



Identifying donkey domestication through changes in cross-sectional geometry of long bones



Laura Shackelford^{a,*}, Fiona Marshall^b, Joris Peters^c

^a Department of Anthropology, University of Illinois at Urbana-Champaign, 607 S. Mathews Ave., Urbana, IL 61801, USA

^b Department of Anthropology, Washington University, St. Louis, MO 63130, USA

^c Institute of Palaeoanatomy, Domestication Research and the History of Veterinary Medicine, Ludwig Maximilian University, Munich and State Collection of Anthropology and Palaeoanatomy, Munich, Germany

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ABSTRACT

The initial phases of donkey domestication are difficult to identify in the archaeological record due to late and inconsistent changes in morphology and body size in the earliest domestics. Use of donkeys for load carrying and the management of captive herds resulted in a distinctive behavioral shift away from the free-ranging speed and mobility characteristic of wild asses toward slower, more steady pacing. Given the ability of bone to adapt to its mechanical environment, bone remodeling in the limbs of wild asses and donkeys are evaluated using cross-sectional geometry to determine whether weight bearing or locomotor differences between the wild and domestic forms may be used to recognize early domestication. Cross-sectional data were collected on the humeri, radii, metacarpals and metatarsals of eight wild ass and six donkey skeletons. Wild ass forelimbs have greater overall strength and more cylindrical humeral diaphyses, indicating better resistance to a varied locomotor repertoire. These results demonstrate that analyses of shaft geometry can provide information on changes in locomotor behavior during domestication. Our finding that shifts in *gait* had greater effects on the morphology of early domestic donkeys than did load-carrying places a new emphasis on understanding selection for gait changes in domestication dynamics.

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1. Introduction

The domestication of donkeys (*Equus asinus*) resulted in the development of mobile responses to climate change by early herders of the Sahara and land-based, long distance trade routes by ancient Egyptians and Sumerians (Marshall, 2007). Donkeys remain an essential pack animal for household transport and trade across Africa, Asia and South America (Fielding and Pearson, 1991; Marshall, 2007; Starkey, 2000). Ancient African wild asses (*Equus africanus*) were the wild ancestors of donkeys with at least two different wild populations recruited to the domestic gene pool (Beja Pereira et al., 2004; Kimura et al., 2011). On the basis of the genetic diversity and distribution of African wild asses and the distribution of ancient herders, it has been argued that African pastoralists were responsible for their domestication (Beja Pereira et al., 2004; Kimura et al., 2011). The lack of sociality of African wild asses and pastoralists' reliance on donkeys for load-carrying

made domestication an especially complex process (Marshall and Asa, 2012; Marshall and Weissbrod, 2011).

Archaeological evidence from the Egyptian Predynastic sites of Maadi and El Omari (ca. 4500 BC) and the early Dynastic site of Abydos (3000 BC) suggests that donkeys were domesticated by at least 6000–5000 years ago (Kimura et al., 2011; Marshall, 2007). Some donkey specimens from Maadi and El Omari are small in size relative to their wild ancestors, a trait often used to identify early stages of domestication. Following this, however, size decreases were inconsistent. Ten donkeys buried in the royal mortuary complex at Abydos, likely during the reign of Horus-Aha, the second pharaoh of the First Dynasty (3000 BC), were large and can be distinguished from African wild asses only by minor differences in metacarpal shaft proportions and vertebral and limb pathologies indicating that they were used to carry heavy burdens (Rossel et al., 2008). Other donkeys buried at Abusir during the reign of a later First Dynasty King were relatively small. However, larger animals similar in size to some of the Abydos donkeys date as late as 2500–1500 BC at Buto in the Nile Delta, Tel Brak in Syria and Wadi Hariq in Sudan (Boessneck et al., 1992; Boessneck and von den Driesch, 1992; Clutton-Brock, 2001; Jesse et al., 2004). Considerably

* Corresponding author. Tel.: +1 217 265 6741.

E-mail address: llshacke@illinois.edu (L. Shackelford).

smaller donkeys are seen once again dating to ca 1700–1600 BC at Avaris or Tel el Daba in the Nile Delta and at sites in the Near East (Bar-Oz et al., 2013; Boessneck, 1976; Clutton-Brock, 1992).

This inconsistency in body size change among the earliest possible domesticates over nearly two millennia has made the origins of donkey domestication particularly difficult to study. Recent research on the behavior of African wild asses and management of donkeys by African pastoralists provides insights into selection processes, helps to explain why morphological change was slow and emphasizes the need for innovative methods for detecting mutualistic relations between humans and donkeys during domestication.

1.1. African wild asses, pastoral settings, and slow morphological change

African wild asses are desert-adapted animals with labile metabolic rates and physiological mechanisms for water sparing. The only stable social group consists of a female and her foal. As a result donkeys thrive in hot and semi-arid environments, and although they are more social than their ancestors, they are not herd animals (Marshall and Weissbrod, 2011). Donkeys are considered essential transport animals but are usually kept in small numbers. When donkeys are not carrying loads, African donkey owners often find it easier to let animals from different households graze unsupervised than to herd or pen individuals or to manage their breeding. The traditional reliance on donkeys for transport rather than for food has also led recent herders to value the size, strength and hardiness of the wild ancestor and to encourage long-term gene flow among captive and wild herds (Marshall and Asa, 2012; Marshall and Weissbrod, 2009, 2011). The deep roots of this tradition are further illustrated by the first century CE agronomist Columella, who discussed the benefits of backcrossing female donkeys with male wild asses in his treatise *De re rustica* (6, 37, 3–7; English translation 1745: 298–301). Together these factors point to relatively low levels of selection and contextualize the lack of consistent size decreases in early domestic donkeys. Management of early captive wild asses or donkeys is also difficult to detect, especially in pastoral settings where the animals are first thought to have been domesticated. If donkeys were not routinely penned after they were first tamed, or if herders moved frequently and kept only a few animals outdoors, even donkey dung would not necessarily accumulate inside ancient settlements in detectable amounts, making it more difficult to use dung to identify donkeys than cattle or other animals kept in larger numbers and more routinely penned. Furthermore, pathologies appear less commonly in household pastoral donkeys than among those used for long distance trade for the First Dynasty royal household (Rossel et al., 2008). To complement these markers, it is clear that new methods are needed for detecting changes in behavior associated with domestication. Here we address the potential of studies of bone remodeling resulting from load carrying and gait changes for recognizing early phases of donkey domestication.

