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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Exploring height estimations of past and present *Equus* from metapodial dimensions

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Methods to estimate withers height, croup height and other body dimensions from skeletal dimensions of *Equus* should be developed because these dimensions, generally taken from living domestic *Equus*, are needed in combination with body mass to determine locomotor ability and thermoregulation. In this study, I applied the so-called hybrid approach to height estimation of past and present *Equus* because there are only few *Equus* for which heights and skeletal dimensions are available for extant and extinct specimens. First, I performed anatomical reconstructions of shoulder joint, hip joint, croup height, and withers heights of extant *Equus* representing all extant species. Second, I generated single-predictor regression equations by regressing these four heights against metapodial lengths and two-predictor equations by regressing them against metapodial lengths and distal-breadth–length ratios. Because two-predictor equations outperformed single-predictor ones in samples of extant *Equus*, I used only two-predictor equations to estimate heights of extinct *Equus*.

Introduction

There is a great deal of interest in the temporal and geographic variation of body size in evolutionary biology, ecology, paleontology, and paleoanthropology. Body mass determines various aspects of physiology (e.g., metabolic rate), life history, ecology, social structure, and behavior (e.g., Damuth & MacFadden 1990, Saarinen *et al.*, 2021, Nacarino-Meneses 2023). Linear dimensions and their proportional relationships (i.e., body shape) combined with body mass affect locomotor ability (Ruff & Niskanen 2018, Niskanen & Bindé 2021) and have implications for thermoregulation through affecting the body surface-area–body-volume ratio (Goldenberg *et al.* 2022). We should aim to estimate body mass and all body dimensions of archaeological and palaeontological equids that can be estimated from skeletal dimensions to gain more information on evolution, phenotypic plasticity, effects of artificial selection, and human–equid relationships.

Body mass of past equids is generally estimated following Scott (1990), Alberdi *et al.* (1995) or Eisenmann and Sondaar (1996). Unfortunately, body mass estimations from skeletal dimensions are only approximations due to regional, seasonal and individual variation in the body-mass–skeletal-size relationship. This affects estimation accuracy even when appropriate and large reference samples of specimens with known body mass are available as is the

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case with osteological studies of humans. There are naturally more problems in body mass estimation of extinct taxa without appropriate reference samples (Ruff & Niskanen 2018). We do not have enough equid specimens with known body mass and skeletal dimensions for sufficient reference samples.

We can expect height estimations to be more accurate than body mass estimations because bone lengths determine limb segment lengths, and summed limb segment lengths representing total limb lengths largely determine total heights at the withers and at the croup in equids and other animals of similar body type. Shoulder-joint height combined with scapular length represents the total forelimb length and largely determines the height at the withers, whereas hip-joint height itself represents the total hindlimb length and largely determines the height at the croup.

Estimating the above linear dimensions is important. For instance, total limb lengths determine step length (the distance between the points of initial contact of the opposite feet) and stride length (the distance between successive contacts of the same foot). Light riding horses and heavy draft horses of the same heights but different body masses demonstrate that total limb lengths relative to body mass combined with differences in limb segment proportions affect locomotion ability (e.g., velocity, jumping ability). The ability to travel long distances at speed is essential for those wild equids, which need extensive foraging ranges due to sparsity of resources.

As already mentioned, the body-mass–limb-length relationship affects the body-surface-area–body-volume ratio, which has implications for thermoregulation. All domestic horses derive from horses of the Pontic-Caspian Steppe, which began dispersing from this steppe region no more than about 4200–4300 years ago (Librado *et al*. 2021, Niskanen 2023). Native types of horses clearly conform to Allen's rule (Allen 1877) but not necessarily to Bergmann's rule (Bergmann 1847). These native horses exhibit relatively short-limbed phenotypes in cold climates and long-limbed ones in hot climates but are not larger overall in cold climate than in hot climate, suggesting that seasonal shortage of forage overrides selection for larger size in high latitudes. Past *Equus* may also have exhibited more ecogeographical patterning in body shape than in body size (*see* van Asperen 2010) but assessing this requires both body mass and total limb length estimations. Unfortunately, most fossil specimens are not represented by adequately complete skeletons for direct determinations of their total limb lengths and heights in addition to body mass estimations.

Although many osteoarchaeological studies include the withers height estimation, there has been very little development of estimation methods. Most researchers still estimate withers height by applying withers-height–limb-bone-length ratios provided by May (1985) based on anatomically reconstructed withers heights of 28 horses and the known withers height of only one horse in Kiesewalter (1888). Some perform these estimations following Vitt (1952) based on a table presenting eight-centimeter withers height classes and corresponding greatest length measurements of bones.

We have been limited to using this 'hybrid approach' where reconstructed heights represent living heights due to a shortage of equids with known living heights and matched skeletal dimensions. Only 15 horses with known withers heights were included in Niskanen (2023) and, as far as I know, no study includes known living heights of other species of *Equus*. Therefore, we cannot be confident that we can accurately estimate living heights of donkeys, wild asses, and zebras from their skeletal dimensions.

Estimating croup height is almost universally neglected. This is unfortunate because this height is a better height measure for interspecies comparisons of *Equus* than withers height, which is affected by variation in the projection of the spinous processes forming the withers above the scapular dorsal border. As a result, there are differences in the croup-height–withers-height ratio among species of *Equus* as well as between different types of domestic horses (Willoughby 1974: table 30).

In this study, I explored the estimation of shoulder joint and hip-joint heights as well as total heights at the withers and at the croup of different species of extant and past *Equus* from metapodial dimensions. I applied the hybrid method due to very small numbers of equids with known living heights as was done by Kiesewalter (1888) in his estimation of withers height of horses, and is increasingly done in studies of estimating statures of past human populations with the 'anatomical method' (e.g., Ruff *et al*. 2012, Niskanen & Ruff 2018). Regressing these anatomically reconstructed heights against limb bone lengths provides equations to estimate heights from these bone lengths for individuals representing past populations.

I selected metapodials for this exploration of height estimation for two reasons. First, these bones are far more often sufficiently preserved to be measured than longer limb bones. Second, the metapodial shape (e.g., breadth–length ratio) reflects the limb segment proportions. Metapodials with small joints relative to their length associate with light build and distal elongation, whereas stout ones associate with heavy build and distal shortening (Niskanen 2023, M. Niskanen & N. Piipponen unpubl. data).

I included distal breadths of metapodials but not shaft breaths and depths in estimations because there is quite a lot of change in shaft thicknesses after the epiphyseal fusion. External diameters and cortical bone walls of bone shafts become thicker with age in adolescents and younger adults as a response to mechanical loading caused by body mass and physical activity. In older adults, external diameters of bone shafts continue to increase through periosteal apposition, but cortical bone walls become thinner due to endosteal bone resorption (Borer 2005). There should be little or no age-related change in joint breadths after the epiphyseal fusion. For example, the vertical diameter of the femoral head increases up to 17 years in human males and up to 15 years in human females, whereas the fusion of the femoral head occurred at 17 years in males and 16 years in females in the same study sample (Rissech *et al*. 2008). I thus expected that there would be little to no age-related changes in distal articular breadths of metapodials, possibly some changes in their distal supra-articular breadths, and considerable changes in their shaft diameters after the distal epiphyseal fusion, which in horses occurs within 8–14 months of age (Rogers *et al*. 2021).

Material and methods

Skeletal samples

The reference sample of height estimation used in this study included 288 equids representing all species of extant *Equus* (Table 1). Minimum requirements for these reference samples were measured lengths of humerus, radius, metacarpal, metatarsal, distal breadths of metacarpals and metatarsals, and an adequate number of phalangeal lengths (at least that of the first phalanx) to allow estimating fetlock height. This reference sample included 285 equids from data made publicly available by Véra Eisenmann (https://vera-eisenmann.com) and three horses with known withers heights from Niskanen (2023). Twelve other modern horses with known living heights from Niskanen (2023)

Table 1. Reference samples of extant *Equus*. All but three are recent zoological specimens measured and made publicly available by Véra Eisenmann (https://vera-eisenmann.com). Three other specimens are warmblood sport horses measured by me.

Sample no.	Common name	Scientific name	Sample size (*n*)
1	Asiatic wild ass	*E. hemionus*	67
2	Donkey	*E. africanus asinus*	28
3	African wild ass	*E. a. africanus* & *E. a. somaliensis*	12
4	Grévy's zebra	*E. grevyi*	26
5	Mountain zebra	*E. zebra*	25
6	Plains zebra	*E. quagga*	35
7	Przewalski's horse	*E. ferus przewalskii*	37
8	Domestic horse	*E. ferus caballus*	44
9	Mule	*E. a. a. + E. f. caballus*	14
			Total 288

were not included in the reference sample due to missing metapodial distal breadth measurements or phalanges, but were included in generating equations to estimate withers height from shoulder-joint height and croup height from hip-joint height. All equids included in my reference sample were fully adult, i.e., specimens with unfused epiphyses of limb bones were not included in this sample.

Osteometric measurements follow the protocol established by Eisenmann (Eisenmann 1986: 39), whose abbreviations are also used for these measurements in regression equations. Full names and abbreviations (including abbreviations used by von den Driesch 1976) of the variables and metapodials measurements are given in Table 2 and Fig. 1, respectively. 'Bd' of von den Driesch (1976: fig. 44a and b) refers to greatest breadth of the distal end, which is generally articular breadth in caballine *Equus* and supra-articular breadth in non-caballine *Equus*.

I replaced the species name *E. caballus* with the species name *E. ferus* in past and present horses because the International Commission on Zoological Nomenclature proposes giving in naming priority to wild animal species over their domestic derivatives (Gentry *et al*. 2003). Therefore, I recognized the domestic horse with the subspecies name *E. f. caballus* and the Przewalski's horse with the subspecies name *E. f. przewalskii*. I included all caballine horses of Eurasia in *E. ferus* as has been done by an increasing number of researchers (e.g., Boulbes & Asperan 2019, Cirilli *et al*. 2022). My sample of modern domestic horses included 14 small ponies less than 120 cm tall, 17 horses and ponies at least 120 cm tall representing different landraces, 12 horses representing warmblood horses (three Arabian horses and 12 warmbloods), and one heavy draft horse. This domestic horse sample was thus not very representative of domestic horses.

I included the kiang as a subspecies of the Asiatic wild ass (*E. hemionus kiang*) following Bennett *et al*. (2017). The Asiatic wild ass sample (*E. hemionus*) included the following subspecies: *E. h. hemionus* (*n* = 9), *E. h. onager* (*n* = 26), *E. h. kulan* (*n* = 11), *E. h. hemippus* (*n* = 3), *E. h. khur* (*n* = 1), and *E. hemionus kiang*

Table 2. Osteometric measurements and variables.

