; Kyle, 1994; Laroche et al., 1995; Laros, 1990; Lim et al., 1999; Lotz et al., 1995; Maquet, 1985; Markolf, 1991; Martini, 1995; Miller, 1996; Miller et al., 2002; Moore, 1985; Mourtada et al., 1996; Neville, 1993; Oatis, 2004; Osborne et al., 1980; Radin et al., 1992; Resnick and Niwawayma, 1988; Rosenthal and Scott, 1983; Schatzker, 1984, 1991; Sinclair and Dangerfield, 1998; Tachdjian, 1990; Van Auwadercke and Van der Perre, 1994; Vander Sloten and Van der Perre, 1989; Venieratos et al., 1987). However, recent authors who have reviewed the historical and/or current use of the trajectorial hypothesis in this context suggest that principal tension and compression stresses or strains do not play a proximate causal role in the formation of these distinctive trabecular patterns (discussed later) (Carter and Beaupré, 2001; Cowin, 2001; Hall, 1985; Huiskes, 2000; Huiskes et al., 1981; Kriz et al., 2002; Roesler, 1981).
Culmann ‘crane’ (compare these drawings in Fig. 1). To our knowledge, however, von Meyer, did not mathematically analyse the course of apparent ‘tension’ and ‘compression’ curvilinear trabecular patterns, and did not further rigorously consider the implications of the non-orthogonal intersections that he illustrated in this drawing of a human proximal femur (Loër and Weigmann, 1992; Zippel, 1992).

Recognizing this discrepancy—with what he perceived to be orthogonal trabecular patterns in his own proximal femoral sections—Wolff admonished von Meyer for not drawing the femoral trabecular patterns “correctly” (Wolff, 1869; this paper was not illustrated). In contrast to von Meyer’s femur drawing (Fig. 1), Wolff’s composite illustration of 1870 shows orthogonally intersecting trabecular arches in a diagrammatic drawing of a coronally sectioned human proximal femur (Fig. 3).1 Wolff, convinced that the similarities between trajectories in Culmann’s ‘crane’ and the arched trabecular patterns in the human proximal femur could not be coincidental, hypothesized that “…the direction and pattern of loading influences, and/or controls, the pattern of the trabecular framework”—hence the origin of Wolff’s emphasis on “mathematical laws” (i.e. that there is a direct mathematical relationship between bone form and skeletal loads) (Bertram and Swartz, 1991; Zippel, 1992).2 Wolff (1892)

Fig. 1. von Meyer’s (1867) composite illustration shows the Culmann ‘crane’ and sections of various human bones with stylized arching trabecular patterns. According to Ruütimann (1992, p. 14), the original figure legend reads: This graphic gives a modification of the curved crane that Prof. Culmann had designed [see Fig. 3 of the current study] under his control with the intention of approximately imitating the shape of the upper end of the femur and the transverse section of the neck and presuming the same wide strain as the head of the femur receives from the socket. (Reproduced from the original with permission of Walter de Gruyter, Berlin, Germany. 1992. Text chapter by Ruütimann In Wolff’s Law and Connective Tissue Regulation. p. 15. Fig. 1).

Fig. 2. Culmann’s (1866, Fig. 107, p. 236) short, cantilevered beam with stress trajectories. This beam is reproduced in several of Wolff’s works (e.g. 1870, 1892, 1986). (Reproduced with the permission of Springer-Verlag, Berlin).

1The provenance of Wolff’s (1870) early illustration of the femur as trajectorial structure has been confused in recent literature. For example, Wolff’s trajectorial femur (see drawing of it in Fig. 3) has been erroneously attributed to G.H. von Meyer (e.g., see Cowin, 1986, 1989b, 2001; Huiskes, 2000; Miller et al., 2002). Thompson (1917, p. 682) also made the same error, but he later corrected it (Thompson, 1943, p. 978). Other authors have re-drawn the Culmann ‘crane’ with non-orthogonal trajectories apparently to resemble those of von Meyer’s femur (Thomason, 1995).

2See the Appendix A for the “proofs” that Wolff offered in support for the trajectory hypothesis in explaining the functional/causal relationships of the arched trabecular patterns in the cancellous bone architecture of the femoral neck.
also suggested that in some cases predominant patterns of trabecular orientation could be ‘transformed’ by alterations in loading patterns (e.g. in a malunited femoral neck fracture, or in an ankylosed knee), and that, in equilibrium, preferred trabecular patterns represent the ‘average’ loading regime experienced by a bone region (Bertram and Swartz, 1991; Pauwels, 1976). Wolff’s contemporaries, typically publishing in German, contested the trajectory hypothesis primarily on their observations of non-orthogonal intersections of cancellous bone trabeculae in various bones (Albert, 1900a; Bähr, 1899; Büdinger, 1903; Solger, 1899; Zschokke, 1892). Despite these contemporary objections and abundant subsequent descriptions of bones exhibiting non-orthogonality (Albert, 1900b; Carey, 1929; Jansen, 1920; Murray, 1936; Triepel, 1922), the apparent mathematical validation by the American anatomist J.C. Koch (1917) seems to have established the palatability of this idea in the English-language literature, which persists in many contemporary investigations and textbooks (Chapman and Zickel, 1988; Elke et al., 1995; Ganey and Ogden, 1998; Kapandji, 1987; Koval and Zuckerman, 2002; Lanyon, 1973, 1974) used in vivo strain measurements on sheep calcanei to show the first ‘clear example’ of the close correspondence between arched trabecular patterns and orientations of principal strains (Bouvier, 1985; Currey, 1984) (Fig. 4). He described this bone as a cantilevered-beam-like structure that typically experiences a relatively simple loading regime exhibiting two quasi-parabolic-shaped trabecular tracts that intersect to form the shape of an arch. Recording strains from rosette gauges attached directly to the bone, Lanyon determined that during ambulation the ‘…principal compressive strain coincided with the trabeculae in the dorsal tract and the principal tensile strain with those in the plantar tract’ (Lanyon, 1973, p. 166). These data have been corroborated in a recent ex vivo study using simulated loading of deer calcanei with up to seven rosette strain gauges on each bone (Su, 1998; Su et al., 1999). Additionally, in these
Several investigators have telemetrically measured in vivo forces imparted to hip endoprostheses during typical ambulatory activities (Bergmann et al., 2001; Davy et al., 1988; Hodge et al., 1986; Rydell, 1966). But using indirect measurements to infer habitual strain distributions are confounded by several variables including the perturbation of the normal loading environment caused by intramedullary loading and altered muscle mechanics. Biewener et al. (1983) provide a poignant example of how indirect or incomplete analyses of a bone’s strain environment can lead to erroneous conclusions about its predominant loading environment. Aamodt et al. (1997) have reported the only in vivo strain measurements on the human proximal femur that we are aware of. In this study one rosette strain gauge was placed laterally on the inferior aspect of the greater trochanter in two adult patients. The data showed that in nearly all loading regimes (e.g. two-legged stance, one-legged stance, walking, and stair climbing) the absolute magnitudes of tensile strain significantly exceeded compressive strain. Such measurements suggest that this region of the femur is subjected to bending and that “…no functional lateral tension band or medially directed force is sufficient to outweigh the bending moment imposed by the joint force” (Aamodt et al., 1997, p. 931).

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compared to orthogonal trabecular intersections, non-orthogonal intersections may represent a more optimal design for accommodating shear stresses that are presumably prevalent in the human femoral neck. In contrast to the human proximal femur, the principal trabecular tracts with orthogonal intersections have been described in calcanei of deer, sheep, and potoroo (Biewener et al., 1996; Skedros and Brady, 2001). In view of these data, it has been suggested that there may be significant differences in the biophysical stimuli and the developmental ‘fields’ that mediate the construction of the curvilinear trabecular patterns in these disparate bone types (Kriz, 2002; Kriz et al., 2002). If mechanical stimuli are significant in the development of the cancellous architecture of these bones, then the differences in trabecular patterns may be related to the notable differences in the relative complexity of their habitual loading: complex multi-directional/multi-axial loading of the human proximal femur vs. relatively simple uni-axial bending of the artiodactyl calcaneus (Kalmey and Lovejoy, 2002; Ryan and Ketcham, 2005a; Skedros et al., 2002). The present study evaluates the trajectorial hypothesis in the context of this dichotomy.

Since the origin of Wolff’s trajectory hypothesis can be traced to Culmann’s short, cantilevered beam (Fig. 2) (Roesler, 1981), we examined adult artiodactyl (sheep and deer) calcanei, which generally appear to be a natural paradigm in this context. Trabecular patterns in adult chimpanzee and human proximal femora were also examined because of their putative disparate loading conditions (human: predominantly compression and torsion; chimpanzee: predominantly bending) (Kalmey and Lovejoy, 2002; Skedros et al., 1999). Analysis of trabecular architecture in these disparate loading conditions may help to clarify the applicability of Wolff’s trajectory hypothesis in skeletal biology and advance our understanding of the mechanisms that are involved in forming and maintaining some anisotropic trabecular patterns in various mammalian bones. Trabecular patterns or stress trajectories in other femora or femur-like structures (e.g. Culmann’s ‘crane’, Culmann’s Fairbairn crane, von Meyer’s femur, and Koch’s femur) (Figs. 5 and 6) that have played an important role in the origin and/or perpetuation of Wolff’s trajectory hypothesis are also evaluated in these comparative contexts. Our intention is to preserve the historical perspective of the often accepted, but inadequately contested, functional analogies drawn between Culmann’s crane or cantilevered beam, the additional trajectorial structures, and the actual femora and calcanei. This approach exposes shortcomings of the trajectorial paradigm that have been evasive—only some bones or bone regions subject to specific loading conditions will exhibit what might be considered trajectorial patterns. By design the present study therefore utilized two-dimensional analysis and equations that could have been used by Wolff or his contemporaries. Limitations of using this approach are also discussed and three-dimensional analyses are proposed that will be subsequently conducted on the bones used herein.