1.2. Biomechanics, shaft geometry and domestication

Very little research has focused specifically on bone structure and shape in the context of recognizing initial animal domestication. A 1970s study evaluated changes in internal bone architecture with domestication of sheep and goats (Drew et al., 1971; MASCA, 1970, 1973). Histological markers from weight-bearing bones indicating the orientation of hydroxyapatite crystals initially appeared to effectively distinguish the bones of wild and domesticated animals (Drew et al., 1971; Perkins and Daly, 1968), but subsequent efforts to verify these results were unsuccessful (Zeder,

2006). However, external morphological features have been widely used. Analyses by Eisenmann and colleagues (Divé and Eisenmann, 1991; Eisenmann, 1986, 1995; Eisenmann and Beckouche, 1986) documented changes in the proportions of the metapodials and phalanges of modern wild asses and donkeys. Rossel et al. (2008) went on to support and amplify these findings by identifying differences in the proportions, but not the size, of ancient Abydos donkeys and modern African wild asses. Both of these research groups argued that the morphological shifts that they documented resulted from changes in load-bearing with domestication. This drew attention to the potential of biomechanical approaches for studying behavioral shifts in load carrying and locomotion with domestication.

Skeletal elements are under variable genetic and environmental influences and as a result inferences from some features are more informative than others about their mechanical environment (Carter and Beaupré, 2001; Lovejoy et al., 1999; Pearson and Lieberman, 2004). Articular surfaces and long bone lengths, for example, are relatively plastic throughout development, but lose that plasticity with skeletal maturity. As a result, they provide little information about the behavior of an individual, but can be informative about the evolutionary history of a population. In contrast, the amount and distribution of cortical bone in long bone diaphyses are highly responsive to mechanical loading and remain responsive to mechanical stimuli throughout life (Lieberman et al., 2001; Martin et al., 1998; Ruff et al., 1991; Sumner and Andriacchi, 1996). Given the plasticity of bone and its response to the environment, variations in bone mass have been related to variations in the mechanical environment, and hence forces generated by activity. This ability of bone to adapt to its mechanical environment has long been a general observation and guiding principle in biology (Roux, 1881; Wolff, 1892, Engl. translation 1986).

The relationship between structural changes in the skeleton and individual life histories are complex (Bertram and Swartz, 1991; Demes et al. 1998; Pearson and Lieberman, 2004), but the results of experimental, clinical and sports medicine research support the general concept of bone functional adaptation. Bone response is stimulated by the strain created when biomechanical movement creates forces through skeletal muscle and ground reaction (Shaw and Stock, 2009). This ability for bone to remodel as the result of activity has been demonstrated in the playing arms of baseball pitchers and tennis players (Bogenschutz et al., 2011; Jones et al., 1977; King et al., 1969; Warden et al., 2009). Cross-sectional geometry has also been used by anthropologists to examine subsistence behaviors in Holocene groups, such as how the introduction of agriculture affected behavior or the division of labor in arctic whaling communities (Bridges, 1989; Bridges et al., 2000; Churchill, 1994; Larsen, 1997; Ruff and Larsen, 1990; Shackelford, 2005). Similar methods have been used to evaluate weapon use in Medieval samples (Rhodes, 2003, 2004; Rhodes and Knüsel, 2004) and use of hunting technology by Neandertals and early modern humans (Churchill, 1994; Churchill et al., 2000a; Holt et al., 2000).

The exact mechanism by which these changes occur, however, is unclear. Although decades of experimental research has correlated mechanical loading with an osteogenic response, it has also demonstrated that bone is most strongly influenced by a subset of factors that include strain magnitude, strain rate, strain frequency, strain gradient, acceleration and rest intervals (Biewener and Bertram, 1993; Biewener and Taylor, 1986; Goodship et al., 1979, 2009; Judex and Carlson, 2009; Judex and Zernicke, 2000; Lanyon et al., 1982; Lanyon and Rubin, 1984, 1985). For example, studies of athletes have shown that only those performing exercises with ground impacts, such as endurance running, sprinting or jumping, are associated with increases in cortical bone, while those involved in high-magnitude (i.e. powerlifting) and non-impact (i.e.

swimming) activities are not (Bennell et al., 1997; Nikander et al., 2010). These various factors are undoubtedly linked, making it difficult to parse out the specific contribution or signal of any one influence on the skeleton. Nevertheless, these studies have suggested that although the magnitude of weight is certainly a factor in bone's reaction to its mechanical environment, the kind of strains acting on a bone might be the greater predictor of an osteogenic response.