Osteometric measurements and variables	Abbreviation (Eisenmann)	Abbreviation (von Driesch)
Greatest length of scapula	SCA1	HS or DHA of scapula
Metacarpal greatest length	MC1	GL of metacarpal
Metacarpal lateral length	MC2	LI pf metacarpal
Metatarsal greatest length	MT1	GL of metatarsal
Metatarsal lateral length	MT2	LI of metatarsal
Distal supra-articular breadth of metacarpal	MC10	Bd of metacarpal
Distal articular breadth of metacarpal	MC11	Bd or BFd of metacarpal
Distal supra-articular breadth of metatarsal	MT10	Bd of metatarsal
Distal articular breadth of metatarsal	MT11	Bd or BFd of metatarsal
Distal supra-articular breadth of metacarpal relative to greatest length	MC10/MC1 × 100	
Distal articular breadth of metacarpal relative to greatest length	MC11/MC1 × 100	
Distal supra-articular breadth of metacarpal relative to lateral length	MC10/MC2 × 100	
Distal articular breadth of metacarpal relative to lateral length	MC11/MC2 × 100	
Distal supra-articular breadth of metatarsal relative to greatest length	MT10/MT1 × 100	
Distal articular breadth of metatarsal relative to greatest length	MT11/MT1 × 100	
Distal supra-articular breadth of metatarsal relative to lateral length	MT10/MT2 × 100	
Distal articular breadth of metatarsal relative to lateral length	MT11/MT2 × 100	
Metatarsal lateral length relative to hip-joint height	MT2/HJH × 100	
Shoulder-joint height	SJH	
Hip-joint height	HJH	
Withers height	WH	
Croup height	CH	
Relative croup height	CH/WH	

(*n* = 6), as well as a group of wild asses with unknown subspecies affiliation (*n* = 11). The African wild ass sample (*E. africanus*) includes both subspecies: *E. a. africanus* (*n* = 2) and *E. a. somaliensis* (*n* = 10). I acknowledged uncertainties regarding delimiting subspecies and even species of these wild asses as well as other past and present *Equus* (Bennett *et al*. 2017, Geigl & Grange 2012).

I included all the Grévy's zebras (*E. grevyi*) in one sample because this species is monotypic. I did not subdivide the plains zebras (*E. quagga*) according to subspecies proposed by Groves and Bell (2004) because Pedersen *et al.* (2018) found that the genetic structure of this zebra species does not coincide with these subspecies. Eisenmann did not divide mountains zebras (*E. zebra*) according to subspecies. Therefore, I included these mountain zebras in one sample.

Metapodial dimensions for past *Equus* were from Eisenmann (https://vera-eisenmann.com). The earliest sample of past equids is *E. simplicidens* (Cope 1892) represented by metapodials from the Hageman quarry in Idaho, USA. These fossils dating younger than 3.4 million years and possibly as young as 3.2 million years (Richmond *et al*. 2002 and references therein) represent late representatives of this earliest recognized *Equus* species, commonly known as the Hagerman horse.

The next oldest fossil material was represented by metapodials of the Mosbach horse, originally *E. mosbachensis* von Reichenau, 1903, but here *E. ferus mosbachensis*, from the Mosbach quarries, Germany, dated to MIS (Marine isotope stages) 15 or 13 (Palombo & Alberdi 2017 and references therein). Therefore, this material dated to within 0.621–0.563 or 0.533–0.478 million years ago, based on dates of MIS in Lisiecki *et al*. (2005), does not represent the earliest Mosbach horses. The first occurrence of this caballine species coincides with the Matuyama-Brunhes reversal approximately 0.781 million years ago (Markova & Vislobakova 2016).

Metapodials from the La Brea Tar Pits from Los Angeles, California, USA, represented the Western horse (*Equus occidentalis*). This Late Pleistocene horse of western North America was related to the extant caballine lineage based on morphological similarity (Barrón-Ortiz *et al.* 2019) but genomic samples from this horse have not yet been examined.

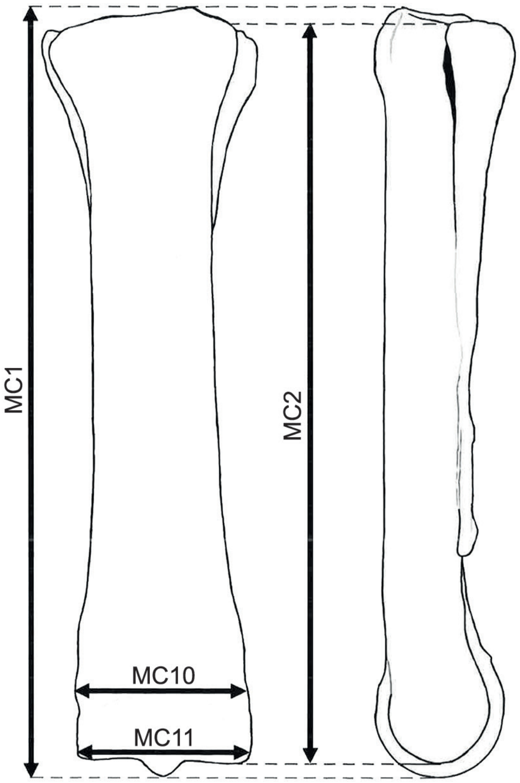

Fig. 1. Metacarpal example of metapodial dimensions used in this study. MC1 = Metacarpal greatest length (GL), MC2 = Metacarpal lateral length (Ll), MC10 = Distal supra-articular breadth of metacarpal, MC11 = Distal articular breadth of metacarpal (BFd). Corresponding metatarsal dimensions are MT1, MT2, MT10, and MT11. Greatest breadth of the distal end (Bd of von den Driesch 1976: fig. 44a and b) generally corresponds with MC11 or MT11 in caballine *Equus* and with MC10 or MT10 in non-caballine *Equus*.

The Late Pleistocene horses of western Eurasia were represented by metapodials of the following subspecies: *E. ferus antunesi* (Antunes' horse), originally, *E. caballus antunesi* from the Iberian Peninsula (Cardoso & Eisenman 1989); *E. ferus gallicus* (Gallic horse), originally *E. caballus gallicus* from Western Europe north of the Pyrenees (Prat 1968); *E. ferus arcelini* (Arcelini horse), originally *E. caballus arcelini*, which replaced *E. f. gallicus* in western Europe during the terminal Pleistocene (Guadelli 1991), and *E. ferus latipes* (Latipes horse), originally *E. latipes* of the South Russian Plain (Gromova

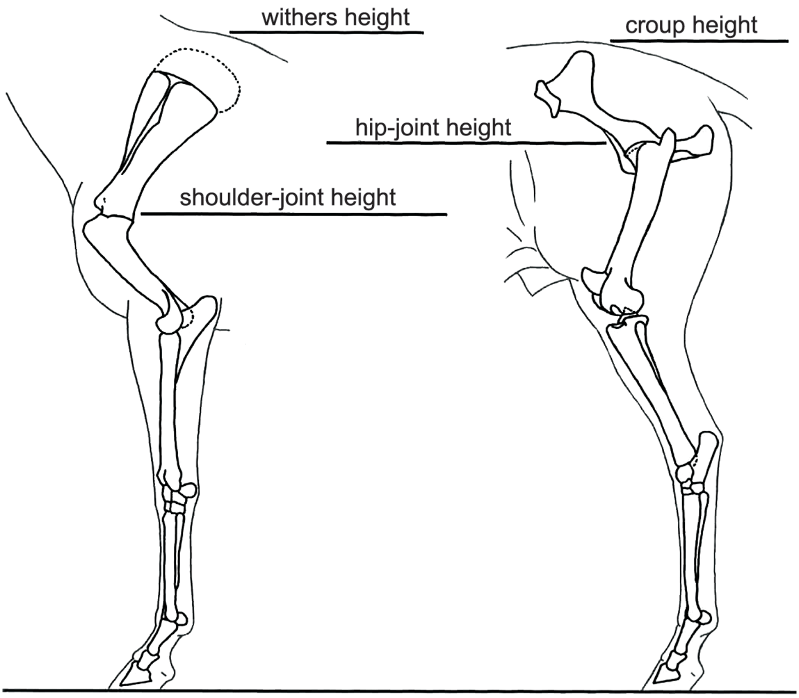

Fig. 2. Heights reconstructed and/or estimated in this study.

1949), which was contemporary with the Gallic horse of western Europe. Subspecies assignations of the above horses are discussed by Eisenmann (2022) and Uzunidis *et al.* (2024).

Anatomical reconstructions of skeletal and living heights

The hybrid method I applied in this study involves reconstructions of skeletal heights represented by shoulder joint and hip-joint heights followed by conversions of these heights to corresponding living heights at the withers and croup, respectively (Fig. 2). I reconstructed shoulder and hip-joint heights representing skeletal heights as in Niskanen (2023: supplementary information B), thus I do not describe these methods here. Instead, I focus on the methods to estimate withers height from shoulder-joint height and croup heigh from hip-joint height because these methods are revisions of those in Niskanen (2023).

I did not include scapular length in the determination of the skeletal height and thus length of the forelimb due to variation in the scapular dorsal border shape. The greatest length of the scapula is usually between the ventral articular angle at the shoulder joint and the caudal angle of the dorsal border but variation in the dorsal border shape results in the most distant point of the scapula being located anywhere between the cranial angle and the caudal angle. Therefore, I included this scapular length as a separate variable in estimating withers height from shoulder-joint height.

The anatomically reconstructed shoulder-joint and hip-joint heights are not exact heights. They are roughly equally affected by the variation in joint angles resulting in the variation in bone shaft inclinations (mostly of humerus, femur, tibia and pasterns), the hoof sole and cup heights, and the joint-cartilage thickness. I expected that there would be some interspecific variation in joint angles, affecting the reconstruction accuracy.

Estimations of withers height and croup height are likely more inaccurate than anatomical reconstructions of shoulder joint and hip-joint heights. There are uncertainties involved in estimating these living heights from shoulder-joint and hip-joint heights, respectively, due to a shortage of individuals with known living heights. Also, these height measurements of living equids are not exact but prone to errors.

Height measurements taken from the same equid at different times and/or by different people can easily vary by a few centimetres (e.g., withers heights of my two mares varied within 157–161 cm and 164–167 cm). Measurement instruments and techniques affect the results (Lamas *et al.* 2007, van de Pol & van Oldruitenborgh-Oosterbaan 2007). Is should also be kept in mind that the trunk of a horse hangs in a muscular sling between the forelimbs without osseus contact (Payne *et al.* 2004), so withers height can change with the level of alertness and physical fitness (Lamas *et al.* 2007, van de Pol & van Oldruitenborgh-Oosterbaan 2007, and author's pers. obs.). The soft tissue thickness at the withers and at the croup also varies. Variation in the adiposity layer thickness affects withers and croup heights by about 1 and 2 cm, respectively (Ojala *et al.* 2007: 160). In addition, the development of the middle gluteal muscle affects croup height (Kersten & Edinger 2004). Hoof trimming affects heights of domestic horses a centimetre or so (own obs.).