We hypothesize that the arched trabecular patterns in adult artiodactyl calcanei (Fig. 4) will correlate with what would be expected if functional bending loads actually mediated their formation along ‘tension/compression’ trajectories. In this context it is predicted that:

1. these arched trabecular patterns can be exactly superimposed on the arched tension/compression stress trajectories in mathematically constructed, short, cantilevered beams (Fig. 7), and
2. the paired quasi-parabolic trabecular tracts in these calcanei and the paired quasi-parabolic stress trajectories in the mathematical beam models will be defined by the same nonlinear equation.

Based on suggestions that the human proximal femur notably differs from a trajectorial structure, we further hypothesize that:

3. the nonlinear equations that best describe the arched trabecular tracts in the human femoral neck will differ from those that best describe the trabecular tracts in the relatively simply loaded calcanei.
4. the trabecular tracts in the chimpanzee femoral neck will differ from those in the human femoral neck and those in the chimpanzee will more strongly resemble those in the relatively simple bending models (the calcanei and short cantilevered beams).

In contrast to the femoral neck regions, it is hypothesized that:

5. the arched trabecular tracts in the trochanteric regions of these two anthropoid femora will have arched trabecular patterns, reflecting adaptations expected in an environment where bending is relatively more prevalent (i.e. symmetric and orthogonal trabecular tracts).

Fig. 5. (A) Culmann’s (1866, Fig. 1 of Plate 11) illustration of a Fairbairn type of crane, which is a freestanding, curvilinear tower crane designed by Sir William Fairbairn (see “Fairbairn vignette” in the Appendix A). This type of crane is referred to in Culmann’s (1866) text in a chapter with the above illustration (a portion of the original plate), which is attributed to Besard. But there is evidence that this engineer (or engineering student) did not have an important role in drawing the stress trajectories in the Culmann ‘crane’ that is illustrated in von Meyer (1867) and Wolff (1870, 1892) (see further discussion in the Appendix A). The tracts indicated with bold and dashed lines and labeled as 1(a,b), 2(a,b), and 3(a,b) (added here) were used in the present study. The intersection of each curve pair is indicated with a bolded dot. As shown by the inset drawing (added here), θ indicates the locations where angle measurements were made. The trajectories toward the free end of Culmann’s ‘crane’ and the Fairbairn crane are not superimposable (compare Figs. 1 and 5). As argued in the Appendix A, this provides additional evidence suggesting that different engineers (Culmann’s students/associates) were involved in the creation of these two drawings. (Modifications made on the original drawing include our addition of the bold and dotted lines and the corresponding symbols.) (B) A Fairbairn crane that can still be seen on the harbor in Bristol, England (reproduced with permission from the original photograph of Alan Goodship, © 2003, All rights reserved).
2. Methods

2.1. Specimen preparation and radiographic analysis

One calcaneus from each of 11 adult male, domesticated sheep (*Ovis aries*; breed is crossed Suffolk/Hampshire and Rambouillet) and 11 adult male, wild Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) were dissected free of soft tissue. The biomechanical ‘length’ of each bone was measured according to published methods (Skedros et al., 1994), and the “free” and “fixed” ends of the bone were considered to be 0% and 100% of this ‘length’, respectively (Fig. 4).

One femur was obtained from each of 16 adult modern Caucasian humans (mean age: 47; age range: 19–62; 8 females, 8 males) and 12 adult chimpanzees.
(Pan troglodytes) (age range: 8–39; 5 females, 5 males, 2 unspecified). All human bones were obtained using standard bone-banking techniques (Bloebaum et al., 1993), which included a pre-selection analysis of standardized roentgenograms to ensure that trochanteric and femoral neck trabecular arches (i.e. secondary and principal tensile and compressive groups, respectively) were present in accordance with Singh grade 6 (i.e. had normal appearing bone density and trabecular architecture) (Singh et al., 1970). The chimpanzee bones were from animals that had been kept in large cages with features of natural habitat. None of the humans or chimpanzees had diseases or conditions that affect the musculo-skeletal system. Soft tissues were removed from all bones with manual dissection. External morphologic parameters of all femora were quantified in previous studies (Kuo et al., 1998, 2003); the human femora had normal cervical-diaphyseal (neck-shaft) and anteversion angles. None of the bones had evidence of significant arthritis of the femoral head or condylar regions. The head and neck regions of the chimpanzee and human femora are referred to as the “free” end of these bones (Kuo et al., 1998; Ruff and Hayes, 1984).

Chimpanzee and human proximal femora were radiographed in internal rotation, so that the proximal femur was in neutral (0°) anteversion (Fig. 8). The bone was placed on the film cassette (fine-detail extremity film) (Kodak Ektascan M Film, Eastman Kodak Company, Rochester, New York), supported with modeling clay in the oriented position (Kuo et al., 1998, 2003; Ruff and Hayes, 1983) and the X-ray beam was focused at the base of the neck (anterior-to-posterior projection, 62–69 kV, 4 mAs, and 101.6 cm source-to-cassette distance).

Using the orientation procedures described by Kuo et al. (1998, 2003) and Ruff and Hayes (1984), the proximal aspect of five femora from each species were also radiographed with the posterior condyles flat, which placed the proximal femur in its natural anteversion. Roentgenograms were also obtained after rotating these five bones 5° and 10° in both internal and external rotation (0° rotation is considered the “condyles flat” position). As discussed below, these additional roentgenograms were used to determine potential sources of error in determining trabecular trajectories.

Finally, radiographs were obtained of a 5 mm-thick section, centered on the mid-coronal plane, which was cut from each femur. To make this section, two cuts were made parallel to the mid-coronal plane (each cut was 2.5 mm from the mid-coronal plane) with the femoral neck in neutral anteversion (i.e. the section was made in the plane of the head and neck; hence, with respect to this portion of the proximal femur this section was coronal) (Backman, 1957). As cutting progressed the direction of sectioning was slightly adjusted (externally rotated) in the area of the neck base so that the trochanteric region was also cut in the true coronal plane; this was done to minimize parallax and projection-effect errors when determining trabecular patterns in roentgenograms in this location (Kothari et al.,...
(1998), and also allowed for one complete section from each bone for subsequent radiographic analysis.

Three independent observers, who were blinded to the objectives of the study, examined all roentgenograms of cut and un-cut femora to determine: (1) if one or more arched trabecular patterns could be detected in the areas of interest, and (2) if arched trabeculae, when present, exhibited a visually obvious point of intersection at the arch apex. Results of this analysis revealed up to six (50%) chimpanzee bones and three (19%) human bones in which arched and/or intersection trabecular patterns could not be readily detected in roentgenograms of intact (un-cut) chimpanzee and human bones. By contrast, there was only one instance (one human bone) where one of the three observers could not detect arched/intersecting tracts in roentgenograms of the same bones.

Fig. 8. (A) Anterior-to-posterior roentgenogram of a thin-sectioned human proximal femur used in the present study. The section was made with the bone in internal rotation, which places the proximal femur in neutral (0°) anteversion. The outline drawing of femur on the right shows arched trabecular tracts that were used in the present study. θ indicates the locations where angle measurements were made. (B) Anterior-to-posterior roentgenogram of a thin-sectioned chimpanzee proximal femur used in the present study. The section was made with the bone in internal rotation, which places the proximal femur in neutral (0°) anteversion. The outline drawing of femur on the right shows arched trabecular tracts that were used in the present study. θ indicates the locations where angle measurements were made.

Similar comparisons were made between roentgenograms of cut and un-cut calcanei. This was done using 5 mm-thick mid-sagittal sections of contralateral deer and sheep calcanei (n = 5 from each species). Each of these calcanei was radiographed (before and after being cut) in the medial-to-lateral projection with the beam focused on 50% bone ‘length’. In contrast to the femora, trabecular arches in cut and un-cut calcanei could be exactly superimposed in all cases, and the three independent observers invariably identified arched/intersecting trabecular patterns in roentgenograms of all bones.

As noted, pilot studies were also conducted to establish the margin of error when determining arched trabecular patterns using roentgenograms of the proximal femora in neutral rotation [posterior condyles flat with whole-bone orientation in accordance with Kuo et al. (1998, 2003), and Ruff and Hayes (1983)], and with 5° external rotation and 5° internal rotation. As described above, this analysis was also done to determine whether roentgenograms of whole proximal femora or sectioned proximal femora should be used in the present study. Results showed that the equations (described below) in trochanteric and femoral neck regions that were obtained from ±5° rotated, un-cut, whole femora were identical in the corresponding regions of the same bones radiographed in neutral rotation. In contrast, ±10° rotation caused changes to occur in several arch pairs in both the human and chimpanzee femora.
These findings suggest that there is an acceptable margin of error (± 5°) when orienting a femoral specimen for radiographing and, hence, subsequent sectioning. This issue may be most relevant in bones with deficient posterior condyles (e.g., arthritic changes) or when only the proximal portion is available (neither of these conditions occurred in the present study).