Cross-sectional geometry is ideal for performing functional comparisons of postcrania because bone has the ability to remodel its diaphyseal structure over an animal's lifetime (Lanyon and Rubin, 1984; Martin et al., 1998; Ruff et al., 2006). This is a non-invasive method in which long bones are modeled as hollow beams, and mathematical formulae that predict the strength of these beams are applied to diaphyseal cross-sections. Analyses of cross-sectional geometry allow for the estimation of the bone's integrity under specific types of loading (Ruff and Hayes, 1983). In particular, the amount of cortical bone in a cross-section approximates the strength of a long bone diaphysis when it is loaded. The shape of a cross-section (indicated by a ratio of principal moments of area) provides information about the direction of forces in the bones, indicating how a limb is being used during locomotion. Steady, linear locomotion creates predictable strains in the loaded limb. Locomotor behavior that includes turning, acceleration and deceleration or other non-steady activities introduces additional bending strains to the loaded limb. Based on the concept of bone functional adaptation, an increase in non-steady locomotor behavior will result in a redistribution of cortical bone in the long bone diaphyses to resist strains in multiple directions, resulting in a relatively circular cross-section (Carlson and Judex, 2007).

Cross-sectional geometric analyses link differences in weight-bearing and types of loading more directly to the distribution of bone in mammalian limbs than descriptive studies of surface anatomy in the limbs. Similar approaches have been used to compare limb loading in a range of terrestrial and arboreal animals (Carlson, 2005; Carlson et al., 2006; Demes and Carlson, 2009; Demes et al., 1998, 2001, 2006) and locomotion and gracilization of Pleistocene wildebeest (Churchill et al., 2000b), but not to domestication. Differences in the loading of wild asses and donkeys provide a promising approach to detecting early domestication prior to long-term size decreases in the archaeological record. In order to derive expectations regarding the direction of change in diaphyseal cortical areas with domestication we summarize below available information on donkey loading and activity patterns and gaits of working donkeys and free-living African wild asses.

1.3. Donkeys and wild asses: differences in locomotion and loading

African wild asses frequent arid, hilly and rocky areas in Eritrea and Ethiopia (Moehlman, 1998, 2002). They are known for their speed and can move as fast as 50 km/h (Library.sandiegozoo.org/factsheets/donkey/donkey.htm). However, animals typically graze at a walking pace from dawn till late morning, rest in the heat of the day, and resume grazing in the late afternoon. Relatively short bursts of activity occur during flight from predators or chases, which are a routine part of courtship and breeding behavior (Asa et al., 2011; Hemmer, 1990; Klingel, 1998). Trotting, galloping, rapid gait, orientation and incline shifts are mostly likely to occur at these times.

Load changes with domestication resulted from the way that ancient villagers used donkeys to carry water and household goods. Farmers also used them to plough, transport harvests and thresh grains. Load carrying was more common, however, than traction. Maasai donkeys in East Africa today often travel 9–14 km to fetch water, carrying a load of 50 kg (Marshall and Weissbrod, 2011)



Fig. 1. Donkeys in the Sudan carrying water-inflated skins and demonstrating pack movement. Image by J. Peters.

(Fig. 1). Similar to saddled horses (Holt et al., 2000), donkeys are fore-loaded such that their center of mass is shifted anteriorly and a greater percentage of weight is placed on the forelimb than on the hindlimb. Documentation of donkey loading devices used by households in Dahkla oasis, Egypt (Förster, 2007), images of loaded pastoral donkeys and donkey conformation (Fig. 2), and analyses of pathologies in the fore- versus hind-limbs of transport animals from archaeological sites (de Cupere et al., 2000; Izeta and Cortés, 2006), suggest much of the weight of loading falls on the forequarters.

Gait changes expected with domestication are harder to assess. Donkeys are known for being sure footed and superior load carriers, especially on rocky or mountainous terrain. Working donkeys generally move at a slow, steady pace. Periods spent carrying loads vary from light pastoral use to transport of heavy goods for hundreds of kilometers. Animals kept by pastoralists or Ethiopian villagers spend some time every day grazing unsupervised and participate in courtship, breeding chases and agonistic interaction with other donkeys (Marshall, per obs). Studies of donkeys and camels note that these desert animals have more energetically efficient locomotion than humans or temperate ungulates of similar sizes (Dijkman, 1991; Jones, 1977; Maloiy et al., 2009; Yousef

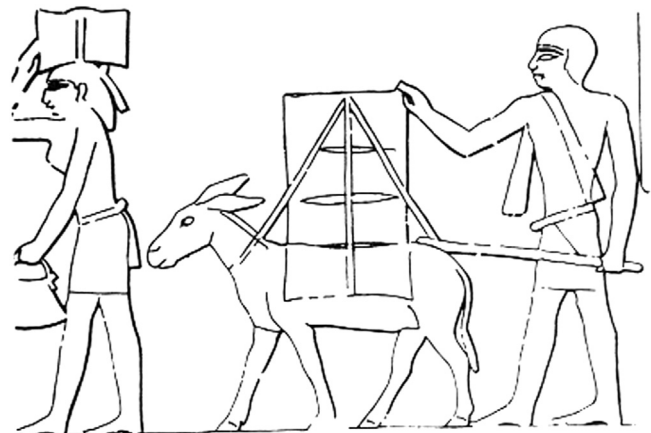


Fig. 2. Image of an ancient Egyptian donkey used for burden carrying from Davies (1901: pl. VII).

et al., 1972), and that donkey walking is more energetically efficient than trotting or galloping (Maloij et al., 2009).