In a sample of 15 horses in Niskanen (2023: supplementary information B) with known withers heights, withers height was strongly correlated with the reconstructed shoulder-joint height ($r = 0.994$), but estimating withers height of horses from the shoulder-joint height with a mean breed/type-specific multipliers (withers-height–shoulder-joint-height ratios) as in Niskanen (2023) results in some directional estimation error because the withers-height–shoulder-joint-height ratio is negatively correlated with the shoulder joint ($r = -0.490$, $n = 52$) and withers heights ($r = -0.279$, $n = 52$) in living horses I personally measured. Also, this ratio approach is likely inapplicable to other species of *Equus* because differences in relative lengths of scapula and spinous processes at the withers result in different withers-height–shoulder-joint-height ratios among species.

Due to the above, I took the greatest length of scapula into account in estimations of withers heights. Subtracting shoulder-joint height from withers height and dividing the difference by greatest length of scapula (*see* Fig. 3) gives a ratio of 1.1576 for five horses with known withers height. My best estimates of this scapular ratio in asses, donkeys, zebras, and Przewalski's horses is 1.1214, and in mules it is 1.1325. These ratios differ due to the differences in the relative lengths of spinous processes forming the withers because the caudal angle of the scapula is generally placed slightly above the transverse process of the 6th thoracic vertebra (Fig. 4). Differences in relative lengths of spinous processes result in domestic horses, especially those bred for riding, tending to have tall withers heights relative to croup heights whereas other equids (including many native breeds of domestic horses) tending to be taller at the croup.

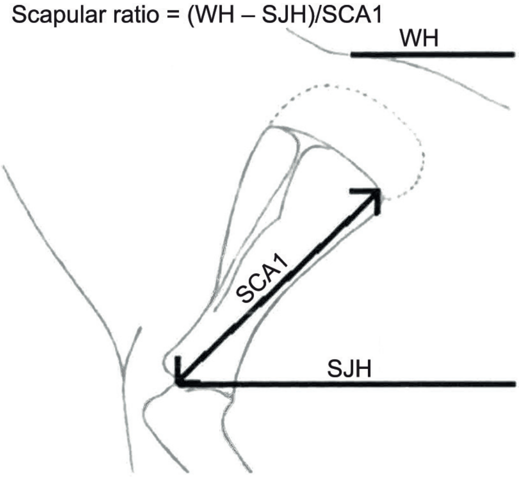

Fig. 3. Calculation of a scapular ratio for estimating withers height (WH) above shoulder-joint height (SJH) from greatest scapular length (SCA1).

I estimated withers heights by multiplying greatest scapular lengths by the above ratios and adding the products to shoulder-joint heights. This procedure provided withers heights for 280 of 288 equids. I estimated withers height from shoulder-joint height for 80 equids without scapular lengths with a reduced-major axis regression equation (withers height = 1.428 × shoulder-joint height – 42.258; $r = 0.989$, SEE = 19.254, $n = 208$). I used sample-specific ratios (*see* Table 1) of withers heights estimated from scapular length and shoulder-joint height and estimates provided by the above regression equation (Table 3) to generate adjusted withers heights for 80 equids without scapular lengths. It was necessary to include these 80 equids because some of the samples would have been too small to be representative. For example, there would have been only 17 domestic horses.

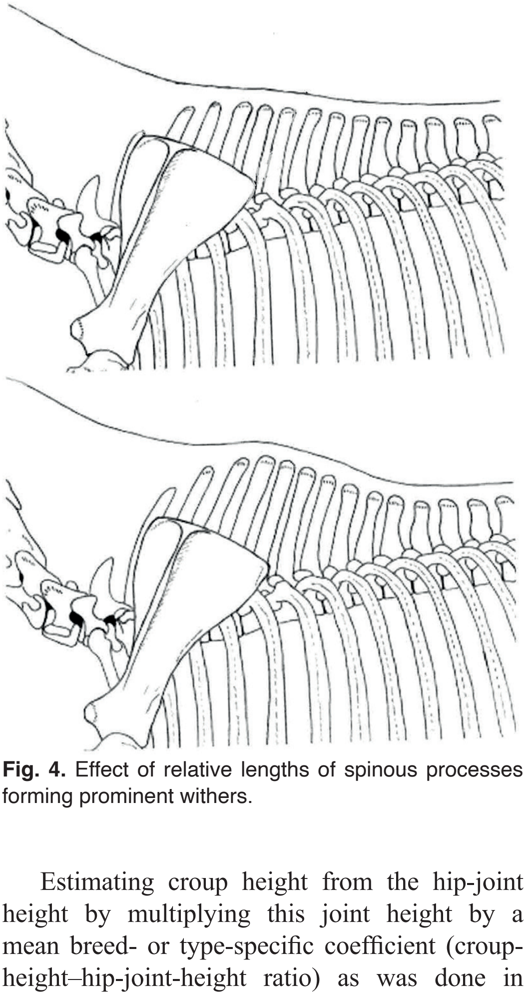

Fig. 4. Effect of relative lengths of spinous processes forming prominent withers.

Estimating croup height from the hip-joint height by multiplying this joint height by a mean breed- or type-specific coefficient (croup-height–hip-joint-height ratio) as was done in Niskanen (2023) resulted in overestimation in tall horses and underestimation in short ones because — as demonstrated by a small sample of 13 horses (one draft horse, two Arabians, two Thoroughbreds, five modern warmbloods, and three pony-sized horses) included in this study — the croup-height–hip-joint-height ratio correlated negatively with both croup height ($r = -0.431$) and hip-joint height ($r = -0.534$). Large horse breeds have lighter newborn foals relative to their dams' body weight than small ones (Walton and Hammond 1938, Platt 1984) which may well explain why taller horses tend to have smaller croup heights relative to hip-joint heights than shorter horses of the same general body type. Smaller newborn foals relative to maternal sizes should have smaller pelvic inlets and thus lower pelvic inlet heights and croup heights relative to their hip-joint heights. Therefore, I estimated croup height from hip-joint height using the following reduced-major-axis regression: croup height = 1.144 × hip-joint height + 65.373; $r = 0.993$, SEE = 21.165, $n = 13$. This regression provided accurate estimates of croup height in a small reference sample of 13 horses but is unlikely to perform equally well in all equids. It may however underestimate croup heights in very heavy draft horses, which generally have steeper pelvis inclinations due to the need to support their heavier body than light riding horses (*see* Willoughby 1974: 433–435, table 18). Combined with larger and thus taller pelvic inlets than those of lighter horses of the same hip-joint height due to bigger newborn foals, this more inclined pelvis likely results in taller croup heights relative to hip-joint heights. Sex differences likely also affect this ratio. Larger vertical diameters of the pelvic inlet of mares (*see* Budras *et al.* 2011: 72) should result in slightly taller croups relative to hip-joint heights than in stallions and geldings of the same size and conformation.

Table 3. Ratios of withers heights estimated from scapular length and shoulder-joint height, and withers heights from a regression equation using shoulder-joint height (withers height = 1.428 × shoulder-joint height – 42.258, $r = 0.989$, SEE = 19.254, $n = 208$); n = specimens with withers heights estimated from shoulder-joint height and scapular length only.

Sample	*n*	Reconstructed/estimated withers height
Asiatic wild ass	49	0.9865
Donkey	14	0.9972
African wild ass	7	1.0095
Grévy's zebra	24	1.0053
Mountain zebra	25	1.0087
Plains zebra	30	1.0033
Przewalski's horse	33	1.0006
Domestic horse	17	1.0208
Mule	9	0.9966

There may be differences in the pelvic configuration among species, which affect the estimation of croup height from hip-joint height. For instance, newborn donkeys and mountain zebras as well as some other species of *Equus* may be lighter relative to their dams' size than those of horses of the same size. Birthweights of newborn foals of a large-sized Martina Franca donkey breed average a little more than 8%

of their dams' body weight based on newborn foals of jennies weighing 380–420 kg averaging 33.4 kg (Carluccio *et al*. 2021). Birthweights of Harmann's mountain zebra foals average almost exactly 6% of their dam's body weight given that foals average 25 kg and mares 276.3 kg (Joubert 1974). For comparison, birthweights of foals of the Arabian horse mares in the United Arab Emirates average 48.1 kg (Wilsher *et al*. 2020: table 2), which is about 11% of their dams' body weight if these Arabian horse mares were average in size for their breed (weighing about 418–432 kg) (Willoughby 1974: 155). There may also be differences in the pelvic configuration among species not related to obstetrical factors and size, which affect the estimation of croup height from hip-joint height.

Values (mean, SD, min., max.) for shoulder-joint height, hip-joint height, withers height, and croup height for nine samples of extant *Equus* (Table 4) are consistent with expectations, as are those for different types of horses (Table 5). The croup-height–withers-height ratios cited here are similar to those presented by Willoughby (1974: table 30). The most notable exception is the only draft horse in the domestic horse sample. This horse's croup-height–withers-height ratio of 0.9727 would be typical for modern warmblood sport horses but very atypical for heavy draft horses. This underestimation of croup height of this heavy draft horse confirms my expectations (*see* above).

Regression equations and statistical procedures

I regressed anatomically reconstructed shoulder-joint height (SJH; Table 6), hip-joint height (HJH; Table 7), withers height (WH; Table 8), and croup height (CH; Table 9), against (1) metapodial length (single-predictor regressions) and (2) metapodial length and metapodial-distal-breadth–length ratios (two-predictor regressions) to produce equations for calculating SJH, HJH WH and CH. It should be noted that regressions based on the reduced-major-axis formula, generally more appropriate for specimens at both extremes of variation, are steeper than ordinary least-square regressions.

To evaluate the regressions, I calculated standard error of estimate (SEE), percent prediction error (%PE = ((reconstructed – estimated)/estimated) × 100; positive and negative values indicate underestimation and overestimation, respectively), absolute %PE (Abs.%PE), and reconstructed–estimated-height ratios (greater than 1 indicate underestimation, smaller than 1 overestimation). All statistical analyses and generating graphs were undertaken with SPSS ver. 27.

Results and discussions

Applying regression equations for estimating height from metapodial dimensions in the reference sample

Mean %PE values for estimates of shoulder-joint height and hip-joint height (Table 10), and withers height and croup height (Table 11) reveal that there was more under- or overestimation if heights were estimated only from metapodial lengths with single-predictor, than if heights were estimated from both metapodial lengths and distal-breadth–length ratios with two-predictor regressions. Therefore, as expected, this resulted in lower mean and median Abs. %PE values (Table 12). In addition, the mean %PE and median Abs. %PE indicate that there is more estimation error in withers height estimation than croup-height estimation reflecting differences in the relative prominence of withers. This is exemplified by underestimated withers heights and accurately estimated croup heights of domestic horses.