2.2. Obtaining traces of trajectorial and trabecular arches

One pair of arched intersecting trabeculae in the roentgenograms of each calcaneus and two pairs in each coronally sectioned femur were traced onto a plastic sheet with a fine-point marker. In each femur one pair of trabecular tracts was selected such that their intersection occurred in the region between the mid-neck to sub-capitus (the “neck region”), and one pair was selected such that its intersection was between the vertical (superior–inferior) distance from the proximal aspect of the calcaneus to the inferior base of the lesser trochanter (the “lesser trochanteric region” or “trochanteric region”) (Fig. 8). In each calcaneus, one pair of trabecular tracts was selected such that their intersection occurred between 40% and 55% of bone ‘length’ (Fig. 4).

Tracings of trabecular tracts were made in a darkened room with the assistance of an illuminated view box and magnifying lens. Using tracings magnified 4 ×, the angle (θ) formed at the apex (i.e., intersection) of each paired trabecular arch was also measured to the nearest 1° with a protractor. The angle was determined by drawing, through the intersection of the curves, two straight lines which were perpendicular to the radius of each curve (Koch, 1917, p. 253). Since the curvilinear trabecular “tracts” are in reality non-continuous, where even plate-like trabeculae have perforations, care was taken to ensure that each of the selected tracts exhibited at least 90% continuity along its analysed length.

The traced trabecular tracts (two tracts, or “curves”, in each arched pair) were digitized and assigned Cartesian coordinates (Digitize-Pro 4.1®, Dr. Y. Dannon, Arad, Israel), which were subsequently used to determine the top-five best-fit equations for these data (Table Curve™ 2D v4, Jandel, San Rafael, CA). The resolution of the digitizing process provided 90 points/cm. One of the two curves from each pair was rotated and inverted so that it followed the same course as its paired curve (i.e., could be exactly, or closely, superimposed on the opposing tract). This was done to reduce error associated with the digitization process. Further explanation of this process is given below in the section on axis definitions (see below). Similar tracings and analyses were conducted on paired stress trajectories in analogous regions of the trajectorial structures and bone drawings (Figs. 4–7). In contrast to the orthogonally end-loaded cantilevered beams, two non-orthogonally loaded beams from Pauwels’ text (1976) were analysed (Fig. 7D). These beams were included since they might have trajectorial patterns that more closely correspond to the trabecular arches in the femoral necks, which are also typically loaded non-orthogonal to the neck axis.

In the orthogonally loaded beams, only the stress trajectories of Roesler were examined. This is because the stress trajectories in Roesler’s beam can be exactly superimposed on the trajectories of all of the other orthogonally loaded beams (Fig. 7B and C). Tracings of arched trabecular tracts in each calcaneus and femur were examined to determine if they could be exactly, or inexacty, superimposed on the stress trajectories of Roesler’s cantilevered beams. In the calcanei the percentage of bone ‘length’ where the trabecular tracts intersect was compared to trajectories that intersected at an equivalent percent length of Roesler’s cantilevered beam.

2.3. Trajectorial analysis: axis definitions and digitization process

The procedure used to reliably obtain a best-fit equation for a curve encompasses at least 8 steps (Fig. 9). Once the desired intersecting arches are traced, they are enlarged 2 × (step 1). After being traced and enlarged, the shorter, post-intersection portion of the curves [i.e., the “short tails” cranial (femora) or distal (calcanei) aspect to intersection] are identified. The post-intersection portions are then measured from the intersection to their respective ends using a pliable wire (step 2). The shorter of the two post-intersection ‘tails’ is determined and its arc length measured. A corresponding length is measured onto the longer post-intersection tail and marked (step 3). A line is then drawn from the tip of the shorter post-intersection tail to the equal arc length mark on the longer post-intersection tail (step 4). The “x”-axis is then drawn as a line passing though the arch intersection (0,0) and forming a 90° angle with the line joining the two short tails (step 5). The y-axis is drawn as a perpendicular to the x-axis at the arch intersection (step 6). If all is done correctly the y-axis should be parallel to the line joining the post-intersection curves and should traverse the arch intersection.

To insure consistency when digitizing the curves, the positive segment of the x-axis is defined as the distance between the y-axis and the line connecting the short tails. The positive y-axis extends the same distance toward the long tail of the arch that is being digitized (step 7). Our pilot studies demonstrated that this reduces operator error in the digitization process and reliably produces a best-fit equation despite potential differences in arch orientation. To make these axis definitions the same for all curves, tracings of the other curve of each pair were inverted and rotated in order to make both curves fit the same axis definitions (step 8). In some trajectorial femora (e.g., Koch’s femur drawing, Fig. 6) there are trajectories that have obvious changes in ‘slope’ (e.g., from concave to convex or vice versa) along their length. In this instance measurements were only made on the curve extending from the superior (cranial) aspect (toward the capitus femoris) to the
approximate point at which this change in slope occurred. The selection of a portion of these curves helps to provide reliable and consistent data for regions of the curve in the area of interest. The present study only deals with the trabecular or trajectorial arches near the arch intersection; therefore, the infrequent distal changes in slope—which only occurred in some trajectorial drawings—were ignored.

Because of the longer lengths of hypothetical trajectories in the femora compared to the traceable trabecular arches in the actual femora, the trajectories were not traced from end to end. Instead, the length of the shortest post intersection tail (which was always at the superior aspect of the arch in the 'trajectorial' femora) was determined and a distance $2 \times$ of that was mapped onto the longer tail of the curve. This ensured that the lengths of trajectories in these structures were more comparable to the traceable length of trabecular curves in the actual bones. This procedure was followed in all cases except for trajectories 1a and 3a of Koch’s ‘trajectorial’ femur and 2a in von Meyer’s femur (Fig. 6) in which a distance of only $1 \times$ the shortest short tail was used. The selected arches in the lateral aspect of the trochanteric region of von Meyer’s femur also required a slight modification in the tracing process. Because these trajectories extend from the lateral intertrochanteric region to the peripheral margins of the femoral head, the superior “end” of these trajectories was considered to be the most medial trochanteric trajectory.

2.4. Additional sources of error and clarifications

Pilot studies showed that nearly identical equations were obtained for all curves in calcanei and beams, but a variety of equations were frequent in the human femora. For example, in pilot studies the equation $y^{-1} = a + b/x$ was the most prevalent equation and seemed to best fit most trabecular curves in the human bones. The congruence of the curvilinear trabecular or trajectorial tracts and their fit to this equation becomes clear on gross observation—these curves fit only a region of the curve (Fig. 10B). The observation that a traced curve fits a portion of a larger or more complex curve and that the same traced region can fit other equations with very little manipulation raises important questions about the limitations of the methods used in this study. Strict axis definition and tracing procedures (steps 1–8, above) need to be followed in order to produce a consistent equation describing curves that closely fit the tracings. Despite rigorous axis definition and tracing procedures, the Table Curve™ program at times supplied the exponential equation $y = a + b/(x/c)$ as the best fit for the traced curve. This exponential equation and the equation $y^{-1} = a + b/x$ describe functions that are very different. They are similar, however, in a small region that corresponds to the trabecular curves (Fig. 10). Unless strict axis definition procedures are followed these equations are assigned interchangeably.

Pilot studies revealed that among the myriad equations in the Table Curve™ program, the “simple equations menu” was most optimal for distinguishing differences between curves within one bone or structure. The simple equations menu also provided comparable data and a clear distinction between dissimilar curves. Other equation menus that were studied contained polynomial, rational, and curve-fit kinetic equations that produced many equations that fit many curves better than $r^2 = 0.99$. However, in most cases these curves were bizarre and/or complexly non-monotonic. Polynomial equations were only exclusively used in one instance (curve fitting in Pauwels’ beams) where the “simple equations menu” equations simply could not provide a close fit ($r^2 < 0.90$). In all cases, all curve fits were visually examined to insure that they: (1) closely fit the graphical plot, and (2) had a very high coefficient of determination (typically $r^2 > 0.97$). Additionally, plots of the residual errors were also examined to ensure that in all cases the curvilinear

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Fig. 9. Eight steps used for axis definitions; see text for descriptions.
relationship between $x$ and $y$ variables did not violate homoscedasticity assumptions (Kachigan 1986). Use of the simple equations menu also helped to avoid the assignment of erroneous equations, whilst producing comparable functions that clearly fit the traced curve.

To ensure that our methods reliably produced consistent equations, $\pm 5^\circ$ and $\pm 10^\circ$ axis rotations in both the clockwise and counterclockwise directions were also performed on traced trabecular arches in three deer calcanei, three sheep calcanei, three human femora (trochanteric and femoral neck) and three chimpanzee femora (trochanteric and femoral neck). All axis definition requirements were followed (steps 1–8) with the exception of the final axis being rotated $5^\circ$ and $10^\circ$ in both the clockwise and counterclockwise direction. Therefore, the “origin” $(0,0)$ of intersection remained the same while the axis was rotated. The $5^\circ$ rotations produced the same equations that had been originally assigned to the curves for all bones. In contrast, $10^\circ$ rotations produced a different equation in one superior trabecular tract in a human femoral neck. Upon gross examination, the equation produced by the rotations of this one curve clearly did not fit. This exception is a result of the greater length of trabecular arches in the superior aspect of the femoral neck region. When this trabecular tract was measured from its proximal tip to an arc length of only $2 \times$ that of the short tail, the equation is the same as that obtained without rotation. As shown by this result, the best-fit curve that results after $10^\circ$ rotation is not expected and is attributable to a large portion of a curving “long tail”. These results demonstrate that $\pm 5^\circ$, which is within our assessment of intra- and inter-observer error, is associated with an acceptable margin of error for determining the axes using definitions in steps 1–8.