When activity patterns, locomotion, and load carrying are examined together, it is clear that changes may have occurred in all of these areas with domestication of African wild asses. External loading in the form of burden carrying is the most unequivocal change. It is generally assumed that burden carrying increases the strain on the limbs of the domesticated donkey relative to the wild ass, particularly since archaeological studies have identified an increase in pathologies associated with draught and transport animals (de Cupere et al., 2000; Izeta and Cortés, 2006; Rossel et al., 2008). With respect to the internal structure of the bone, however, experimental studies of a range of mammals indicate that limbs respond to the types of strain created by an animal's locomotion. This suggests that cortical bone is more responsive to an active strain environment created by locomotor variability (such as that demonstrated by the natural movement of the wild ass) than a less active or routine strain environment (such as that induced by the steady pacing that characterizes the domesticated donkey) (Judex and Zernicke, 2000; Lanyon and Rubin, 1984, 1985; Robling et al., 2001; Turner, 1998). Furthermore, an animal experiencing a more active, unpredictable strain environment will have a more circular cross-section than one that experiences a predictable strain pattern in a single plane.

Whether burden carrying or locomotor changes affected wild ass morphology with domestication can be empirically tested by examining differences between cortical area and diaphyseal shape. We hypothesize that wild asses demonstrate greater behavioral variability within their locomotor repertoire than donkeys, including more high-intensity activities and non-steady behaviors like jumping, acceleration, deceleration and turning. The locomotion of domestic donkeys, we argue, is limited to slower, linear pacing during load-bearing. As a result, we propose that wild ass locomotion is characterized by greater diaphyseal strength (as quantified by greater resistance to axial and bending strains in the limb bones) than that of slower moving domestic donkeys. Correspondingly, we hypothesize that the cross-sectional shape of the forelimb diaphyses in the wild ass will be more circular than those of the donkey, indicating better resistance to bending deformations from multiple directions.

An alternate hypothesis is that burden carrying was the primary factor in cortical bone remodeling. This is not suggested by experimental research, but would be supported if domestic donkeys have greater cortical area and greater resistance to strains in the forelimbs than wild asses.

2. Materials and methods

Metric and biomechanical data were collected on as many donkey and wild ass skeletons as possible. African wild asses are critically endangered, with as few as 400 remaining in the wild. As few as ten confirmed African wild ass skeletons exist in museums worldwide. We were able to collect data on eight available specimens (Table 1). Donkeys are common, but their skeletons are rare in museum collections; as such, data were collected on six skeletons (Table 1).

Forelimbs have been a particular focus of comparative study in equid domestication and are associated with changes in weight-bearing in transport donkeys (Eisenmann, 1986; Divé and Eisenmann, 1991). As a result we sampled a range of forelimb elements. However, changes in metatarsal proportions have also been considered in relation to equid domestication (Eisenmann, 1986). Furthermore, the relative roles of weight and locomotion were unknown at the beginning of this study. As a result metatarsals were also included in this analysis, as a sample of the hindlimb. For

Table 1
Specimens used for analysis.

Specimen number ^a	Description	Provenience
Equus asinus		
SAPM 4	Adult female donkey (c. 15 yrs)	Lesbos, Greece
SAPM 5	Adult female donkey (15 yrs)	Naxos, Greece
SAPM 17	Adult female donkey (22 yrs)	Nurnberg (Zoo animal)
ZSM 1968.696	Adult female donkey (16 yrs)	Naxos, Greece
FMNH 57271	Young adult donkey	Iraq (Reed, 1954)
WU 1	Adult donkey	Lesbos, Greece
Equus africanus		
SAPM 1	Male adult wild ass (10 yrs)	Zoo-born (2nd generation wild ass)
SAPM 3	Male adult wild ass (6 yrs)	Zoo-born (2nd generation wild ass)
ZSM 1952.9	Adult female Somali wild ass	Eritrea (wild caught)
ZSM 1963.133	Adult male Somali wild ass (>30 yrs)	Eritrea (wild caught)
ZSM 1963.134	Adult male Somali wild ass (5–6 yrs)	Zoo-born (1st generation wild ass)
ZSM 1964.23	Female Somali wild ass	Zoo-born (1st generation wild ass)
FMNH 1427	Young, male Somali wild ass	Somalia
FMNH 18851	Adult male Somali wild ass	Berbera, east of Halle, Somalia (Akley, 1896)

^a ZSM = Bavarian State Collection of Zoology, Munich; SAPM = State Collection of Anthropology and Palaeoanatomy, Munich; FMNH = Field Museum of Natural History, Chicago; WU = Washington University in St Louis.

each specimen, linear measurements were collected for the humeri, radii, metacarpals and metatarsals, as available, following Eisenmann (1986) and von den Driesch (1976) (Table 2). Cross-sections were taken at the midshaft of each bone, with the midshaft measurement taken at the point of the smallest diaphysis breadth. This convention allows this method to be used even in the case of fragmentary long bone remains. Length and breadth measurements were taken to the nearest millimeter using an osteometric board and digital calipers.

Cross-sectional data were collected on one humerus, radius, metacarpal and metatarsal from each individual (data were collected from the right side unless it was unavailable) (Section 2.1). Geometric properties measuring overall axial and bending strength of each bone were evaluated (Section 2.2). Relevant properties of bone strength and robusticity were analyzed and compared for the samples of wild asses and domestic donkeys using independent

Table 2
Linear measurements used in analysis.