The finding that using metapodial length and distal-breadth–length ratio in regressions provides more accurate estimates than including metapodial length alone was expected because metapodials with small joints relative to their length tend to be long relative to height and *vice versa* (Niskanen, 2023). This is apparent when comparing mean values of metatarsal lateral length relative to hip-join height (MT2/HJH × 100), and distal articular breadth of metatarsal relative to lateral length (MT2/MT2 × 100). Correlations between these two variables are also negative in all nine samples (Table 13), demonstrating that this is typical to individual equids within each sample. Plotting regressions for nine mean values of these two variables and values for 288 individual equids (Fig. 5), further demonstrated that metapodial shape strongly reflects metapodial length relative to height both

Table 4. Shoulder-joint heights (SJH), hip-joint heights (HJH), withers heights (WH), croup heights (CH) and CH-to-WH ratios in extant *Equus*; for samples sizes *see* Table 1.

	SJH (mm)	HJH (mm)	WH (mm)	CH (mm)	CH/WH
Asiatic wild ass					
mean	873.9	1020.4	1189.1	1232.8	1.0371
SD	43.2	46.3	58.0	53.0	0.0147
min.	759.9	875.4	1016.7	1066.8	1.0037
max.	982.6	1129.6	1335.8	1357.6	1.0821
Donkey					
mean	815.2	957.9	1117.4	1161.3	1.0403
SD	119.3	140.1	161.0	160.2	0.0151
min.	625.8	746.0	849.0	918.7	1.0113
max.	1069.8	1251.3	1456.7	1496.9	1.0822
African wild ass					
mean	848.5	1003.2	1180.5	1213.1	1.0275
SD	32.2	46.8	47.0	53.5	0.0121
min.	761.5	870.2	1053.1	1060.8	1.0073
max.	878.6	1043.7	1220.8	1259.3	1.0455
Grévy's zebra					
mean	970.7	1138.4	1350.9	1367.7	1.0126
SD	23.0	24.1	33.8	27.5	0.0117
min.	924.5	1089.4	1286.1	1311.7	0.9917
max.	1012.4	1177.3	1410.8	1412.2	1.0442
Mountain zebra					
mean	875.1	1037.5	1217.8	1252.3	1.0287
SD	33.1	36.0	51.3	41.2	0.0144
min.	817.0	971.8	1143.2	1177.2	1.0066
max.	944.4	1126.1	1321.2	1353.6	1.0702
Plains zebra					
mean	863.0	1029.6	1193.9	1243.2	1.0418
SD	32.2	32.0	46.0	36.6	0.0181
min.	807.1	973.5	1113.9	1179.0	1.0006
max.	923.9	1085.9	1272.6	1307.6	1.0825
Przewalski's horse					
mean	919.2	1073.8	1271.1	1293.8	1.0180
SD	28.5	33.9	42.2	41.1	0.0171
min.	866.4	1002.9	1179.3	1212.6	0.9912
max.	973.9	1155.9	1353.9	1387.8	1.0595
Domestic horse					
mean	930.5	1093.9	1312.1	1316.7	1.0074
SD	176.2	200.1	251.5	229.0	0.0254
min.	558.6	674.2	771.1	836.6	0.9727
max.	1296.5	1517.7	1852.2	1801.6	1.0849
Mule					
mean	963.4	1124.6	1328.8	1351.9	1.0187
SD	119.5	138.3	169.6	158.2	0.0191
min.	809.2	941.2	1119.4	1142.9	0.9796
max.	1158.4	1355.4	1625.0	1615.9	1.0505
Overall (all 288 specimens)					
mean	893.5	1050.0	1235.6	1266.6	1.0267
SD	97.2	110.8	140.7	126.7	0.0213
min.	558.6	674.2	771.1	836.6	0.9727
max.	1296.5	1517.7	1852.2	1801.6	1.0849

among and within species, subspecies, and populations of extant *Equus*.

Height estimations can be corrected by multiplying them by reconstructed-height–estimated-height ratios (Tables 14 and 15). For example, generally underestimated withers heights of domestic horses can be corrected by multiplying these estimates by these ratios. Overestimated

Table 5. Shoulder-joint height (SJH), hip-joint height (HJH), withers height (WH), croup height (CH) and CH-to-WH ratio in domestic horses. Small ponies include all < 1200 mm tall specimens.

	n	SJH (mm)	HJH (mm)	WH (mm)	CH (mm)	CH/WH
Small ponies						
mean	14	727.0	863.8	1022.0	1053.5	1.0331
SD		85.0	92.4	120.3	105.7	0.0266
min.		558.6	674.2	771.1	836.6	0.9837
max.		832.5	976.4	1191.1	1182.4	1.0849
Landrace horses						
mean	17	938.6	1103.2	1324.2	1327.4	1.0025
SD		41.9	54.1	62.3	61.7	0.0116
min.		879.4	1014.8	1238.8	1226.3	0.9782
max.		1040.9	1212.6	1474.2	1452.6	1.0212
Warmblood horses						
mean	12	1126.0	1313.7	1588.3	1568.3	0.9874
SD		59.8	75.3	86.1	86.1	0.0081
min.		1030.3	1197.7	1458.8	1435.5	0.9741
max.		1207.5	1415.7	1717.1	1684.9	1.0001
Draft horses						
mean	1	1296.5	1517.7	1852.2	1801.6	0.9727
All horses						
mean	44	930.5	1093.9	1312.1	1316.7	1.0074
SD		176.2	200.1	251.5	229.0	0.0254
min.		558.6	674.2	771.1	836.6	0.9727
max.		1296.5	1517.7	1852.2	1801.6	1.0849

Table 6. Regression equations for estimating shoulder-joint height (SJH) from metapodial length and metapodial-distal-breadth–length ratio. Reduced-major-axis (RMA) formula was used in Eqs. 5–8 (single-predictor regressions), and least-square (LS) formula in all others (single-predictor and two-predictor regressions).

Equation	*r*	Standard error of estimate (SEE)
1: SJH = 3.965 × MC1 + 52.120	0.935	34.545
2: SJH = 4.047 × MC2 + 63.675	0.924	37.215
3: SJH = 3.560 × MT1 + 8.948	0.929	35.995
4: SJH = 3.628 × MT2 + 15.252	0.923	37.532
5: SJH = 4.241 × MC1 – 6.380	0.935	35.060
6: SJH = 4.380 × MC2 – 4.698	0.924	37.881
7: SJH = 3.832 × MT1 – 58.666	0.929	36.588
8: SJH = 3.931 × MT2 – 58.140	0.923	38.210
9: SJH = 4.158 × MC1 + 14.883 × MC10/MC1 × 100 – 288.729	0.968	24.501
10: SJH = 4.170 × MC1 + 14.345 × MC11/MC1 × 100 – 280.520	0.971	23.405
11: SJH = 4.314 × MC2 + 15.658 × MC10/MC2 × 100 – 317.718	0.966	25.050
12: SJH = 4.330 × MC2 + 15.099 × MC11/MC2 × 100 – 309.486	0.970	23.752
13: SJH = 3.598 × MT1 + 16.629 × MT10/MT1 × 100 – 286.597	0.970	23.568
14: SJH = 3.648 × MT1 + 15.791 × MT11/MT1 × 100 – 281.148	0.966	25.251
15: SJH = 3.694 × MT2 + 17.039 × MT10/MT2 × 100 – 301.926	0.971	23.497
16: SJH = 3.756 × MT2 + 16.425 × MT11/MT2 × 100 – 302.057	0.967	24.848

withers heights of Asiatic wild asses, for example, can be similarly corrected. Unfortunately, correcting estimates using these ratios corrects estimates of individuals of average height in each sample but cannot correct directional estimation error within samples. Regression slopes for specific samples represented by different species, subspecies or even population are usually steeper or shallower than those for pooled samples of, for example, related species (Smith 2002 and references therein). Ordinary least squares regression lines for the three largest samples of wild equids (Przewalski's horses, plains zebras, and Asiatic wild asses) to estimate with-

Table 7. Regression equations to estimate hip-joint height (HJH) from metapodial length and metapodial-distal-breadth–length ratio. Reduced-major-axis (RMA) formula was used in Eqs. 5–8 (single-predictor regressions), and least-square (LS) formula in all others (single-predictor and two-predictor regressions).

Equation	*r*	Standard error of estimate (SEE)
1: $HJH = 4.443 \times MC1 + 107.267$	0.920	43.494
2: $HJH = 4.525 \times MC2 + 122.160$	0.907	46.635
3: $HJH = 3.969 \times MT1 + 63.934$	0.910	46.092
4: $HJH = 4.042 \times MT2 + 71.662$	0.903	47.743
5: $HJH = 4.829 \times MC1 + 25.414$	0.920	44.310
6: $HJH = 4.989 \times MC2 + 26.976$	0.907	47.681
7: $HJH = 4.362 \times MT1 - 33.686$	0.910	47.081
8: $HJH = 4.476 \times MT2 - 33.517$	0.903	48.857
9: $HJH = 4.708 \times MC1 + 20.424 \times MC10/MC1 \times 100 - 360.487$	0.968	27.813
10: $HJH = 4.714 \times MC1 + 18.981 \times MC11/MC1 \times 100 - 332.897$	0.969	27.580
11: $HJH = 4.884 \times MC2 + 21.031 \times MC10/MC2 \times 100 - 390.104$	0.967	28.412
12: $HJH = 4.893 \times MC2 + 19.643 \times MC11/MC2 \times 100 - 363.302$	0.968	28.020
13: $HJH = 4.019 \times MT1 + 22.461 \times MT10/MT1 \times 100 - 335.262$	0.968	27.809
14: $HJH = 4.088 \times MT1 + 21.401 \times MT11/MT1 \times 100 - 329.211$	0.962	30.252
15: $HJH = 4.130 \times MT2 + 22.693 \times MT10/MT2 \times 100 - 350.777$	0.969	27.554
16: $HJH = 4.211 \times MT2 + 21.857 \times MT11/MT2 \times 100 - 350.584$	0.964	29.624

Table 8. Regression equations to estimate withers height (WH) from metapodial length and metapodial-distal-breadth–length ratio. Reduced-major-axis (RMA) formula was used in Eqs. 5–8 (single-predictor regressions), and least-square (LS) formula in all others (single-predictor and two-predictor regressions).