![Figure 10](image-url)

Fig. 10. Curve fits for the two most-common equations for the traced trabecular tracts obtained from human femoral neck regions. The darkened portion of each curve represents the length of the traced trabecular tract. The equations are: (A) $y = a + b/(x^c)$, (B) $y^{-1} = a + b/x$. 
2.5. Statistical analyses for paired comparisons

A one-way ANOVA design was used to evaluate comparisons of trabecular tract intersection angles. The level of statistical significance was considered to be $p \leq 0.05$.

3. Results

Calcanei (Tables 1 and 2): All calcanei showed the presence of obvious arched trabecular tracts (Fig. 4). Supporting hypotheses 1 and 2, the dorsal (“compression”) and plantar (“tension”) trabecular tracts of all sheep and deer calcanei could be exactly superimposed on trajectories in Roesler’s beam at proportionally similar percentages of diaphyseal or beam ‘length’ (Figs. 4 and 7A). In turn, the arched trabecular patterns in the calcanei and the stress trajectories of the cantilevered beams can be described by the same nonlinear equation ($y^{-1} = a + b/x$, Table 1). Only one curve obtained from a plant calcaneal tract exhibited a relatively lower $r^2$ value ($< 0.97$).

Trabecular tract intersections in the calcanei are typically orthogonal to quasi-orthogonal (90° ± 7°; range: 70°–102°), with 90° ± 5° in 76% of arches and exactly 90° in 33% of arches (Table 2).

Human femora (Table 2): In all cases, the three independent observers recognized arched trabecular patterns and intersections in the neck of each of the (thin sectioned) human femora. However, there were two bones where one of the three investigators could not identify trabecular arch intersections in the trochanteric region. In 62.5% (10/16) of the human femoral necks, the nonlinear equations describing the inferior trabecular tracts were different from the nonlinear equations describing the trabecular tracts in the calcanei and the stress trajectories in the cantilevered beams (Table 2). Also in support of hypothesis 3, trabecular tract intersections in the human femoral necks were non-orthogonal, and these tracts also had shapes that often differed from the trabecular tracts in the calcanei and the stress trajectories in the simply loaded beams. The superior aspect of the human femoral neck varied only once (1/16) when compared to these simply loaded structures. In the human bones there were three curves (3/78) where the $r^2$ value was less than 0.97 (all three curves are from the superior (“tension”) tracts of the femoral necks); in these cases high-order polynomial functions provided a better fit of the data.

In support of hypothesis 5, all of the medial and lateral trabecular tracts in the human trochanteric region best fit the same equation that best fit the trajectories in the beams. Additionally in support of hypotheses 3 and 5, respectively, trabecular intersections in the human proximal femora are typically non-orthogonal in the neck (69° ± 12°; range: 51–90°) and typically quasi-orthogonal in the trochanteric region (92° ± 6°; range: 82–105°) ($p = 0.0001$).

Chimpanzee femora (Table 2): In all cases, the three independent observers recognized arched trabecular patterns and intersections in the neck and trochanteric regions of each of the (thin sectioned) chimpanzee femora. In 83.3% (10/12) of the chimpanzee femoral necks, the nonlinear equations describing the inferior trabecular tracts differed from the nonlinear equations describing the trabecular tracts in the calcanei and the stress trajectories in the cantilevered beams (Table 2). In contrast, the superior tracts in the chimpanzee femoral neck never varied when compared to these simply loaded structures. In the chimpanzee femora there were four curves (4/48) where the $r^2$ value was less than 0.97 (three curves in the trochanteric region and one in the superior femoral neck); in these cases high-order polynomial functions provided a better fit of the data.

In all but one chimpanzee bone (i.e. a medial trochanteric tract) the trabecular tracts from the medial and lateral trochanteric region matched the equations for the cantilevered beams. Trabecular intersections in the chimpanzees are typically non-orthogonal in the femoral neck (70° ± 12°; range: 45–85°) and obtuse in the trochanteric region (117° ± 10°; range: 100–132° ($p = 0.001$); these findings do not support hypotheses 4 and 5, respectively.

Table 1
Comparisons of best-fit equations for trajectories in: (A) beams, (B) calcanei, and (C) cranes

<table>
<thead>
<tr>
<th>Trajectorial structures</th>
<th>Mean $r^2$ values (range)</th>
<th>Mean intersection angles</th>
<th>Equations</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Beams</td>
<td></td>
<td></td>
<td>$y^{-1} = a + bx$</td>
</tr>
<tr>
<td>Roesler’s cantilevered beam</td>
<td>0.993 (0.986–0.999)</td>
<td>90°</td>
<td>100%</td>
</tr>
<tr>
<td>Pauwels’ cantilevered beam</td>
<td>0.945 (0.757–0.999)</td>
<td>90°</td>
<td>100%</td>
</tr>
<tr>
<td>B. Calcanei</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deer calcanei</td>
<td>0.993 (0.954–0.999)</td>
<td>89° ± 8°</td>
<td>100%</td>
</tr>
<tr>
<td>Sheep calcanei</td>
<td>0.995 (0.984–0.999)</td>
<td>90° ± 6°</td>
<td>100%</td>
</tr>
<tr>
<td>C. Cranes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culmann’s ‘crane’</td>
<td>0.961 (0.876–0.999)</td>
<td>88°*</td>
<td>100%</td>
</tr>
<tr>
<td>Fairbairn crane</td>
<td>0.990 (0.978–0.999)</td>
<td>90°</td>
<td>100%</td>
</tr>
</tbody>
</table>

*The intersections are 90° in two locations and 84° in one location (Fig. 4). These data show that trajectories in Roesler’s beam (Fig. 7A) can be described by the same equations for trabecular tracts in the calcanei, trajectories in one of Pauwels’ non-orthogonally loaded beams (Fig. 7, D2), and the Fairbairn crane and Culmann ‘crane’ (Figs. 3, 5, and 6).
Human and chimpanzee femora comparisons: Statistical comparisons of intersection angles between chimpanzees and humans showed the following results: (1) $p = 0.003$ for chimpanzee trochanteric vs. human trochanteric, and (2) $p = 0.8$ for chimpanzee femoral neck vs. human femoral neck.

3.1. von Meyer’s femur, trajectorial femora, and “cranes” (Tables 2 and 3)

Nearly all of the ‘trajectories’ analysed in von Meyer’s (1867), Wolff’s (1870), and Koch’s (1917) femora best fit the same nonlinear equation in the calcanei. The only exceptions were the trajectories in the inferior neck region of von Meyer’s drawing (Fig. 6). Equations in this region matched those that best fit the chimpanzee and human inferior femoral neck trabecular tracts. Trajectorial intersection angles were generally orthogonal except in von Meyer’s femur where a mean of $73^\circ$ was observed, which is similar to the values found in the actual femora (Tables 2 and 3). The $r^2$ values are much lower in Koch’s (0.927) and Wolff’s (0.974) femora (compared to von Meyer’s at 0.982). Plots of residual errors also showed greater amplitudes of the residuals in these cases. These lower $r^2$ values are a result of subtle curvature changes in the longer trajectories. The curve fits in these two trajectorial femora improved when only the central portions of the trajectories were traced.

All trajectories analysed in both Culmann’s ‘crane’ and the Fairbairn crane best fit the same nonlinear equation that best fit the trabecular curves in the calcanei (Table 1). However, the trajectories in the Fairbairn crane had notably higher $r^2$ values than those in the Culmann ‘crane’ (e.g. mean values: 0.990 vs. 0.961, respectively). The $r^2$ values were typically lower when compared to the human and chimpanzee femora, which is the consequence of a.

Table 2

<table>
<thead>
<tr>
<th>Trabecular tract</th>
<th>Best-fit equations and intersection angles of: (A) human and chimpanzee femora, and (B) sheep and deer calcanei</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Femora</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Human femora</strong></td>
<td></td>
</tr>
<tr>
<td>Equations</td>
<td>Superior</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Superior</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Superior</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Superior</td>
</tr>
<tr>
<td>Mean angle of intersection</td>
<td>Superior</td>
</tr>
<tr>
<td>Range of angles of intersection</td>
<td>Superior</td>
</tr>
<tr>
<td><strong>Chimp femora</strong></td>
<td></td>
</tr>
<tr>
<td>Equations</td>
<td>Superior</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Superior</td>
</tr>
<tr>
<td>$y = a + bx$</td>
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<td>Mean angle of intersection</td>
<td>Superior</td>
</tr>
<tr>
<td>Range of angles of intersection</td>
<td>Superior</td>
</tr>
<tr>
<td><strong>B. Calcanei</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Sheep calcanei</strong></td>
<td></td>
</tr>
<tr>
<td>Equations</td>
<td>Dorsal</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Dorsal</td>
</tr>
<tr>
<td>Mean angle of intersection</td>
<td>Dorsal</td>
</tr>
<tr>
<td>Range of angles of intersection</td>
<td>Dorsal</td>
</tr>
<tr>
<td><strong>Deer calcanei</strong></td>
<td></td>
</tr>
<tr>
<td>Equations</td>
<td>Dorsal</td>
</tr>
<tr>
<td>$y = a + bx$</td>
<td>Dorsal</td>
</tr>
<tr>
<td>Mean angle of intersection</td>
<td>Dorsal</td>
</tr>
<tr>
<td>Range of angles of intersection</td>
<td>Dorsal</td>
</tr>
</tbody>
</table>
greater length of the trajectories. Plots of residual errors also showed greater amplitudes of the residuals in these cases. The trajectories in the Fairbairn crane intersected at 90°, while some of the trajectories in Culmann’s ‘crane’ intersected at ~84°.