Bone	Msmt. ^a	Bone	Msmt. ^a
Humerus		Metacarpal	
Greatest length	GL (E1)	Greatest length	GL (E1)
Section breadth	E3	Section breadth	E3
Section depth	E4	Section depth	E4
Distal articular breadth	E6	Proximal breadth	Bp (E5)
		Proximal depth	E6
Radius/Ulna		Metatarsal	
Greatest length	GL (E1)	Greatest length	GL (E1)
Section breadth	E3	Section breadth	E3
Section depth	E4	Section depth	E4
Proximal articular breadth	BFp (E5)	Proximal breadth	BP (E5)
Proximal articular depth	E6	Proximal depth	E6

^a E = Eisenmann; all else, von den Driesch.

samples *t*-tests. All statistical analyses were performed using SPSS Statistics 17.0.

2.1. Cross-sectional data collection

Cross-sections were obtained by combining external contour molds of each bone shaft with biplanar radiography. This method has been used by other researchers studying postcranial biomechanics to reconstruct comparable data in modern and fossil primate and human populations (Ruff and Hayes, 1983; Shackelford, 2005; Trinkaus and Ruff, 1999a,b). Each bone was oriented in anatomical position and the midshaft (50% proximo-distal) section was determined based on the maximum length of the bone. For the radius, the midshaft section was sometimes artificially enlarged by the additional bone contributed by the ulna. In these cases, the section was moved just distal to midshaft in order to avoid the contribution of the ulna. If the splint bones were still attached to the metacarpals or metatarsals, section measurements were taken without these.

A mold of Polysiloxane putty (Cuttersil putty Plus, Heraeus Kulzer, Inc.) was placed around the external contour of each bone at the identified section, with the mediolateral plane of the bone marked directly on the mold (Fig. 3). Anteroposterior (AP) and

mediolateral (ML) diameters of the bone were measured at this level, after which time the mold was cut away from the bone. Each mold was photocopied to create a two-dimensional picture of the external section contour after verifying that the photocopy did not distort its size and shape (Fig. 4).

Each bone was radiographed in posteroanterior and mediolateral planes to measure cortical thicknesses. Radiographs were taken using a portable veterinary X-ray machine and Kodak Ready-pack X-ray film with a radio-opaque marker present in each image to identify the measured section. Each bone was positioned so that the diaphyseal axis was parallel to the X-ray film in an anatomically accurate plane. After development, AP and ML diameters of each bone were measured on the radiographs at the designated section levels using digital calipers, and parallax corrections were performed when necessary by multiplying the cortical thickness measured from the radiograph by the bone/radiograph ratio. Anterior, posterior, medial and lateral cortical thicknesses for each section were measured on the radiographs using digital calipers. The measured cortical thicknesses were combined with the photocopied subperiosteal molds to interpolate endosteal contours for each section (Fig. 4). Each reconstructed section was then photographed with a scale for size and orientation. Slide images of the reconstructed cross sections were projected onto a Summagraphics two-dimensional digitizing tablet. The endosteal and periosteal boundaries were traced as input for SLICE (Nagurka and Hayes, 1980), and cross-sectional properties were calculated using a PC version (Eschman, 1992) of SLICE. Each section was digitized twice, and the resulting values for each section were averaged to minimize tracing error.

Cross-sectional data can also be generated using computed tomography (CT) and an imaging program such as AMIRA (Mercury Computing Systems, Chelmsford, MA) or BoneJ, an open source ImageJ plugin (Doubé et al., 2010) (for complete methods see Shackelford, 2005). The low-tech, low-cost, portable method of data collection used in the present study demonstrates its widespread applicability to zooarchaeological questions when CT imaging is unavailable.

2.2. Cross-sectional geometric properties

Cross-sectional geometry provides a method for estimating the mechanical loading history of long bones by modeling bones as hollow beams (Ruff and Hayes, 1983). Using this theory, the amount of cortical bone in the cross-section of a long bone approximates its resistance to loading in tension or compression (Nordin and Frankel, 2000). Pure axial loading of the long bones is rare, however, due to shape constraints, superimposed loading forces and bone curvature (Lanyon, 1980; Rubin, 1984; Rubin et al., 1990). Instead, bending is the predominant loading pattern (Bertram and Biewener, 1988; Biewener et al., 1983; Lanyon and Rubin, 1980; Rubin and Lanyon, 1982, 1984; Rubin et al., 1990). In bending, a bone's mechanical behavior will be a function of both the amount and distribution of cortical bone in a cross-section, measured by the second moment of area (or area moment of inertia, I) (Nordin and Frankel, 2000). Resistance to bending (bending rigidity) may be evaluated along anatomical axes (e.g. I_x and I_y) or principal axes (I_{max} and I_{min}) of a cross-section. I_x and I_y estimate the bending strength of a cross section along the AP and ML axes, respectively, as measured from the centroid of the section. The distribution of bone around the principal axes gives an indication of the bending loads going through the bone. An animal that moves in a typical or repeated fashion presumably adapts sufficient rigidity in a diaphyseal cross-section to prevent bending or fracture in any plane that is loaded. The maximum second moment of area or maximum rigidity (I_{max}) approximates the magnitude of these bending loads.



Fig. 3. Top: Humeri (latero-medial view) of donkey (ZSM, 1968.696) and Somali wild ass (ZSM, 1963.133) with putty molds identifying the midshafts (50% section) of the bones. Bottom: Two-dimensional outline of donkey (696) and Somali wild ass (133) midshaft cross-sections. Horizontal line represents mediolateral axis.