Equation	*r*	Standard error of estimate (SEE)
1: $WH = 5.536 \times MC1 + 60.928$	0.902	60.722
2: $WH = 5.627 \times MC2 + 81.733$	0.888	64.713
3: $WH = 4.980 \times MT1 - 1.693$	0.899	61.852
4: $WH = 5.058 \times MT2 + 11.263$	0.889	64.445
5: $WH = 6.137 \times MC1 - 66.555$	0.902	62.162
6: $WH = 6.337 \times MC2 - 63.885$	0.888	66.497
7: $WH = 5.539 \times MT1 - 140.543$	0.899	63.353
8: $WH = 5.690 \times MT2 - 141.839$	0.889	66.208
9: $WH = 5.892 \times MC1 + 27.408 \times MC10/MC1 \times 100 - 566.774$	0.957	40.920
10: $WH = 5.919 \times MC1 + 26.835 \times MC11/MC1 \times 100 - 561.360$	0.964	37.763
11: $WH = 6.107 \times MC2 + 28.104 \times MC10/MC2 \times 100 - 602.785$	0.955	41.796
12: $WH = 6.142 \times MC2 + 27.470 \times MC11/MC2 \times 100 - 597.150$	0.962	38.338
13: $WH = 5.047 \times MT1 + 29.687 \times MT10/MT1 \times 100 - 529.301$	0.963	38.286
14: $WH = 5.145 \times MT1 + 29.477 \times MT11/MT1 \times 100 - 543.192$	0.961	39.124
15: $WH = 5.175 \times MT2 + 30.058 \times MT10/MT2 \times 100 - 548.276$	0.962	38.558
16: $WH = 5.291 \times MT2 + 30.028 \times MT11/MT2 \times 100 - 568.836$	0.961	38.818

ers height from metacarpal lateral length are all less steep than that for pooled samples (Fig. 6). This resulted in overestimation and underestimation of heights of tall and short individuals, respectively. Sample-specific reduced major axis regression lines for Przewalski's horses, plains zebras, and Asiatic wild asses (not shown here) are very similar to each other and about as steep as the ordinary least squares regression line for the pooled sample.

Applying height-estimation equations to Pliocene and Pleistocene equids

I do not present here the results of height estimations of the past *Equus* from metapodial length because these single-predictor equations perform poorly in comparison with two-predictor equations of estimating these heights from metapodial length and distal-breadth–length ratio. I report the results of using the two-predictor regression equations to estimate shoulder and hip-joint heights (Table 16) and heights at the withers and at the croup (Table 17) in past *Equus*.

Estimated shoulder and hip-joint heights (Table 16) can be corrected by multiplying them by reconstructed-height–estimated-height ratios (given in Table 14), and estimated withers heights and croup heights (Table 17) by multiplying them by reconstructed-height–estimated-height ratios (given in Table 15) assuming that any of the extant *Equus* samples would be an appropriate reference for a particular sample of past *Equus*. Differences in shoulder-joint and hip-joint heights estimated from metatarsal dimensions divided by these height ratios estimated from metacarpal dimensions are not remarkable given considerable ranges of variation within each sample of extant *Equus*, and that samples of past *Equus* do not include metacarpals and metatarsals that can be matched to individual specimens (Table 18).

Especially hip-joint heights can be used to estimate step and stride lengths of the past *Equus* because it represents the total hind limb length. This limb length combined with body mass estimates would allow estimating locomotion abilities and assessing climatic adaptation. Relatively light and linear body design would reflect adaptation to travel long distances relatively fast and/or adaptation to hot climate, whereas the reverse would reflect reduced need to travel long distances with speed and/or adaptation to cold climate.

Results of estimating shoulder-joint and hip-joint heights (Table 18) are not discussed further

Table 9. Regression equations to estimate croup height (CH) from metapodial length and metapodial-distal-breadth–length ratio. Reduced-major-axis (RMA) formula was used in Eqs. 5–8 (single-predictor regressions), and least-square (LS) formula in all others (single-predictor and two-predictor regressions).

Equation	*r*	Standard error of estimate (SEE)
1: $CH = 5.083 \times MC1 + 188.087$	0.920	49.757
2: $CH = 5.176 \times MC2 + 205.124$	0.907	53.350
3: $CH = 4.541 \times MT1 + 138.513$	0.910	52.730
4: $CH = 4.623 \times MT2 + 147.355$	0.903	54.618
5: $CH = 5.525 \times MC1 + 94.315$	0.920	50.694
6: $CH = 5.707 \times MC2 + 96.319$	0.907	54.546
7: $CH = 4.990 \times MT1 + 26.869$	0.910	53.860
8: $CH = 5.120 \times MT2 + 27161$	0.903	55.889
9: $CH = 5.386 \times MC1 + 23.365 \times MC10/MC1 \times 100 - 347.024$	0.968	31.818
10: $CH = 5.393 \times MC1 + 21.715 \times MC11/MC1 \times 100 - 315.462$	0.969	31.551
11: $CH = 5.587 \times MC2 + 24.060 \times MC10/MC2 \times 100 - 380.906$	0.967	32.504
12: $CH = 5.598 \times MC2 + 22.472 \times MC11/MC2 \times 100 - 350.244$	0.968	32.055
13: $CH = 4.598 \times MT1 + 25.696 \times MT10/MT1 \times 100 - 318.167$	0.968	31.814
14: $CH = 4.677 \times MT1 + 24.483 \times MT11/MT1 \times 100 - 311.244$	0.962	34.609
15: $CH = 4.725 \times MT2 + 25.961 \times MT10/MT2 \times 100 - 335.916$	0.969	31.522
16: $CH = 4.818 \times MT2 + 25.004 \times MT11/MT2 \times 100 - 335.695$	0.964	33.890

here because the results of estimating withers height and croup height (Table 17) provide essentially the same information. The latter do not present any surprises. Estimates of croup heights are likely more accurate than those of withers heights. The results are discussed in chronological order from the oldest sample to the youngest.

The Hagerman horse (*E. simplicidens*) was about 137.4 cm and 139.4 cm tall at the withers and croup, respectively (Table 18). It was thus perhaps a little taller than the extant Grévy's zebra, which is here estimated to be 135.1 cm and 136.8 cm tall at the withers and croup, respectively (Table 5). The height estimates of the Hagerman horse could be corrected by multiplying them by reconstructed-height–estimated-height ratios for the extant zebra species (probably Grévy's zebra) with most similar limb-segment proportions to those in specimens from the Hagerman quarry (*see* https://vera-eisenmann.com).

The Mosbach horse (*E. mocbachensis*) was about 157.4 cm tall at the withers and 157.3 cm tall at the croup (Table 17). It was considerably taller than the extant wild *Equus* (Table 5) and about the same height as the warmblood horses in my skeletal sample, being on average 158.8 cm and 156.8 cm tall at the withers and croup, respectively (Table 6). One could

Table 10. Mean percent prediction errors (%PE = (reconstructed – estimated)/estimated) × 100) of estimating SJH and HJH; positive and negative values indicate underestimation and overestimation, respectively; samples as in Table 1.

	Sample								
	1	2	3	4	5	6	7	8	9
SJH Eq.1	–4.28	1.20	–0.13	–0.43	2.44	–1.40	0.78	4.33	2.77
SJH Eq.2	–4.77	1.03	–0.59	–0.71	2.63	–1.41	1.50	4.74	2.89
SJH Eq.3	–4.37	0.24	–0.67	0.95	5.98	1.77	–1.18	1.99	1.19
SJH Eq.4	–4.67	–0.38	–1.02	0.43	6.40	1.58	–0.75	2.57	1.86
SJH Eq.5	–4.40	2.10	0.23	–1.00	2.78	–1.25	0.64	4.62	2.53
SJH Eq.6	–4.96	2.07	–0.19	–1.40	3.05	–1.23	1.40	5.12	2.61
SJH Eq.7	–4.51	1.12	–0.31	0.41	6.66	2.20	–1.47	2.10	0.79
SJH Eq.8	–4.85	0.52	–0.65	–0.19	7.19	2.03	–1.03	2.73	1.49
SJH Eq.9	–1.15	3.06	0.24	–0.10	0.11	–2.97	–0.53	1.56	3.36
SJH Eq.10	–1.05	3.32	0.88	–0.05	0.64	–2.22	–0.90	0.46	3.22
SJH Eq.11	–1.25	3.21	–0.02	–0.33	0.07	–3.09	–0.17	0.59	3.49
SJH Eq.12	–1.16	3.51	0.69	–0.29	0.66	–2.27	–0.57	0.41	3.33
SJH Eq.13	–0.73	2.53	0.01	0.82	2.61	–1.00	–2.40	–0.18	1.71
SJH Eq.14	–0.84	2.54	–0.29	0.92	3.56	–0.20	–2.36	–1.28	1.83
SJH Eq.15	–0.76	2.29	–0.17	0.42	2.73	–1.22	–2.19	0.10	2.16
SJH Eq.16	–0.84	2.34	–0.48	0.50	3.73	–0.42	–2.16	–1.10	2.32
HJH Eq.1	–4.78	0.62	0.20	–0.23	3.13	0.01	0.26	4.33	2.26
HJH Eq.2	–5.25	0.44	–0.24	–0.49	3.30	0.00	0.95	4.72	2.38
HJH Eq.3	–4.87	–0.33	–0.35	1.12	6.47	3.04	–1.59	2.10	0.79
HJH Eq.4	–5.15	–0.92	–0.67	0.63	6.87	2.85	–1.18	2.66	1.43
HJH Eq.5	–4.93	1.67	0.63	–0.92	3.54	0.20	0.10	4.66	1.97
HJH Eq.6	–5.47	1.65	0.23	–1.31	3.81	0.22	0.83	5.15	2.05
HJH Eq.7	–5.04	0.73	0.09	0.45	7.31	3.57	–1.94	2.22	0.30
HJH Eq.8	–5.37	0.16	–0.23	–0.14	7.83	3.41	–1.52	2.84	0.97
HJH Eq.9	–1.12	2.75	0.62	0.15	0.41	–1.83	–1.27	1.11	2.94
HJH Eq.10	–1.15	2.96	1.34	0.19	1.11	–0.92	–1.63	0.01	2.76
HJH Eq.11	–1.21	2.89	0.41	–0.05	0.38	–1.93	–0.95	1.14	3.05
HJH Eq.12	–1.24	3.13	1.17	–0.02	1.12	–0.96	–1.33	–0.04	2.86
HJH Eq.13	–0.67	2.25	0.45	0.97	2.62	–0.16	–2.98	–0.39	1.39
HJH Eq.14	–0.78	2.28	0.09	1.09	3.70	0.75	–2.94	–1.65	1.53
HJH Eq.15	–0.71	2.06	0.30	0.62	2.73	–0.34	–2.80	–0.14	1.76
HJH Eq.16	–0.80	2.11	–0.06	0.71	3.85	0.58	–2.77	–1.48	1.95

possibly use reconstructed-croup-height–estimated-croup-height ratio of warmblood horses to correct croup height estimates of the Mosbach horse, but the Mosbach horse was likely lower at the withers relative to the height at the croup than the modern warmblood riding horses. There may be enough limb bones other than metapodial from the Mosbach quarries (*see* https://vera-eisenmann.com) to estimate heights anatomically by using mean lengths of relevant bones.