3.2. Cantilevered beams

All trajectories analysed in Roesler’s cantilevered beam best fit the same nonlinear equations for the calcanei with an $r^2$ value $>0.986$ ($y^{-1} = a + b/x$, Table 1). The intersections in Roesler’s beam were also invariably orthogonal.

Although all the trajectories measured in Pauwels’ two non-orthogonally loaded cantilevered beams formed 90° intersections (Fig. 7), the $r^2$ values were typically lower ($r^2 < 0.945$) when they were fit to either of the two most common equations used in the calcanei and femora. High-order polynomial equations were required for achieving fits of $r^2 > 0.97$ for the trajectories analysed in Pauwels’ beams.

4. Discussion

4.1. Trabecular patterns in the human femoral neck are clearly not trajectorial

Results in the sheep and deer calcanei showed that the same nonlinear equation invariably best fit their dorsal (“compression”) and plantar (“tension”) trabecular tracts, and that these tracts could be superimposed on the corresponding mathematically derived compression and tension stress trajectories of the simply loaded cantilevered beams. Additionally, the opposing calcaneal trabecular tracts typically formed orthogonal to quasi-orthogonal intersections. In contrast, trabecular tracts in the human femoral necks were non-orthogonal, and also had shapes that often differed from the trabecular tracts in the calcanei and the stress trajectories in the simply loaded beams. However, the trabecular tracts in the chimpanzee femoral neck were also non-orthogonal, resembling those in the human femoral neck. These results suggest that the trabecular patterns in the calcanei satisfy basic tenets of the trajectorial hypothesis, while those in these anthropoid femoral necks do not. As discussed below, it is suggested that, in contrast to the calcanei and simple beams, the anthropoid femoral necks deviate significantly from the trajectorial paradigm since they receive relatively prevalent shear stresses, which are best accommodated by non-orthogonal trabecular tracts. We also consider the possibilities that asymmetrical trabecular patterns in these proximal femora may reflect the different developmental ‘fields’ (trochanteric vs. neck vs. head) that formed these regions—of which there is no parallel in the calcanei.

In the human femoral neck, the trabecular tracts exhibited acute (mean ± SD: 69° ± 12°) intersections. Similar acute intersections are depicted in von Meyer’s anatomical drawing of a proximal femur but not in the trajectories of Culmann’s ‘crane’, the Fairbairn crane, or the theoretical trajectorial/trabecular patterns in Koch’s and Wolff’s femur. Based on similar observations of this non-orthogonal construction in actual human femora, past
and recent investigations have also questioned the conception of the human proximal femur as a trajectorial structure. For example, in computational analyses Carter, Jacobs, and co-workers (Jacobs et al., 1997) calculated magnitudes of normal stresses in various locations throughout a two-dimensional model of a mid-cortically sectioned human proximal femur. Using a nonlinear weighting scheme, they determined the orientation of trabecular tracts in these locations, and noted that one consequence of this “time-averaged” principal stress construction (which they state is similar to Wolff’s principal stress concept if there is no variation in direction of cyclically applied loads) is that it becomes possible to “…form cancellous bone tracts with principal orientations that are not perpendicular to each other” (Carter and Beaupré, 2001, p. 149). Additionally, using simulated loading imparted to a two-dimensional mid-cortical slice through the human proximal femur, Carter, Beaupré and co-workers showed that the “arcuate system of trabeculae” experiences both tension and compression stresses along the principal orientation of the trabeculae, and “…the predicted orientations of trabecular architecture throughout the proximal femur match the early drawings of von Meyer [1867]” (Beaupré et al., 1990; Carter and Beaupré, 2001, p. 152). As noted, and discussed further below, the finite element analysis of Pidaparti and Turner (1997) suggests that these non-orthogonal intersections in the human femoral neck may represent adaptation for shear stresses engendered by prevalent complex/torsional loading—Wolff’s trajectorial paradigm does not include shear as an important mechanical correlate of trabecular architectural anisotropy.

**Neck vs. trochanteric trajectories:** In contrast to those of the human femoral neck, the trabecular tracts in the human trochanteric region often closely resembled the orthogonally intersecting trabecular tracts in the calcanei and the stress trajectories in the beams (Fig. 8, Tables 1–3). In the context of Wolff’s trajectorial paradigm, orthogonally intersecting trabeculae correlate with a medial-to-lateral bending moment in this region of the human femur. However, in the presumably similarly loaded chimpanzee trochanteric region the trabecular tracts typically formed obtuse intersections (117° ± 10°). This unexpected architectural arrangement is difficult to reconcile in a simple mechanical context. This architecture also seems inconsistent with predominant collagen fiber orientation data in cortical bone suggesting that the chimpanzee neck, and hence the proximal diaphysis with which it is continuous, receives relatively more prevalent bending than the human femoral neck (Kalmy and Lovejoy, 2002; Lovejoy, 2005). In the chimpanzee trochanteric region, a structure/function relationship between habitual loading and obtuse trabecular intersections might be clarified by considering Heft’s (Heft, 1992, 1994) functional interpretation of predominant trabecular patterns. Heft (1992, 1994) suggests that in a metaphyseal/epiphysial region of a weight-bearing bone, such as the human femur, the trabeculae form “paired” oblique angles, where each principal tract corresponds to the compressive predominant joint load vectors near the extremes of a typical range of joint excursion. In turn, these oblique trabecular tracts may appear as quasi-parabolic arches. This interpretation precludes an important role for tension trajectories (Figs. 11 and 12). In this context the formation of obtuse trochanter intersections in chimpanzees may then be strongly influenced by extremes of predominant load vectors produced by their Trendelenburg-type gait patterns (Elftman and Manter, 1935; Jenkins, 1972; Kalmy and Lovejoy, 2002; Lovejoy, 2005). In contrast to humans, chimpanzees habitually shift their center of mass of the head, arm, and trunk laterally (over the supporting limb) (i.e. Trendelenburg gait) in order to achieve equilibrium during single-leg support phase (Lovejoy, 2005). As noted by Kalmy and Lovejoy (2002), this gait pattern occurs because non-human primates (including hominoids) lack a specialized adductor apparatus (gluteus minimus and medius, pyriformis, etc.) that minimizes pelvic drop, which...
is especially pronounced during bipedal locomotion. Although bipedal gait is relatively uncommon in chimpanzees (Alexander, 2004; D’Aout et al., 2004; Schmitt, 2003; Thorpe et al., 1999), their typical ambulatory activities also incur significant pitching of the trunk—a tension system oriented in the direction of the inserting muscles and a pressure system resulting from pressure of the apophysis against the diaphysis. (Reproduced from Heft (1994) with permission of the publisher, Elsevier Science, New York).

4.2. The ‘adaptability’ and biomechanics of cancellous bone: do non-orthogonal femoral neck arches reflect ‘shear-priority’ adaptations?

In a review of the literature on trabecular bone mechanical properties, Keaveny (2001, pp. 16–2) states that “The strength of trabecular bone depends on volume fraction, architecture [e.g. trabecular orientation, thickness, and connectivity], and the tissue material properties, in that order of importance.” Ford and Keaveny (1996) further point out that “…shear may be a dominant failure mode during off-axis loading of trabecular bone in vivo….” These facts are relevant in the context of functional adaptation of the anthropoid hip since this region is habitually loaded “off axis” (e.g. in humans, loading is typically ~22–37° superior to the femoral neck axis) (Bergmann et al., 1993; Davy et al., 1988). Hence, it seems that the anthropoid femoral neck especially in the human hip (because of the relatively long femoral neck), would be in a precarious situation without functional adaptations that accommodate prevalent/predominant shear produced by the habitual co-existence of bending and torsion. Specific functional adaptations for shear are expected in this region because experimental data have shown that, when tested to failure in tension, compression, and shear, trabecular bone is notably weakest in shear (Ford and Keaveny, 1996; Keaveny and Hayes, 1993; Keaveny et al., 2001, 1994) (Fig. 13).

In view of this disparity, we invoke the idea that shear loads, which are minimally considered in the Wolffian paradigm, are important considerations for interpreting adaptation of trabecular architecture. Experimental studies

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Fig. 12. Heft’s (1992) drawing of a human proximal femur. The original figure legend reads: Interpretation of the architecture of the spongiosa at the upper end of the femur. The two principal trabecular systems in the neck are exposed to pressure [compression]. Their direction corresponds to the marginal force of the fan of resultant forces acting on the articular end of the bone. Two trabecular systems are developing in the apophysis—a tension system oriented in the direction of the inserting muscles and a pressure system resulting from pressure of the apophysis against the diaphysis. (Reproduced from Heft (1994) with permission of the publisher, Elsevier Science, New York).