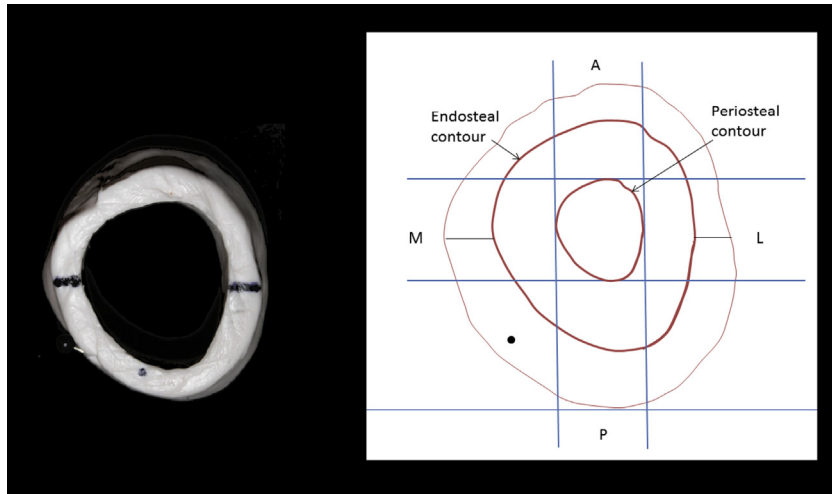


Fig. 4. Left: Polysiloxane putty mold of midshaft external contour of left donkey humerus (WU 1) after being removed from the bone. Horizontal marks indicate the mediolateral plane of the cross-section (distal view). Right: Two-dimensional image of the midshaft cross-section of left humerus (WU 1). External contour is transferred from the external mold on the left by photocopying. Internal contour is interpolated from the anterior, posterior, medial and lateral cortical thicknesses measured on the radiographs (blue lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Alternatively, in planes where bending loads are relatively low, less rigidity may be adapted, and this minimum rigidity is estimated by I_{\min} of a cross-section. The sum of any two second moments of area calculated about orthogonal axes (e.g. $I_x + I_y$ or $I_{\min} + I_{\max}$) is the polar moment of area (J) (Nordin and Frankel, 2000). The polar moment of area reflects overall bending or torsional rigidity of a cross-section (Ruff, 2000; Daegling, 2002).

Long bone strength was evaluated using cortical area (CA) as a measure of axial strength and the polar moment of area (J) as a measure of overall bending and torsional strength. A ratio of principal moments of area (I_{\max}/I_{\min}) was used to estimate the shape (circularity) of a cross-section by quantifying the amount of uniformity between its maximum and minimum bending rigidity. This ratio of principal moments of area (PMA) was used to infer the variability in loading regimes on the limbs of wild and domestic forms during locomotion.

2.3. Body mass estimation

Diaphyseal variables are highly correlated with body mass; for this reason, without proper size standardization, relatively heavier individuals have the potential to appear “robust.” This is especially

important in the current analysis given that domesticates are generally smaller than their wild ancestors. Body mass for each individual was estimated using a regression equation derived by Scott (1990) from a large reference sample of equids. Maximum humeral length was used as a predictor of body mass for each individual. Cortical area was scaled to body mass given its proportional relationship to the compressive and tensile strength of a bone in axial loading (Ruff et al., 1993). Polar moments of area were scaled to the product of body mass and moment arm length (i.e. bone length) given that the bending moment is the product of a force and its perpendicular distance from its point of application at the cross-section (Polk et al., 2000; Ruff, 2000).

3. Results

3.1. Measures of axial and bending strength

In almost all measures of long bone robusticity analyzed, significant differences were identified between the donkey and wild ass samples (Table 3). Axial strength in these samples, as estimated by cortical areas of the cross-sections, is significantly different for the humeri, radii and metatarsals ($\alpha = 0.05$), with the limbs of the

Table 3
Standardized cross-sectional geometric properties for domestic donkey and African wild ass.

		Humeri		Radii		Metacarpals		Metatarsals	
		Donkey	Wild ass	Donkey	Wild ass	Donkey	Wild ass	Donkey	Wild ass
CA	Mean	11.09	13.70	8.91	10.94	7.427	8.501	8.015	9.178
	SE	0.497	0.420	0.211	0.597	0.359	0.418	0.254	0.443
	N	6	7	5	7	6	7	6	5
J	Mean	104.4	180.9	35.2	67.8	37.2	56.3	35.8	53.2
	SE	6.29	13.24	2.083	7.302	2.479	5.060	2.53	3.60
	N	6	7	5	7	6	7	6	5
I_x	Mean	80.7	133.9	16.9	31.9	22.4	32.6	23.8	35.8
	SE	8.22	7.61	2.81	10.4	4.07	4.92	2.02	2.21
	N	6	7	5	7	6	7	6	5
I_y	Mean	23.6	47.0	18.2	35.8	14.8	23.7	11.9	17.4
	SE	3.96	16.8	2.19	9.59	2.90	7.02	1.02	1.12
	N	6	7	5	7	6	7	6	5
I_{\max}/I_{\min}	Mean	1.125	1.104	1.016	1.031	1.050	1.040	1.074	1.075
	SE	0.007	0.007	0.010	0.008	0.007	0.007	0.006	0.006
	N	6	7	5	7	6	7	6	5

wild asses having greater strength than those of the donkeys. The metacarpals of the two samples were also significantly different at a less stringent significance level ($\alpha = 0.10$). Similarly, measures of bending and torsional strength (J) are significantly greater in the wild ass than in the donkey sample for all bones analyzed ($\alpha = 0.05$). These differences were maintained when bending strength was evaluated along AP (I_x) and ML (I_y) axes.

These results are consistent with the hypothesis that wild asses demonstrate greater long bone strength than slower moving, domestic donkeys as measured by both cortical areas (axial strength) and polar moments of area (bending and torsional strength). This does not fit with the expectations of the secondary hypothesis that burden-bearing associated with donkey domestication increased the strength of the donkey's limb bones relative to the wild ass.