The Western horse (*E. occidentalis*) was on average 150.5 cm and 151.0 cm tall at withers and croup, respectively (Table 17). This close relative or a separate lineage of caballine horses was thus taller than all extant wild *Equus* (Table 5). There is enough skeletal material from Rancho La Brea (*see* https://vera-eisenmann.com) to reconstruct heights of an average specimen anatomically as was done by David P. Willoughby. His reconstruction of a typical specimen stands 146.98 cm tall at the withers and 151.50 cm at the croup (Willoughby 1974: fig. 248). This suggests that estimations of withers height from metapodial dimensions of the Western horse are likely too high but those of croup height accurate.

All four Late Pleistocene wild horses of Europe were on average shorter than the Mosbach horse and the Western horse (*see* above)

Table 11. Mean percent prediction errors (%PE = (reconstructed – estimated)/estimated) × 100) of estimating WH and CH; positive and negative values indicate underestimation and overestimation, respectively; samples as in Table 1.

	Sample								
	1	2	3	4	5	6	7	8	9
WH Eq.1	–5.82	0.46	0.51	0.13	3.14	–1.34	0.76	6.38	2.44
WH Eq.2	–6.30	0.24	0.03	–0.12	3.31	–1.36	1.50	6.78	2.57
WH Eq.3	–5.91	–0.48	–0.03	1.51	6.75	1.88	–1.22	3.96	0.84
WH Eq.4	–6.20	–1.14	–0.39	1.01	7.16	1.66	–0.77	4.56	1.53
WH Eq.5	–6.01	1.89	1.10	–0.77	3.69	–1.09	0.55	6.87	2.07
WH Eq.6	–6.58	1.86	0.65	–1.19	3.97	–1.07	1.35	7.40	2.15
WH Eq.7	–6.12	0.84	0.52	0.71	7.78	2.52	–1.64	4.15	0.26
WH Eq.8	–6.47	0.23	0.16	0.07	8.36	2.35	–1.19	4.83	0.98
WH Eq.9	–1.67	2.97	1.02	0.58	0.04	–3.42	–0.97	2.65	3.24
WH Eq.10	–1.47	3.35	1.91	0.65	0.71	–2.44	–1.49	1.12	3.05
WH Eq.11	–1.74	3.11	0.79	0.38	0.00	–3.52	–0.65	2.67	3.36
WH Eq.12	–1.56	3.53	1.74	0.44	0.72	–2.48	–1.21	1.06	3.15
WH Eq.13	–1.23	2.51	0.88	1.35	2.42	–1.67	–2.78	1.14	1.53
WH Eq.14	–1.15	2.65	0.50	1.48	3.49	–0.76	–2.80	–0.47	1.72
WH Eq.15	–1.24	2.30	0.72	1.00	2.48	–0.89	–2.59	1.38	1.93
WH Eq.16	–1.15	2.48	0.34	1.11	3.62	–0.95	–2.62	–0.32	2.16
CH Eq.1	–4.54	0.60	0.19	–0.22	2.96	0.01	0.24	4.11	2.15
CH Eq.2	–4.99	0.43	–0.23	–0.47	3.12	0.00	0.90	4.48	2.27
CH Eq.3	–4.62	–0.29	–0.33	1.06	6.11	2.87	–1.51	2.01	0.76
CH Eq.4	–4.89	–0.85	–0.63	0.60	6.48	2.69	–1.12	2.53	1.37
CH Eq.5	–4.68	1.58	0.60	–0.87	3.35	0.19	0.09	4.41	1.87
CH Eq.6	–5.19	1.56	0.22	–1.25	3.60	0.21	0.78	4.86	1.94
CH Eq.7	–4.79	0.70	0.09	0.43	6.90	3.38	–1.85	2.10	0.29
CH Eq.8	–5.10	0.16	–.22	–.13	7.39	3.22	–1.45	2.69	0.92
CH Eq.9	–1.06	2.59	0.59	0.15	0.39	–1.74	–1.20	1.07	2.79
CH Eq.10	–1.09	2.79	1.26	0.18	1.05	–0.87	–1.55	0.02	2.62
CH Eq.11	–1.15	2.72	0.38	–0.05	0.36	–1.84	–0.91	1.10	2.90
CH Eq.12	–1.18	2.95	1.11	–0.02	1.06	–0.91	–1.27	–0.02	2.72
CH Eq.13	–0.63	2.13	0.42	0.92	2.48	–0.15	–2.84	–0.35	1.32
CH Eq.14	–0.74	2.16	0.08	1.03	3.50	0.71	–2.80	–1.55	1.46
CH Eq.15	–0.67	1.94	0.28	0.59	2.58	–0.33	–2.66	–0.12	1.68
CH Eq.16	–0.76	2.00	–0.06	0.67	3.64	0.54	–2.63	–1.39	1.85

and taller than extant Przewalski's horse, which according to my results was on average 127.1 cm tall at the withers and 129.4 cm at the croup (Table 5). Antunes' horse from the Iberian Peninsula was 130.3 cm and 132.8 cm tall at the withers and croup, respectively (Table 17).

Table 12. Mean and median absolute percent prediction error (abs. %PE) values for pooled samples.

Equation	Abs. %PE		Equation	Abs. %PE	
	mean	median		mean	median
SJH Eq.1	3.04	2.50	WH Eq.1	3.87	3.24
SJH Eq.2	3.26	2.74	WH Eq.2	4.08	3.65
SJH Eq.3	3.14	2.53	WH Eq.3	3.92	3.23
SJH Eq.4	3.29	2.66	WH Eq.4	4.12	3.59
SJH Eq.5	3.15	2.62	WH Eq.5	4.06	3.23
SJH Eq.6	3.40	2.79	WH Eq.6	4.31	3.67
SJH Eq.7	3.21	2.57	WH Eq.7	4.05	3.15
SJH Eq.8	3.38	2.73	WH Eq.8	4.28	3.54
SJH Eq.9	2.28	2.00	WH Eq.9	2.71	3.34
SJH Eq.10	2.11	1.74	WH Eq.10	2.48	2.08
SJH Eq.11	2.32	1.96	WH Eq.11	2.77	2.40
SJH Eq.12	2.13	1.79	WH Eq.12	2.49	2.03
SJH Eq.13	2.06	1.71	WH Eq.13	2.47	1.98
SJH Eq.14	2.34	1.80	WH Eq.14	2.56	2.22
SJH Eq.15	2.10	1.75	WH Eq.15	2.47	2.01
SJH Eq.16	2.32	1.89	WH Eq.16	2.56	2.16
HJH Eq.1	3.18	2.73	CH Eq.1	3.01	2.59
HJH Eq.2	3.39	2.95	CH Eq.2	3.21	2.80
HJH Eq.3	3.51	3.20	CH Eq.3	3.33	3.03
HJH Eq.4	3.66	3.28	CH Eq.4	3.47	3.11
HJH Eq.5	3.29	2.65	CH Eq.5	3.12	2.51
HJH Eq.6	3.54	2.86	CH Eq.6	3.36	2.71
HJH Eq.7	3.60	2.88	CH Eq.7	3.41	2.72
HJH Eq.8	3.75	3.25	CH Eq.8	3.56	3.09
HJH Eq.9	2.12	1.71	CH Eq.9	2.01	1.62
HJH Eq.10	2.08	1.75	CH Eq.10	1.97	1.66
HJH Eq.11	2.15	1.70	CH Eq.11	2.04	1.61
HJH Eq.12	2.10	1.77	CH Eq.12	1.99	1.68
HJH Eq.13	2.08	1.68	CH Eq.13	1.97	1.60
HJH Eq.14	2.23	1.72	CH Eq.14	2.11	1.64
HJH Eq.15	2.09	1.76	CH Eq.15	1.98	1.67
HJH Eq.16	2.20	1.68	CH Eq.16	2.08	1.59

Table 13. Average metatarsal lateral length relative to hip join height (MT2/HJH × 100) and distal articular breadth of metatarsal relative to lateral length (MT11/MT2 × 100) ratios and their correlations; sample sizes as in Table 1.

Sample	MT2/HJH × 100	MT11/MT2 × 100	*r*
Asiatic wild ass	24.3577	15.2198	–0.688
Donkey	23.1330	16.3650	–0.783
African wild ass	23.1498	17.2448	–0.621
Grévy's zebra	23.0401	17.2334	–0.698
Mountain zebra	21.8680	18.8680	–0.518
Plains zebra	22.3410	18.5666	–0.279
Przewalski's horse	23.3970	18.1747	–0.625
Domestic horse	22.4527	19.4343	–0.525
Mule	22.8221	17.1135	–0.780
Total	23.0829	17.4363	–0.792

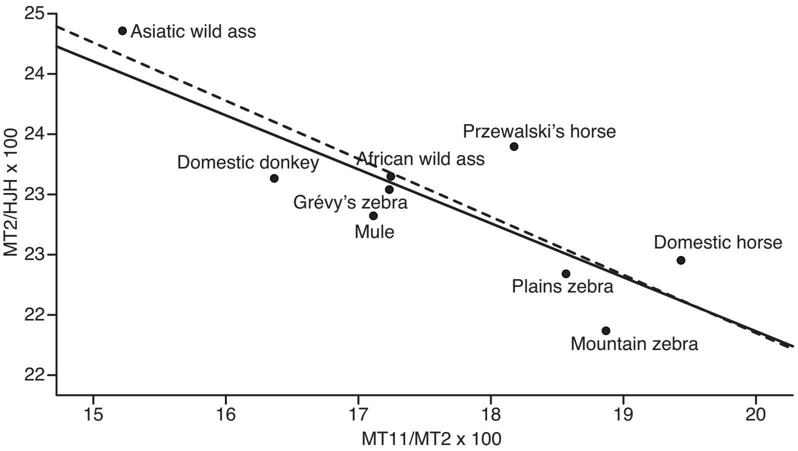

Fig. 5. Metatarsal length relative to hip-joint height (MT2/HJH × 100) regressed against distal articular breadth of metatarsal relative to lateral length (MT2/MT2 × 100). Solid line = least squares regression using sample mean values (MT2/HJH × 100 = –0.448 × MT11/MT2 × 100 + 30.824; $r = -0.828$, SEE = 0.427, $n = 9$ samples); dashed line = least squares regression using values of individual equids not shown in this graph (MT2/HJHx100 = –0.482 × MT11/MT2 × 100 + 31.490; $r = -0.792$, SEE = 0.641, $n = 288$ equids).