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6Elastic modulus (stiffness) and failure stress of cancellous bone depends primarily on apparent density (the product of volume fraction and bone tissue density, the latter being essentially constant at about 2 g/cm³) (Keaveny et al., 2001).
of Keaveny and co-workers (Keaveny, 2001) have contributed most significantly to the development of the idea that shear loads—by being potentially more deleterious than tension or compression loads—may have "priority" among these naturally selective stimuli in affecting the emergence of developmental adaptations in cancellous bone. This hypothesis is also supported by experimental data showing differences in microdamage accumulation in trabecular bone when loaded "on-axis" in compression vs. "off-axis" in shear (Wang and Niebur, 2006), and studies suggesting that shear loads are important in the etiology of osteoporosis-related fragility fractures of the proximal femur (Greenspan et al., 1998; Pinilla et al., 1996) and vertebral bodies (Myers and Wilson, 1997). At the tissue/cellular level, shear can also be distinguished from other strain modes by differences in deformation of the cell body or by evoking different biophysical stimuli (e.g. streaming potentials or fluid-flow dynamics) (Carter and Wong, 1988; Judex et al., 1997; Rubin et al., 1996).

Additional observations supporting the idea that prevalent/predominant shear loads have "priority" over tension and compression in producing developmental adaptation also include yield stress data for bovine tibial trabecular bone loaded in longitudinal vs. transverse directions, and their strength anisotropy ratio (SAR) data, plotted as a function of apparent density for three different loading modes (compression, tension, shear) (Keaveny et al., 2001). These data, shown as curves in Fig. 14, demonstrate that strength (dashed lines) always increases with increasing volume fraction and depends critically on loading direction and mode. Furthermore, the strength anisotropy ratio varies from 2 to 10; it depends on volume fraction and loading mode, being greatest for compression and least for shear. Hence, trabecular orientation may have a relatively greater influence on trabecular bone strength when loaded in prevalent/predominant shear. In view of these data, we suggest that regional modifications in volume fraction are not sufficient for accommodating the shear stresses that are common in the proximal femur. Consequently, if the non-orthogonal trabecular intersections are adaptive in the anthropoid femoral necks examined in this study, then it is plausible that they are configured in ways that ultimately help accommodate shear stresses in this region. This is consistent with results of the finite element analysis of Pidaparti and Turner (1997, p. 981) (see also Fernandes et al., 1999).

Our analyses show that non-orthogonal trabecular orientations [in the human femoral neck] reduce shear coupling under multiaxial loading, e.g. bone near a synovial joint, but under predominant uniaxial or biaxial loading, e.g. bone near a tendon insertion, orthogonal trabecular orientations that align with the loading direction minimize shear coupling. These observations suggest that optimal trabecular orientations near joint surfaces (like the proximal femur) may be different than those near tendon insertions (like the potoroo’s calcaneus).

As discussed further below, these and other investigators draw an important distinction in functional environments that correlate with trabecular morphologies within traction apophyses (e.g. the trochanteric region and calcanei) vs. those that are within epiphyseal regions like the femoral neck (Heft, 1992; Tsubota et al., 2002).

4.3. Tension/shear and cartilage: the cartilaginous growth plate is "protected"

Metaphyseal/epiphyseal trabecular architectural anisotropy, such as the arched patterns shown in the calcanei and femora in this study, might also be the circumstantial consequence of the disproportionate importance (Fig. 13) of minimizing the deleterious effects of tension and shear stress on cartilaginous growth plates (Inman, 1947; Moen...
This helps to avoid epiphyseal separation while enabling growth by avoiding excessive compression, consistent with the Hueter–Volkmann “law” (Mehlman et al., 1997; Moss-Salentijn, 1992). Biomechanical constraints on growth-plate orientation, in turn, could play an important role in governing the development of the trabecular patterns that subsequently form in these bones. Consequently, their trabecular patterns might be strongly, but less directly, correlated with mechanical stimuli—perhaps these stimuli primarily influence the cartilaginous growth plates that produce the trabeculae. If this interpretation is correct, then some trabecular patterns (e.g. see Swartz et al., 1998; Smith, 1962a) might not be as strongly associated with mechanical stimuli as conveyed by conventional wisdom. This supports shifting conventional emphasis from commonly ascribed, but nevertheless putative, roles for mechanobiological stimuli in the emergence of trabecular bone morphology (e.g. Carter and Beaupré, 2001; Tanck et al., 2006) to programmed pattern development that might more directly mediate the development of epiphyseal growth plates (Frost, 1990; Hamrick, 1999; Lovejoy, 2005).

But even this explanation is confounded by the fact that the ‘weak’ growth plate is progressively strengthened during ontogeny by formation of a stout perichondral ring (Chung et al., 1976), and the chance of epiphyseal separation is further reduced by greater tensile modulus than shear modulus of growth-plate cartilage (Cohen et al., 1992; Williams et al., 1999). Numerous observations suggest that a common characteristic of mammalian limb bones is that epiphyseal growth plates are generally oriented parallel to one of the principal stresses that occur in the region during normal activity (Smith, 1962a,b; Thompson, 1902). Consequently, in the human proximal femur and artiodactyl calcaneus the alignment of tensile

Fig. 14. Yield stress for longitudinal vs. transverse loading, and their ratio, plotted as a function of apparent density (i.e. bone volume fraction) for these different loading modes (compression, tension, and shear). The curves, based on data from bovine tibial trabecular bone (Keaveny et al., 1999), demonstrate the complexity of the strength properties of trabecular bone. Strength (dashed lines) always increases with increasing density and depends critically on loading direction and mode. The strength anisotropy ratio (solid lines) varies from approximately 2–10. It, too, depends on density and loading mode, being greatest for compression and least for shear. (Reproduced from Keaveny (2001) with permission of CRC press, Boca Raton, FL).
stress along their epiphyseal growth plates is a reasonable trade-off for avoiding the potentially more deleterious consequences if prevalent/predominant shear stresses were aligned along the growth plate.

Differing developmental ‘fields’ for trochanteric and neck regions. The biomechanical environments of the developing human and chimpanzee proximal femoral chondroepiphysis also significantly differ from artiodactyl calcanei since in these femora the apophyseal (greater trochanter) and epiphyseal (head) portions of the growth plate form in different developmental ‘fields’ (Kriz et al., 2002; Ogden, 1981, 1990; Reno et al., 2002; Siffert, 1983). During growth, the trochanteric and head regions progressively separate from what was previously a contiguous growth plate. The trochanteric region (mostly the greater trochanter) becomes a traction apophysis as a result of the loads that it receives from the gluteus medius. In contrast, the femoral head portion of the growth plate remains within the joint capsule and tends to become oriented orthogonal to the predominant compression loads across the hip joint (Smith, 1962a). The intervening cartilage (the ‘inter-epiphyseal’ region) gives rise to the arcuate (“tension”) trabecular tracts and the superior neck cortex of the sub-adult femur (Kriz et al., 2002; Ogden, 1981; Reno et al., 2002). These observations again demonstrate the inherent developmental/biomechanical complexities of the human proximal femur that render it an inadequate approximation of a natural trajectorial structure. Lovejoy (2004, p. 116) also emphasizes the possibility that, in contrast to the Wolffian paradigm, the arched trabecular pattern of the human proximal femur can be “…readily explicable by interactive growth within its three physes—those of the head, greater trochanter, and the interepiphyseal “band”.” We speculate that trabeculae that form in traction apophyses more closely approximate strain-mode-related loading patterns whereas trabeculae that form in articular regions may be more strongly influenced by developmental constraints arising from patterning of the growth plate and articular surface geometries (Lovejoy et al., 2003). The idea that in some cases the developmental emergence of regional trabecular architectural anisotropy is not strongly influenced by mechanobiologic stimuli appears consistent with findings of Swartz et al. (1998) who were able to identify trabecular homologies across various species (mostly small mammals), suggesting a heritable program regulating the position of individual trabeculae.

4.4. Functional adaptation and pattern formation in the emergence of trabecular patterns: optimal, adequate, or circumstantial morphology?

Essentially, Wolff suggested that bone architecture was an answer to requirements of optimal stress transfer, pairing maximal strength to minimum weight, according to particular mathematical design rules (Huiskes, 2000). Huiskes (2000, pp. 153–154) states that even though sophisticated finite element models support Wolff’s trajectorial hypothesis in continuous materials this:

...in no way implies that bone cells actually use trajectorial information to form bone. As Cowin (1997) has pointed out again, this idea is sheer nonsense; any trabeculisation, any discontinuity in the material, would alter the stress trajectories, and the cells would forever chase their own tails trying to capture them in hard material. The correspondence between trabecular architecture and stress trajectories in models using continuous material representations is circumstantial, not causal.