3.2. Diaphyseal shape and direction of greatest bending strength

For each element, comparisons between the two samples were evaluated qualitatively and graphically. There are no significant differences between species in this ratio for the radii, metacarpals or metatarsals. There are, however, significant differences in the shape of the humeri ($\alpha = 0.10$) as indicated by the PMA ratio, which gives an indication of how the limb was used. The wild asses have a more circular diaphysis as indicated by a lower PMA, while the donkeys are more elliptical, on average (Table 3). This structural difference is obvious when the values are examined quantitatively (Table 4) and in Fig. 5 (also see Fig. 3). In the scatterplot shown in Fig. 5, the samples are completely separated from one another with the donkey sample distributed in a lower position relative to the wild ass sample (or the donkey sample having more similar maximum and minimum second moments of area). Based on these shape differences, it is reasonable to infer that wild ass and donkey humeri are experiencing different patterns of strain in their humeri. A more circular diaphysis (a ratio closer to 1) as seen in the humerus of the wild ass is characteristic of an animal experiencing a greater range of forces over the full array of its locomotor behavior. In contrast, the more oval humeral shafts of the donkeys indicate a more consistent pattern of strains through the humeri.

4. Discussion

This study was undertaken in order to evaluate whether differences in locomotion or differences in burden-carrying between wild asses and domestic donkeys could be identified by changes in cross-sectional geometry of the limbs, independent of the body size of the animals. Sample sizes are small but differences identified in cross-sectional properties, and therefore in diaphyseal strength, in the limbs of African wild asses and donkeys suggest that analyses of shaft geometry can be used to isolate the behavioral shifts associated with domestication.

Consistent with the stated hypothesis, slower and more linear movement in donkeys resulted in lower axial and bending strains in their limbs; these results occur despite the added weight of load

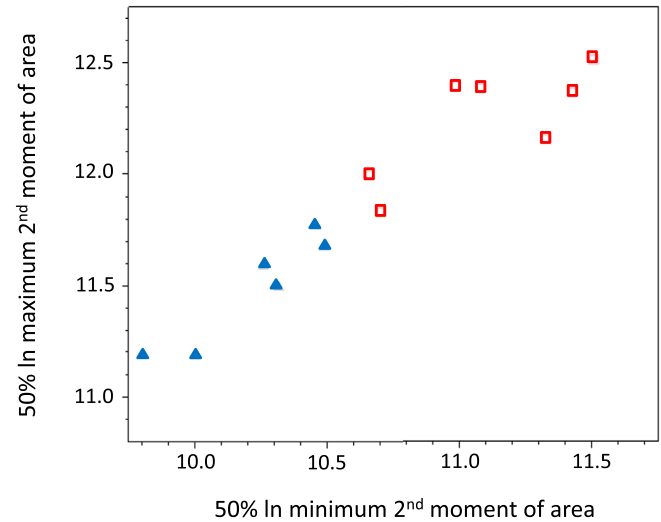


Fig. 5. Bivariate plot of humeral 50% In maximum second moments of area versus 50% In minimum second moments of area for wild asses (red squares) and donkeys (blue triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

carrying. Conversely, wild asses have greater axial and bending strength in their skeletal elements, and their forelimb diaphysis are more circular. These results may be interpreted as a reflection of the relative variability in locomotor behavior demonstrated by wild asses during daily activities. Studies of animals in the wild (Carlson et al., 2006, 2011) as well as animals performing natural and restricted movements (Biewener et al., 1981, 1983; Carlson and Judex, 2007; Demes and Carlson, 2009; Demes et al., 2006; Judex and Carlson, 2009; Moreno et al., 2008) indicate that non-steady behaviors (i.e. jumping, sudden accelerations, decelerations and directional changes) generate a greater range and distribution of external bending loads in the limbs than steady-speed locomotion. This behavioral variability within an animal's locomotor repertoire is subsequently reflected in greater amounts of cortical bone in the loaded limbs. This is also consistent with findings that an increase in the magnitude of loads being carried will not necessarily result in increased bone response of the support limbs; instead, a loading environment that produces high-magnitude, dynamic strains in unusual distributions is more effective in initiating adaptive responses than is a less active, static or routine strain environment (Judex and Zernicke, 2000; Lanyon and Rubin, 1984, 1985; Robling et al., 2001; Turner, 1998).

The differences between donkey and wild ass samples are particularly marked for the humerus as demonstrated by shape of the diaphyses. Wild ass diaphyses are more circular than those of donkeys, which were expected because a cylindrical shaft is best able to resist bending strains oriented in multiple directions. When strains on a limb are more consistent, a more elliptical diaphysis may emerge to maximize bending rigidity in the most-loaded plane as a preventative response to bone failure and minimize bone material in planes under less strain.

Taken together the results of this study provide a first step toward demonstrating that analyses of diaphyseal shaft geometry can provide information on gait changes during domestication. Eisenmann (1986, 1995, Eisenmann and Beckouche, 1986; Divé and Eisenmann, 1991) argued that differences in the proportions of modern African wild ass and donkey lower limbs were the result of the way that donkeys were used to carry heavy loads. Rossel (Rossel et al., 2008) also attributed small scale proportional shifts in the lower limbs of morphologically wild donkeys at Abydos to their use

Table 4
Results from cross-sectional analyses.