Table 14. Mean reconstructed–estimated-height ratios of SJH and HJH; values greater than 1 indicate underestimation and smaller than 1 overestimation; samples as in Table 1.

	Sample								
	1	2	3	4	5	6	7	8	9
SJH Eq.1	0.9572	1.0120	0.9987	0.9957	1.0244	0.9860	1.0078	1.0433	1.0277
SJH Eq.2	0.9523	1.0103	0.9941	0.9929	1.0263	0.9859	1.0150	1.0474	1.0289
SJH Eq.3	0.9563	1.0024	0.9933	1.0095	1.0598	1.0177	0.9882	1.0199	1.0119
SJH Eq.4	0.9533	0.9962	0.9898	1.0043	1.0640	1.0158	0.9925	1.0257	1.0186
SJH Eq.5	0.9560	1.0210	1.0023	0.9900	1.0278	0.9875	1.0064	1.0462	1.0253
SJH Eq.6	0.9504	1.0207	0.9981	0.9860	1.0305	0.9877	1.0140	1.0512	1.0261
SJH Eq.7	0.9549	1.0112	0.9969	1.0041	1.0666	1.0220	0.9853	1.0210	1.0079
SJH Eq.8	0.9515	1.0052	0.9935	0.9981	1.0719	1.0203	0.9897	1.0273	1.0149
SJH Eq.9	0.9885	1.0306	1.0024	0.9990	1.0011	0.9703	0.9947	1.0156	1.0336
SJH Eq.10	0.9895	1.0332	1.0088	0.9995	1.0064	0.9778	0.9910	1.0046	1.0322
SJH Eq.11	0.9875	1.0321	0.9998	0.9967	1.0007	0.9691	0.9983	1.0159	1.0349
SJH Eq.12	0.9884	1.0351	1.0069	0.9971	1.0066	0.9773	0.9943	1.0041	1.0333
SJH Eq.13	0.9927	1.0253	1.0001	1.0082	1.0261	0.9900	0.9760	0.9982	1.0171
SJH Eq.14	0.9916	1.0254	0.9971	1.0092	1.0356	0.9980	0.9764	0.9872	1.0183
SJH Eq.15	0.9924	1.0229	0.9983	1.0042	1.0273	0.9878	0.9781	1.0010	1.0216
SJH Eq.16	0.9916	1.0234	0.9952	1.0050	1.0373	0.9958	0.9784	0.9890	1.0232
HJH Eq.1	0.9522	1.0062	1.0020	0.9977	1.0313	1.0001	1.0026	1.0433	1.0226
HJH Eq.2	0.9475	1.0044	0.9976	0.9951	1.0330	1.0000	1.0095	1.0472	1.0238
HJH Eq.3	0.9513	0.9967	0.9965	1.0112	1.0647	1.0304	0.9841	1.0210	1.0079
HJH Eq.4	0.9485	0.9908	0.9933	1.0063	1.0687	1.0285	0.9882	1.0266	1.0143
HJH Eq.5	0.9507	1.0167	1.0063	0.9908	1.0354	1.0020	1.0010	1.0466	1.0197
HJH Eq.6	0.9453	1.0165	1.0023	0.9869	1.0381	1.0022	1.0083	1.0515	1.0205
HJH Eq.7	0.9496	1.0073	1.0009	1.0045	1.0731	1.0357	0.9806	1.0222	1.0030
HJH Eq.8	0.9463	1.0016	0.9977	0.9986	1.0783	1.0341	0.9848	1.0284	1.0097
HJH Eq.9	0.9888	1.0275	1.0062	1.0015	1.0041	0.9817	0.9873	1.0111	1.0294
HJH Eq.10	0.9885	1.0296	1.0134	1.0019	1.0111	0.9908	0.9837	1.0001	1.0276
HJH Eq.11	0.9879	1.0289	1.0041	0.9995	1.0038	0.9807	0.9905	1.0114	1.0305
HJH Eq.12	0.9876	1.0313	1.0117	0.9998	1.0112	0.9904	0.9867	0.9996	1.0286
HJH Eq.13	0.9933	1.0225	1.0045	1.0097	1.0262	0.9984	0.9702	0.9961	1.0139
HJH Eq.14	0.9922	1.0228	1.0009	1.0109	1.0370	1.0075	0.9706	0.9835	1.0153
HJH Eq.15	0.9929	1.0206	1.0030	1.0062	1.0273	0.9966	0.9720	0.9986	1.0176
HJH Eq.16	0.9920	1.0211	0.9994	1.0071	1.0385	1.0058	0.9723	0.9852	1.0195

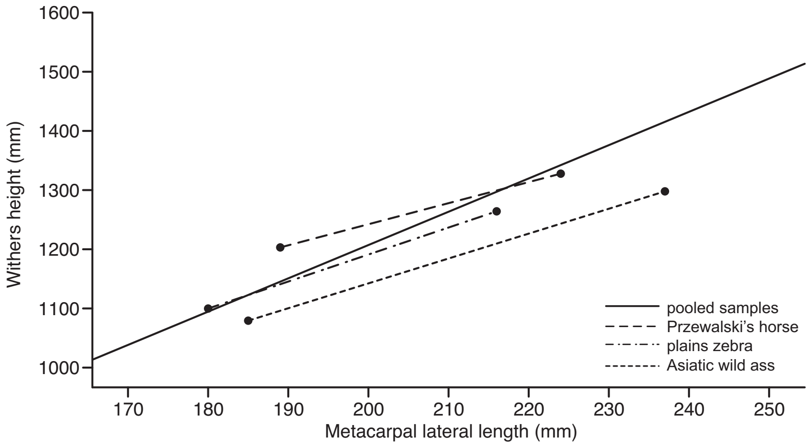

Fig. 6. Differences in slopes of regression lines of regressing withers height (WH) against metacarpal lateral length (MC2) between pooled samples (WH = 5.627 × MC2 + 81.733; $r = 0.902$, $n = 288$) and three largest samples of wild equids: Przewalski's horse (WH = 3.561 × MC2 + 530.081; $r = 0.578$, $n = 37$), plains zebra (WH = 4.564 × MC2 + 278.293; $r = 0.859$, $n = 35$), and Asiatic wild ass (WH = 4.203 × MC2 + 301.757; $r = 0.882$, $n = 67$).

Table 15. Mean reconstructed–estimated-height ratios of WH and CH; values greater than 1 indicate underestimation and smaller than 1 overestimation; samples as in Table 1.

	Sample								
	1	2	3	4	5	6	7	8	9
WH Eq.1	0.9418	1.0046	1.0051	1.0013	1.0314	0.9866	1.0076	1.0638	1.0244
WH Eq.2	0.9370	1.0024	1.0003	0.9988	1.0331	0.9864	1.0150	1.0678	1.0257
WH Eq.3	0.9409	0.9952	0.9997	1.0151	1.0675	1.0188	0.9878	1.0396	1.0084
WH Eq.4	0.9380	0.9886	0.9961	1.0101	1.0716	1.0166	0.9923	1.0456	1.0153
WH Eq.5	0.9399	1.0189	1.0110	0.9923	1.0369	0.9891	1.0055	1.0687	1.0207
WH Eq.6	0.9342	1.0186	1.0065	0.9881	1.0397	0.9893	1.0135	1.0740	1.0215
WH Eq.7	0.9388	1.0084	1.0052	1.0071	1.0778	1.0252	0.9836	1.0415	1.0026
WH Eq.8	0.9353	1.0023	1.0016	1.0007	1.0836	1.0235	0.9881	1.0483	1.0098
WH Eq.9	0.9833	1.0297	1.0102	1.0058	1.0004	0.9658	0.9903	1.0265	1.0324
WH Eq.10	0.9853	1.0335	1.0191	1.0065	1.0071	0.9756	0.9851	1.0112	1.0305
WH Eq.11	0.9826	1.0311	1.0079	1.0038	1.0000	0.9648	0.9935	1.0267	1.0336
WH Eq.12	0.9844	1.0353	1.0174	1.0044	1.0072	0.9752	0.9879	1.0106	1.0315
WH Eq.13	0.9877	1.0251	1.0088	1.0135	1.0242	0.9833	0.9722	1.0114	1.0153
WH Eq.14	0.9885	1.0265	1.0050	1.0148	1.0349	0.9924	0.9720	0.9953	1.0172
WH Eq.15	0.9876	1.0230	1.0072	1.0100	1.0248	0.9811	0.9741	1.0138	1.0193
WH Eq.16	0.9885	1.0248	1.0034	1.0111	1.0362	0.9905	0.9738	0.9968	1.0216
CH Eq.1	0.9546	1.0060	1.0019	0.9978	1.0296	1.0001	1.0024	1.0411	1.0215
CH Eq.2	0.9501	1.0043	0.9977	0.9953	1.0312	1.0000	1.0090	1.0448	1.0227
CH Eq.3	0.9538	0.9971	0.9967	1.0106	1.0611	1.0287	0.9849	1.0201	1.0076
CH Eq.4	0.9511	0.9915	0.9937	1.0060	1.0648	1.0269	0.9888	1.0253	1.0137
CH Eq.5	0.9532	1.0158	1.0060	0.9913	1.0335	1.0019	1.0009	1.0441	1.0187
CH Eq.6	0.9481	1.0156	1.0022	0.9875	1.0360	1.0021	1.0078	1.0486	1.0194
CH Eq.7	0.9521	1.0070	1.0009	1.0043	1.0690	1.0338	0.9815	1.0210	1.0029
CH Eq.8	0.9490	1.0016	0.9978	0.9987	1.0739	1.0322	0.9855	1.0269	1.0092
CH Eq.9	0.9894	1.0259	1.0059	1.0015	1.0039	0.9826	0.9880	1.0107	1.0279
CH Eq.10	0.9891	1.0279	1.0126	1.0018	1.0105	0.9913	0.9845	1.0002	1.0262
CH Eq.11	0.9885	1.0272	1.0038	0.9995	1.0036	0.9816	0.9909	1.0110	1.0290
CH Eq.12	0.9882	1.0295	1.0111	0.9998	1.0106	0.9909	0.9873	0.9998	1.0272
CH Eq.13	0.9937	1.0213	1.0042	1.0092	1.0248	0.9985	0.9716	0.9965	1.0132
CH Eq.14	0.9926	1.0216	1.0008	1.0103	1.0350	1.0071	0.9720	0.9845	1.0146
CH Eq.15	0.9933	1.0194	1.0028	1.0059	1.0258	0.9967	0.9734	0.9988	1.0168
CH Eq.16	0.9924	1.0200	0.9994	1.0067	1.0364	1.0054	0.9737	0.9861	1.0185

It was thus about the same size as the recent Icelandic horse, which averaged 133.2 cm and 133.1 cm tall at the withers and at the croup, respectively (Árnason & Bjarnason 1994: table 3). The Antunes's horse sample is unfortunately too small for reconstructing heights from all directly contributing skeletal elements.