This reflects the well-known fact that cortical and trabecular bone violate important assumptions of the trajectory hypothesis when applied in a strict/ideal context; namely, the material must be homogeneous, continuous, and isotropic (Brand et al., 2003; Cowin, 1989c; Harrigan et al., 1988; Heft, 1992; Murray, 1936). In fact, as stated by Keaveny et al. (2001, p. 317), “…the [mechanical] properties of trabecular bone are heterogeneous (vary with age, site, disease, etc), anisotropic (depend on loading direction), and asymmetric (differ in tension versus compression versus shear).” Consequently, results of the present study showing that although all of the selected trabecular tracts in the calcanei and all of the stress trajectories in the simple beams are described by the equation \( y^{-1} = a + b/x \), this equation probably does not have biophysical significance. Previous investigators have also suggested that such trabecular anisotropy may develop in a predetermined, minimally mechanically influenced fashion that circumstantially resembles stress/strain trajectories (Ascenzi and Bell, 1972; Huiskes, 2000; Jansen, 1920; Lovejoy, 2005; Lovejoy et al., 2002; Murray, 1936; Triepel, 1922). This appears to be supported by the fact that in developing deer and sheep calcanei the orientation of the epiphyseal growth plate and the plantar (“tension”) trabecular tracts are also described by the same nonlinear equation throughout ontogeny (from fetus to adult) (Skedros and Brady, 2001). But predictable patterns of dorsal-plantar stresses from muscle loading and other mechanobiologic stimuli probably exist and are likely present in utero, which might imply an important role for muscle loading in the emergence of this distinctive morphology (Carter and Beaupré, 2001; Skerry, 2000). For example, Skerry (2000) describes the unpublished qualitative observation of Lanyon and Goodship who, after transecting the Achilles tendon of a living fetal lamb, noted that subsequent prenatal growth produced disorganized trabeculae in the experimental calcaneus compared to the contralateral control. Although this isolated observation warrants confirmation, it suggests that prenatal loading might play an important role in the formation of the arched patterns described in the present study. Alternatively, the systematic expression of genetically derived positional information may be more directly important to a bone’s development.
than any individual effects of strain transduction. In this context, Lovejoy et al. (2002) state:

Mounting evidence suggests that the role of mechanotransduction, especially in the developing/growing skeleton, is to provide necessary threshold values required for implementation or maintenance of patterns of growth guided principally by positional information, and it seems increasingly likely that this maxim holds as much for cancellous bone (i.e. trabecular distribution and orientation) as it does for cortex.

This view minimizes, or at least significantly reduces, the putative role that mechanical stimuli have in causally mediating the arched trabecular patterns in the human proximal femur and other bones. Additional studies examining this “developmental hypothesis” are warranted.

4.5. Impediments posed by the trajectory hypothesis and Wolff’s “law

Recent scholars agree that the often vague or poor understanding of what Wolff’s “law” actually is and the enormously variable ways that this nebulous rubric is used to explain normal and pathologic bone “transformation” processes (i.e. modeling and remodeling) are impediments to progress in understanding how mechanical stimuli and other biologic factors mediate normal skeletal development, maintenance, and adaptation (Bertram and Swartz, 1991; Cowin, 1997, 2001; Currey, 1997; Holt et al., 2004; Huiskes, 2000; Ruff et al., 2006). The historical acceptance of Wolff’s “law” is partially rooted in orthopaedists’ view that the human proximal femur and other bones and bone regions are subject to habitual ‘tension/compression’ stressing. This conception will be difficult to uproot, since, as noted by Hall (1985, p. xxv) “...specialists such as orthopaedic and oral surgeons and orthodontists spend their working lives manipulating the skeleton in conformity with the trajectory theory,...”. This view reflects both: (1) the trajectorial hypothesis, and (2) a broader view (hence Hall’s inclusion of “orthodontists”) that Wolff’s “law” includes consideration of putative trophic influences of material anisotropy could provide additional important biomechanical information (e.g. determining how variations in the degree of connectivity influence trabecular stress distribution). For example, in a study of high-resolution, materially nonlinear finite element models (used to obtain yield strains in both tension and compression) in 12 adult human femoral neck trabecular specimens, Bayraktar and Keaveny (2004) reported that “The highly oriented structure of trabecular bone results in equivalence of apparent-level yield and tissue-level strains for tensile loading but not from compression.” This discrepancy was attributed to combined effects of the asymmetric strength of trabecular tissue (see Fig. 14) and the presence of slightly oblique trabeculae, causing tissue-level yield to occur first in tension for apparent compression loading. We suggest that this is a fundamental reason why three-dimensional morphologic differences would be expected between ‘tension’ and ‘compression’ trabecular regions, and especially in the intervening ‘neutral axis’ region or in regions generally subject to complex/multidirectional loading where shear stresses are prevalent/predominant. Addition-
ally, by carrying off-axis loads, some measures of trabecular connectivity and oblique cross struts can help reduce deleterious stress concentrations and shear deformations, and other nonlinear deformations such as bending and buckling that can be especially notable when trabecular volume fraction is low (e.g. with aging/osteoporosis) (Bayraktar and Keaveny, 2004; Ding et al., 2002; Parkinson and Fazzalari, 2003; Stauber et al., 2006; Van Rietbergen et al., 2003; Wang and Niebur, 2006).

Some of these morphologic characteristics might evade recognition in the context of the traditional trajectorial paradigm. Micron-level imaging techniques coupled with computer modeling can allow for these more rigorous analyses of three-dimensional reconstructions (Bousson et al., 2004; Fajardo and Muller, 2001; Huiskes et al., 2000; Issever et al., 2003; Nuzzo et al., 2003; Odgaard, 2001; Van Rietbergen et al., 2003). Studies such as these are currently being conducted on the bones used in the present study.

A fourth limitation lies in our focus on Wolff’s view of habitual loading of the hip. In this loading regime the angle of the joint contact force with respect to the femoral neck is relatively constant. There is evidence that the orientation of joint contact force is relatively consistent in many activities of daily living (Pedersen et al., 1997), and presumably, such habitual loading conditions drive bone adaptation. But less-frequent loading conditions may also produce strains (tensile and compressive) suggesting that higher magnitude stresses contrast with the idea that trabeculae tend to align with the predominant principal stress directions (both compressive and tensile), suggesting that higher magnitude stresses will have a disproportionately greater effect upon bone adaptation than smaller stresses (Biewener et al., 1996; Cheal et al., 1987; Frost, 1964, 1986; Hayes and Snyder, 1981; Lanyon, 1974; Lovejoy, 2005; Ryan and Ketcham, 2005b; Skerry and Lanyon, 1995; Turner, 1992).

5. Conclusion

Compared to the arched trabecular patterns in the cancellous bone of the human and chimpanzee femoral neck regions, the arched trabecular patterns in the sheep and deer calcanei more closely resemble stress trajectories in idealized, short, cantilevered beams. These beams also closely resemble Culmann’s cantilevered beam—the historical ‘origin’ of Wolff’s trajectorial hypothesis. The striking dichotomy between the arched trabecular patterns in these artiodactyl calcanei (orthogonal and symmetric) and these anthropoid femoral necks (nonorthogonal and asymmetric) might reflect differences in their developmental histories and habitual loading complexities. Biomechanical constraints associated with the orientation of cartilaginous growth plates, which may be disproportionately more important in cartilage than in cancellous bone, must also be considered because this directly influences the development of trabecular morphology. Furthermore, non-orthogonal patterns may reflect the relative “priority” that shear has over tension and compression (especially in trabecular bone) in causally mediating the emergence of developmental limb-bone adaptations. However, using quasi-parabolic trabecular patterns in these anthropoid bones to interpret loading history, and generalizing their utility for interpreting adaptation in other bones that are also not simply loaded, can be misleading because such architectural patterns can be variously influenced by diverse factors that often do not appear to have straightforward relationships with functional/mechanical stimuli. These results suggest that only some bones or bone regions subject to specific and relatively simple loading conditions (e.g. the calcanei) will exhibit what might be considered trajectorial patterns. Consequently, it is unfortunate that the relatively complexly loaded human femoral neck region has historically, and is often currently, modeled as a structure that generally conforms to Wolff’s trajectorial paradigm. Further investigations are needed to determine the mechanisms that causally mediate functional adaptation of trabecular bone in the appendicular skeleton.

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Appendix A

Wolff’s “law” : The concept of a causal form–function relationship expressed in cancellous architecture and causally mediated by dynamic loads that seem evident in bone growth is primarily the idea of Wolff’s contemporary Wilhelm Roux (Dibbets, 1992; Fung, 1990; Huiskes, 2000;
Roesler, 1987). Contemporary application of Wolff’s law of bone transformation can be summarized in three basic principles (Martin et al., 1998): (1) optimization of strength with respect to weight, (2) alignment of trabeculae with principal stress direction, and (3) self-regulation of bone structure by cells responding to a mechanical stimulus. Several authors provide further discussion of the origins, broad applications, common misconceptions, and notable inconsistencies of Wolff’s “law” (Bertram and Swartz, 1991; Cowin, 2001; Currey, 1997; Dibbets, 1992; Lee and Taylor, 1999; Roesler, 1981; Trehan, 1981). Furthermore, as noted by Stanford and Brand (1999, p. 553), the use of “mathematical laws” in this context must be questioned since:

Mathematical descriptions of natural phenomena never reflect causation, but rather merely describe and often accurately predict. Confusing description with causation has often led to the misunderstanding that mathematical “laws” “govern” or control or explain natural phenomena.