	Humeri	Radii	Metacarpals	Metatarsals
Standardized CA	0.002 ^a	0.020 ^a	0.082 ^b	0.041 ^a
Standardized J	0.001 ^a	0.005 ^a	0.008 ^a	0.003 ^a
Standardized I_x	<0.001 ^a	0.008 ^a	0.008 ^a	0.003 ^a
Standardized I_y	0.001 ^a	0.002 ^a	0.015 ^a	0.006 ^a
I_{\max}/I_{\min}	0.056 ^b	0.264	0.320	0.954

^a Significant at $\alpha = 0.05$.

^b Significant at $\alpha = 0.10$.

by ancient Egyptians for load-carrying. Our results indicate, however, that changes in *gait* with domestication and transport use had more significant morphological effects than did the distribution of burdens carried by ancient donkeys. Given this result, further exploration of the skeleton – including additional hindlimb elements – will help to clarify the changes in locomotion that accompanied domestication.

4.1. Perspectives on gait changes with domestication

The finding that shifts in *gait* and a less active, more routine strain environment had greater effects on the morphology of early domestic donkeys than did load-carrying, places a new emphasis on understanding the context for changing donkey locomotion in pastoral settings during domestication. Archaeology, ethnography and ethology provide long-term perspectives on this process. Archaeological data demonstrate that a reliance on donkeys as pack animals has been consistent through history, with the direction of selection during domestication being for load carrying and traction rather than for speed. Herding and night penning led to shorter distances traveled by donkeys than African wild asses, as well as reduced territories and mobility and slower gaits to accommodate groups. Increased sociality is a hallmark of domestication, which in the long-term results in fewer agonistic encounters, and consequently fewer episodes of rapid gait change (Marshall and Asa, 2012; Marshall and Weissbrod, 2011). Lower incidences of predation would have the same effect. The movement of contemporary pastoral donkeys is, therefore, slower, more restricted and characterized by fewer and shorter bursts of activity than that of wild asses.

In addition to selection acting on small groups of pastoral and household donkeys, a large number of donkeys were subject to selective forces specific to ancient cities and states, especially for use in trade. Information on intensive use of donkeys on long-distance trade routes in ancient states suggests that this played a key role in selection for slower gaits and more linear locomotion. Large numbers of tightly packed animals traveled with heavy loads and little water on long-distance desert routes (Greenfield et al., 2012; Marshall, 2007; Potts, 2011). In ancient Egypt, 50–1000 donkeys carried ebony, ivory and gold over the 400 km Abu Ballas Trail (Förster, 2007). The Sumerians relied on donkeys and mules to carry tin and textiles over the Taurus Mountains (Postgate, 1986, 1992). Donkeys operated at the boundaries of their physiological abilities to cope with loading in desert environments on such routes and even today mortality can be high in African donkeys used on trade routes. Under such conditions pace is affected by the speed of the animal in front. Maloiy (Maloiy et al., 2009; Yousef et al., 1972) observed that working donkeys are often required to move at relatively slow speeds, which might differ from those preferred by the animals. There is also strong selection for donkeys to rely on their most energetically efficient gait—the walk—in order to survive. Archaeological and ethological data together identify a range of areas on which selection acted in pastoral and trade settings. There have, however, been very few quantitative studies of locomotion that would provide more detailed information on contrasts between donkeys and wild asses, and none on the locomotion patterns of donkeys or other domestic animals living in pastoral villages.

The role of donkeys in ancient cities and states also highlights the applicability of using long bone data to investigate questions about domestication. Since it appears that donkeys were used for traction and transportation of household goods rather than for food from the first, their skeletons were often discarded *in toto* after service. Their role as status animals, for warfare or for provisioning luxury goods helps explain why equids were deposited inside

archaeological features associated with elite households, such as the royal cemetery of Abydos in Middle Egypt (Rossel et al., 2008), the Hyksos capital of Avaris in the Nile Delta (von den Driesch and Peters, 2002) or the elite site of Umm el-Marra near Aleppo (Weber, 2008). Old World camels are of interest as well, because these animals were also discarded and sometimes even buried. In the Arabian Peninsula, for example, complete (but decapitated) animals were deposited intentionally in pits in Classical times (Vogt, 1994). In these and similar archaeological situations, cross-sectional analyses of the long bones of load-carrying animals such as donkeys, horses and their hybrids as well as one- and two-humped camels and their hybrids have the potential to clarify their domestication status and possible use through time.

5. Conclusion

The load carrying role of donkeys has been more emphasized by scholars of domestication than gait changes associated with ranging, grazing or the management of animals. Our findings suggest that changes in gait with domestication are an important area for future study. They also support using shaft geometry to identify shifts in diaphyseal strength in the limbs of African wild asses with domestication. Wild ass forelimbs have greater amounts of cortical bone than donkeys, and their humeral diaphyses are more cylindrical, indicating better resistance to a varied locomotor repertoire. Data collection is non-invasive and non-destructive and can be performed with portable machinery, and with favorable political conditions and local collaborations it should be possible to apply this method to specimens from Abydos, Abusir and ancient donkey burials in southwest Asia. Furthermore, because locomotion and gait changes have proven to be the key shifts mirrored in shaft geometry, rather than loads, this approach need not be confined to donkeys or even to transport animals. The gaits of transport animals are likely to be particularly affected by their load carrying and handling, and this method has the potential to be an effective indicator of domestication or human intervention with horses, cattle, dromedaries, Bactrian camels, llamas and yaks. However, shifts in locomotion have been little explored among large domestic mammals. Depending on the intensity of management, confinement in pens and herding of animals in dense groups at slow paces, is likely to have affected locomotory patterns of a wide range of domesticates including cattle, sheep and goats.

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