The Gallic horse and the Latipes horse from western Europe north of the Pyrenees and in the South Russian Plain, respectively, were taller than Antunes' horse. The Gallic horse stood 139.4 cm and 140.7 cm tall at the withers and croup, respectively. The Latipes horse was about the same height averaging 140.4 cm and

Table 16. Estimated shoulder-joint height (HJH) and hip-joint height (HJH) of Pliocene and Pleistocene *Equus* from metacarpal (MC) and metatarsal (MT) dimension with two-predictor equations.

	SJH from			HJH from		
	MC	MT	MC & MT	MC	MT	MC & MT
Hagerman horse						
n	48	48	96	48	48	96
mean (mm)	1006.7	982.6	994.2	1174.8	1148.2	1161.5
SD (mm)	20.5	21.7	24.2	23.0	24.1	27.0
min. (mm)	963.2	934.5	934.5	1127.7	1094.1	1094.1
max. (mm)	1060.0	1022.7	1060.0	1236.1	1195.0	1236.2
Mosbach horse						
n	30	34	64	30	34	64
mean (mm)	1116.7	1135.9	1126.9	1307.2	1326.8	1317.6
SD (mm)	25.3	27.6	28.0	28.9	31.6	31.7
min. (mm)	1066.1	1074.9	1066.1	1246.9	1256.9	1246.9
max. (mm)	1161.4	1189.4	1189.4	1358.1	1388.0	1388.0
Western horse						
n	32	29	61	32	29	61
mean (mm)	1076.7	1079.6	1078.1	1259.9	1265.0	1262.3
SD (mm)	29.1	30.5	29.6	33.5	34.2	33.6
min. (mm)	1027.9	1025.7	1025.7	1206.2	1203.2	1203.2
max. (mm)	1129.9	1129.8	1129.9	1317.4	1322.6	1322.6
Antunes' horse						
n	8	4	10	8	4	10
mean (mm)	928.1	966.7	941.2	1088.9	1134.7	1104.0
SD (mm)	33.3	32.9	38.7	38.5	38.5	45.3
min. (mm)	871.3	935.2	871.3	1023.3	1095.9	1023.3
max. (mm)	973.2	1013.0	1013.0	1142.7	1188.0	1188.0
Gallic horse						
n	32	28	60	32	28	60
mean (mm)	982.2	1006.6	993.6	1159.1	1186.0	1171.6
SD (mm)	34.4	30.9	34.8	39.9	35.6	40.0
min. (mm)	896.8	956.4	896.8	1059.6	1126.2	1059.6
max. (mm)	1047.8	1066.7	1066.7	1159.1	1255.1	1255.1
Latipes horse						
n	8	6	14	8	6	14
mean (mm)	987.4	1019.0	1001.0	1166.1	1201.0	1181.1
SD (mm)	30.6	31.6	33.9	33.4	37.1	38.1
min. (mm)	940.3	979.6	940.3	1114.7	1155.0	1114.7
max. (mm)	1024.3	1051.6	1051.6	1207.6	1240.4	1240.6
Arcelini horse						
n	30		30	30		30
mean (mm)	934.4		934.4	1102.1		1102.1
SD (mm)	35.6		35.6	40.9		40.9
min. (mm)	827.9		827.9	977.9		977.9
max. (mm)	988.1		988.1	1164.7		1164.7

141.7 cm tall at the withers and at the croup, respectively (Table 17). These two horses were thus about the same height as the modern Icelandic horses, which are on average about 141 cm tall at the withers (Stefánsdóttir *et al*. 2014). Reconstructing heights from all directly contributing skeletal elements is possible for some of the Gallic horses because there are some complete enough skeletons (*see* Crégut-Bonnoure *et al*. 2018: fig. 19). In any event, there are enough different limb bones to use average values in reconstructing heights of both of these Late Pleistocene horses (*see* https://vera-eisenmann.com).

Table 17. Estimated withers heights (WH) and croup heights (CH) of Pliocene and Pleistocene *Equus* from metacarpal (MC) and metatarsal (MT) dimension with two-predictor equations.

	WH from			CH from		
	MC	MT	MC & MT	MC	MT	MC & MT
Hagerman horse						
n	48	48	96	48	48	96
mean (mm)	1389.2	1357.8	1373.5	1409.4	1378.9	1394.1
SD (mm)	28.7	30.3	33.3	26.3	27.6	30.9
min. (mm)	1331.8	1289.5	1289.5	1355.4	1317.0	1317.0
max. (mm)	1467.0	1417.6	1467.0	1479.5	1432.5	1479.5
Mosbach horse						
n	30	34	64	30	34	64
mean (mm)	1561.2	1586.1	1574.4	1560.8	1583.3	1572.5
SD (mm)	36.5	40.1	40.1	33.0	36.2	36.3
min. (mm)	1483.4	1497.6	1483.4	1491.8	1503.3	1491.7
max. (mm)	1625.1	1662.7	1662.7	1619.0	1653.2	1653.2
Western horse						
n	32	29	61	32	29	61
mean (mm)	1501.1	1509.4	1505.0	1506.7	1512.5	1509.5
SD (mm)	42.5	43.0	42.6	38.3	39.1	38.5
min. (mm)	1433.2	1431.0	1431.0	1445.3	1441.8	1441.8
max. (mm)	1573.6	1582.3	1582.3	1572.2	1578.4	1578.4
Antunes' horse						
n	8	4	10	8	4	10
mean (mm)	1284.3	1343.4	1303.4	1311.1	1363.5	1328.3
SD (mm)	49.0	49.0	57.8	44.1	44.1	51.8
min. (mm)	1200.9	1292.9	1200.9	1236.0	1319.1	1236.0
max. (mm)	1353.6	1410.4	1410.4	1372.7	1424.4	1424.4
Gallic horse						
n	32	28	60	32	28	60
mean (mm)	1379.4	1411.6	1394.4	1391.4	1422.1	1405.7
SD (mm)	50.8	45.2	50.6	45.6	40.7	45.7
min. (mm)	1252.6	1334.6	1252.6	1277.5	1353.8	1277.5
max. (mm)	1474.6	1499.4	1499.4	1477.1	1501.1	1501.3
Latipes horse						
n	8	6	14	8	6	14
mean (mm)	1388.9	1431.3	1407.1	1399.4	1439.4	1416.5
SD (mm)	40.8	47.6	47.3	38.3	42.4	43.6
min. (mm)	1326.7	1371.9	1326.7	1340.6	1386.6	1340.6
max. (mm)	1440.5	1482.6	1482.6	1446.9	1484.6	1484.6
Arcelini horse						
n	30		30	30		30
mean (mm)	1305.8		1305.8	1326.2		1326.2
SD (mm)	52.0		52.0	46.8		46.8
min. (mm)	1146.8		1146.8	1184.1		1184.1
max. (mm)	1386.0		1386.0	1397.8		1397.8

The Arcelini horse succeeded the Gallic horse in western Europe north of the Pyrenees during the very Late Glacial period. This horse was about the same height as Antunes' horse of the Iberian Peninsula, but shorter than the Gallic horse and the Latipes horse. Estimated heights at the withers and at the croup of this horse are 130.6 cm and 132.6 cm, respectively (Table 17). Average height of the western European wild horses thus decreased during the terminal glacial period at least north of the Pyrenees. There should be enough different limb bones of the Arcelini horse for these reconstructions of an average specimen, even though there are no complete skeletons.

Concluding remarks

Estimation methods presented herein are tentative and should be properly tested and revised accordingly. Skeletal dimensions of larger numbers of horses and other *Equus* with and known living heights are obviously needed to develop more "definite" estimation methods. Anatomical reconstructions of shoulder- and hip-joint heights based on measurements of domestic horses with known living dimensions and skeletal dimensions should be reasonably accurate for domestic horses but whether these are equally accurate for other *Equus* species is unknown. Measurements and other observations of living animals are required to determine, for example, joint angles, which influence vertical heights between joints by affecting bone shaft inclinations.

Although subject to revision, anatomically reconstructed shoulder- and hip-joint heights are almost certainly more accurate than withers heights and croup heights derived from these heights. There is insufficient information especially in the case of the former total height. More accurate estimations of these two heights require samples representing different species with measured withers heights, croup heights and relevant skeletal dimensions including lengths of spinous processes and measurements from articulated pelvises in anatomically correct orientations. Because body mass likely affects variation in the croup-height–hip-joint-height ratio, a proxy of body mass (e.g. joint size) should probably be included in the croup height estimation. In addition, this ratio is likely affected by sex- and species-specific differences in the pelvic configuration not related to size.

There is no need to be limited to estimating only heights and body masses of past and present equids from skeletal dimensions. It is possible to estimate body length, chest girth and cannon girth of domestic horses with surprisingly high accuracy just from metacarpal length and relative distal articular breadth (M. Niskanen & N. Piipponen unpubl. data). These estimation methods

Table 18. Shoulder-joint (SJH) and hip-joint (HJH) height ratios estimated from metatarsal dimensions divided by those estimated from metacarpal dimensions in past and present *Equus*; sample sizes of extant *Equus* as in Table 1.

	SJH from MT/SJH from MC × 100				HJH from MT/HJH from MT × 100			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Asiatic wild ass	99.64	1.36	97.05	103.51	99.56	1.33	96.91	103.35
Donkey	100.84	1.49	97.95	103.57	100.76	1.51	98.02	103.78
African wild ass	100.69	1.00	99.23	102.34	100.70	1.51	98.02	103.78
Grévy's zebra	99.16	0.94	97.28	101.00	99.23	0.94	97.31	101.04
Mountain zebra	97.31	1.35	95.08	100.78	97.62	1.38	95.27	101.05
Plains zebra	98.09	1.92	89.67	100.90	98.01	1.94	90.17	101.34
Przewalski's horse	101.78	1.07	99.47	104.29	101.63	1.05	99.18	104.33
Domestic horse	101.63	1.37	98.90	104.29	101.49	1.33	98.93	104.13
Mule	101.33	1.64	98.95	104.19	101.25	1.59	98.68	103.98
Hagerman horse	97.61	–	–	–	97.94	–	–	–
Mosbach horse	101.72	–	–	–	101.50	–	–	–
Western horse	100.27	–	–	–	100.40	–	–	–
Gallic horse	102.48				102.32	–	–	–

should be tested and modified to be more applicable for different taxa. Accurate estimations of body size and shape of past equids are not possible unless we can make accurate body size and shape estimations for extant *Equus* species.

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