Bone “Transformation” vs. “Remodeling” vs. “Change in Conformation”: During Wolff’s time the concept of osteon-mediated remodeling was not known. Remodeling in this context is defined below. What Wolff referred to as “changes” or “transformation(s)” in bone architecture would actually be better translated as modeling (see below). It should also be noted that Wolff strongly ascribed to the concept of interstitial bone growth (Dibbets, 1992). The concept of modeling-mediated resorption vs. formation was debated in Wolff’s time, but Wolff did not accept the somewhat limited evidence supporting the existence of modeling. Therefore, the processes of “remodeling”, or “modeling” are not accurate translations of what Wolff referred to as “transformation” of bone. Wolff also considered his ‘law’ of bone transformation to apply to both cancellous and cortical bone, since cortical bone represented locations of high stress trajectory density, and these two tissues were basically the ‘same’, differing only in their porosities. Contemporary investigators have challenged this idea (Huiskes et al., 1987; Rice et al., 1988).

Modeling: Modeling activities affect the formation and/or resorption of secondary or non-secondary bone (e.g. primary bone, and trabecular bone in some cases) on periosteal or endosteal surfaces. They are detected as changes and/or differences in a bone’s curvature, cross-sectional shape and/or regional cortical thickness. Consequently, modeling is a concept describing a combination of non-proximate, though coordinated, resorption and formation drifts whose net result is, typically, to change the distribution of bone (Jee et al., 1991). Such drifts are called macro-modeling in cortical bone and mini-modeling in cancellous bone (Frost, 1988a; Kobayashi et al., 2003). The re-alignment of trabecular tracts along the lines of stress would be a consequence of mini-modeling.

Remodeling: Remodeling activities affect the replacement of intracortical bone; this is achieved through the activation of basic multicellular units (BMUs = osteoclasts and osteoblasts) that create secondary osteons (Haversian systems) in cortical bone and secondary osteons or hemi-osteons in trabecular bone (Frost, 1986; Jee et al., 1991; Parfitt et al., 1996). During Wolff’s time the concept of osteon-mediated remodeling was not known.

Wolff’s “proof” that the human proximal femur is a natural trajectorial structure: The basic principles of Wolff’s “law of bone transformation” were laid out in his papers published in 1869, 1870, 1872, and 1874. In 1869, Wolff argued that cancellous bone modeling adhered to mathematical rules, which he could prove corresponded to the principal stress trajectories in the Culmann ‘crane’. As stated by Roesler (1981), Wolff’s “proof” consisted of the following (Wolff, 1870, 1872):

(1) The irrefutable similarity between the two drawings recognizable “at the first sight” [compare Culmann’s ‘crane’ and Wolff’s femur in Figs. 3 and 6 of the present study],

(2) The crossing at right angles (orthogonal intersections) of the lines in the drawing of the cancellous bone structure he had made from frontal [coronal] sections of the human femur (Figs. 3 and 6),

(3) The corresponding crossing at right angles of the principal stress trajectories in the drawing of Culmann’s ‘crane’,

(4) The construction of Culmann’s ‘crane’ itself, the trajectories of which were obtained from the same load conditions as those of the human femur carrying the weight of the body.

As noted by Roesler (1981), these conditions may be necessary, but are not sufficient to prove Wolff’s trajectory ‘theory’. Therefore, it is more accurately referred to as the trajectory hypothesis.

On the origins of Culmann’s ‘crane’ (Figs. 1, 3, and 6): Presumably under Culmann’s supervision, one of his graduate students was primarily responsible for constructing the stress trajectories in this ‘crane’ in a manner (presumably) similar to that employed in drawing the stress trajectories in a Fairbairn crane (see “Fairbairn vignette” below) that Culmann had also illustrated in his textbook (Culmann, 1866; Rüttimann, 1992; Thompson, 1917, 1943) (Fig. 5A). Our examination of Culmann’s text, however, suggests that different engineers may have determined the course of the curved trajectories in the Fairbairn crane and those in the Culmann ‘crane’. Roesler states (1981, p. 35) that:

No details about the construction of the famous crane [Culmann’s ‘crane’] have been handed down to us from Culmann himself … He [Wolff], however, claims that Culmann himself had gone over those parts of his publication which referred to the construction of the
crane, and therefore they can be considered to be an authorized description. But it cannot be derived from Wolff’s paper that Culmann also read the parts that contain Wolff’s own deductions and conclusions from the drawing of the crane. Thus we must assume that Wolff made these deductions without the assistance of Culmann, who possibly could have helped to avoid at least the major misinterpretations of the trajectories of the crane.

Rüttimann quotes Rudolf Fick’s recollection (italics) of the Culmann-Meyer meeting at the gathering of the Society for Natural Science in Zurich, July, 1866 with a correction of his own (non-italics):

He (von Meyer) drew a crane similar to the shape of the upper end of the femur and asked …Culmann to draw in the tension and pressure lines to be calculated by him for this purpose, having already drawn trabeculae that were significant—in his opinion—on another piece of paper. Culmann had one of his pupils, Dr. Hedenaüer, make the calculation and drawing and, just imagine, it corresponded with the one of H. Meyer…

The above-named assistant was not Dr. Hedenaüer, but Dr. Andreas Rudolf Harlacher…

However, we have recognized that Culmann’s associate (or student?) “Bessard” (only the eponym is noted in the text) supervised the illustration of a Fairbairn crane, which appears in Culmann’s text (plate 11, Fig. 1) (Fig. 5A of the present study). This plate is referenced in Section 3, chapter 4 (pp. 264–270) of Culmann’s text. The description of the mathematics for calculating stress trajectories appear in Section 2, chapter 4 (pp. 231–237). (Wolff (1870) primarily cites portions of Section 3, chapter 1 (pp. 209–226), which deals with mathematics and proofs related to calculating stress trajectories.) In contrast, Harlacher appears to have been responsible for plate 8 of Culmann’s text, and for portions of Section 3, chapters 1 (pp. 219–223) and 2 (pp. 231–235); this section includes an illustration of the construction of the forces (Kräfte) within a rail resembling an I-beam. In this perspective it is plausible that there are different provenances of the stress trajectories of the Culmann ‘crane’ (Harlacher?) and Fairbairn crane (Bessard?). Additionally, the fact that the trajectories toward the free end of Culmann’s ‘crane’ and the Fairbairn ‘crane’ are not superimposable (compare Figs. 1 and 5, Table 2) is consistent with our suggestion that different engineers (Culmann’s “students”) were involved in their creation. In turn, we speculate that the stress trajectories in the Fairbairn crane, being drawn at least 1 year before the publication of von Meyer’s (1867) article (which includes the first published illustration of the Culmann ‘crane’ that we are aware of), were not constructed using methods identical to those used to draw the stress trajectories in the Culmann ‘crane’.

Roesler’s reconstruction of the Culmann ‘crane’—the probable incorrect transition from beam to ‘crane’: The calcanei examined in the present study closely resemble the structures used in the initial formulation of the trajectorial paradigm—short, cantilevered beams loaded transversely at their free ends (Figs. 2, 4 and 7). Not only did Culmann’s (1866) analyses on this topic originate from cantilevered beams, but the Culmann ‘crane’, popularized by Wolff, also appears to have a similar provenance (Roesler, 1981). In fact, Roesler (1981) suggests that the Culmann ‘crane’ was incorrectly constructed, citing two main engineering errors. Lee and Taylor (1999) summarize these as:

(1) Culmann’s ‘crane’ was probably based on a straight cantilever having parabolic shearing stress distribution at its free end that, to make the geometry more consistent with the proximal femur, some curvature was added to this free end. However, no change was made to the stress distribution to allow for this curvature.

(2) To describe the state of stress in a curved bar with a parabolic or near-parabolic distribution of shearing stresses along its free end, three different stress components are required. Culmann’s model involved only two components, a two-dimensional solution.

Roesler (1981) suggests that the creator of this ‘crane’ simply serially transected segments of a plane, straight cantilever, staggered them into the shape of a curve that approximated the shape of a Fairbairn crane, and added the missing trajectory segments, perhaps with a French curve. Hence, the Culmann ‘crane’ appears to be no more than a good first estimate of the stresses in the proximal femur. Wolff’s mistake was to read more into analysis that was used to create the ‘crane’ than was technically justified. In this perspective, it is unfortunate that the trajectorial hypothesis has historically focused on the cancellous architecture of the comparatively complexly loaded human proximal femur.

Although Roesler’s (Roesler, 1981) analysis seems generally plausible, there is evidence that the stress distribution was modified in both the Culmann ‘crane’ and the Fairbairn crane: Examination of these structures in Figs. 3 and 6 shows that the stress trajectories do not intersect on the neutral axis of the “neck” regions of either structure. In other words, it appears that a purposeful adjustment was made in the location of the neutral axis, which would be expected to be most obvious in the curvilinear portion of the beam (Mourtada et al., 1996). These structures nevertheless do not account for the loading complexity that is habitually experienced by the proximal femur, which was not well understood in Wolff’s time.

Fairbairn vignette: Sir William Fairbairn (1789–1874) was a notable structural engineer who helped pioneer the use of iron in construction projects, especially bridges (Stephen and Lee, 1964). Since Fairbairn cranes (Fig. 5) are no longer in use, discussions about how they differed from other tower cranes can be found in encyclopaedias from the

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