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METHODOLOGY FOR THE DETERMINATION OF MODERN AND FOSSIL HORSE GAITS FROM TRACKWAYS

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ABSTRACT

The authors here present a methodology for the analysis of fossil horse trackways in order to determine the gait and velocity. The methodology presents recommended measurements to take on trackways, ways of distinguishing front feet (*manus*) from hind feet (*pes*) in order to determine footfall patterns, tables and figures noting how gaits can be distinguished based upon trackway patterns and measurements, formulae for estimating the speed of gait, and ways of determining likely trackmaker species and height at withers. In order to develop this methodology the authors undertook a study of twenty-five horses of different breeds and sizes in various gaits, and found six ratios determinable from trackways that can help identify horse gait and velocity: step symmetry, stride length/front hoof length, ipsilateral step distance/stride length, diagonal step distance/stride length, diagonal/ipsilateral step distance, and interior straddle/hind hoof width. Also noted were the effects of three key variables that could increase the amount of overstep of ipsilateral feet in different gaits: velocity of gait, height of trackmaker at the withers, and gleno-acetabular distance of trackmaker (distance between center of hip to center of shoulder).

Keywords: megafauna; microfauna; sinkhole; rappelling; vertical rope techniques; stratigraphy; pollen; volcanic ash

RESUMO [in Portuguese]

Os autores apresentam uma metodologia para análise de pegadas de cavalos fósseis, de modo a determinar o tipo de marcha e a velocidade. A metodologia aqui apresentada demonstra o tipo de medidas a fazer para trilhos de pegadas e seus padrões, formas de distinguir os pés dianteiros (manus) dos traseiros (pes), para determinar o tipo de marcha, e apresentamos também tabelas e figuras de como os trilhos podem ser distinguidos com base em padrões e medidas , fórmulas para estimar a velocidade da marcha, e formas de determinar as espécies prováveis de dos trilhos de pegadas e a altura ao garrote. Para desenvolver esta metodologia, os autores empreenderam um estudo de vinte e cinco cavalos de diferentes raças e tamanhos com vários tipos de marcha, e encontraram seis rácios determináveis a partir de pistas que podem ajudar a identificar o andar e a velocidade do cavalo, são estes: a simetria dos passos, o comprimento do passo/comprimento do casco dianteiro, a distância do passo/comprimento do passo ipsilateral, a distância do passo/comprimento do passo diagonal, a distância do passo diagonal/ipsilateral, e a largura do passo interior/largura do casco traseiro. Também foram notados os efeitos de três variáveis-chave que poderiam aumentar a quantidade de passo em excesso dos pés ipsilaterais em diferentes andamentos: a velocidade de marcha, a altura do animal que fez o trilho no garrote, e a distância gleno-acetabular do animal que fez o trilho (distância entre o centro da anca e o centro do ombro).

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INTRODUCTION

Determining the gait of quadrupedal fossil species from trackways is challenging (Kienapfel et al., 2014; Stevens et al., 2016). Quadrupeds are capable of a large variety of gaits, including both laterally and diagonally coordinated walking and running gaits, as well as asymmetrical bounding gaits. Such gaits can leave trackways that look superficially similar (for example, walks, trots, and slow racks which all form trackways with ipsilateral foot pairs landing near each other). Furthermore, one typically does not know such key parameters of the trackmaker as height, gleno-acetabular distance, or leg length, and so theoretical modeling, estimations of these parameters from the trackway, and best-fit calculations are often employed to determine gait (as in Lallensack and Falkingham, 2022; Stevens et al., 2022).

Still, we are in a somewhat better position when it comes to horses, as there are extant species of various sizes that can be studied in different gaits. We have previously examined the trackways left behind by contemporary horses in various gaits in order to investigate fossil horse gaits (Renders, 1984a,b; Renders and Sondaar, 1987; Vincelette, 2021). We here expand upon our earlier studies in order to refine and develop a best methodology for the elucidation of fossil horse gaits and speed.

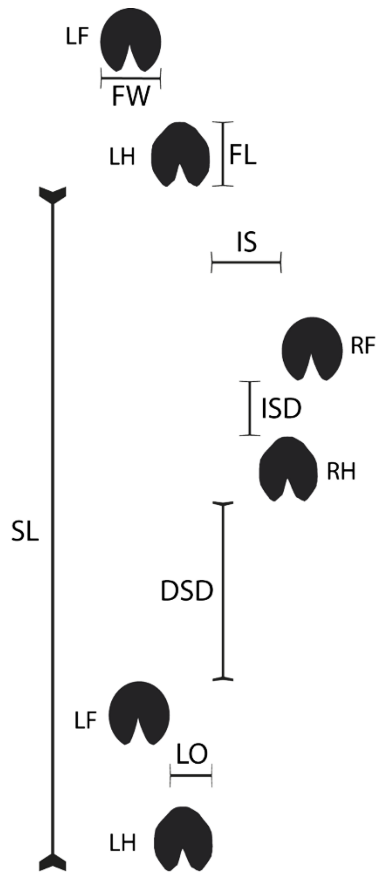

Figure 1. Measurements taken of horse trackway. Footfall abbreviations: LH=Left Hind Hoof; LF=Left Front Hoof; RH=Right Hind Hoof; RF=Right Front Hoof. Measurement Abbreviations: ISD=Ipsilateral Step Distance (Distance between ipsilateral feet parallel to direction of travel); DSD=Diagonal Step Distance (Distance between diagonal feet parallel to direction of travel); LO=Lateral Offset (Distance ipsilateral feet out of parallel alignment with each other); IS=Interior Straddle (distance between diagonal feet perpendicular to direction of travel); SL=Stride Length (distance between successive contacts of left hind hooves).

Such a methodology involves a set of measurements to be taken on the trackway, a means for estimating trackmaker height based upon footprint data alone (as well as upon fossil horse exemplars), a revised Alexander formula for estimating horse gait velocities, as well as tables and figures of six ratios that can identify horse gaits (step symmetry, stride length/front hoof length, ipsilateral step distance/stride length, lateral step distance/stride length, interior straddle/hind hoof width). This methodology was developed through the study of the trackways laid down by twenty-five horses of different sizes in diverse gaits. We also looked at three key variables (velocity, trackmaker height at the withers, and gleno-acetabular distance (distance between center of shoulder to center of hip) and their effect on amount of overstep of ipsilateral feet. This analysis is meant to pave the way for future studies on fossil horse gaits (and gaits of other quadrupeds) by providing a reliable methodology.

Horse gaits

Typical horse breeds are capable of walking, trotting, cantering, and galloping gaits. In horses the walk is a slow lateral-sequence single-foot gait. It is a lateral-sequence gait as locomotion begins with a hind foot (or pes) stepping forward followed by the ipsilateral front foot (or manus), which is then repeated on the other side of the horse (hence such a gait is also called symmetrical). And it is a single-foot gait (or "square" in equestrian terminology) as it is a four-beat gait wherein each limb moves in a fairly independent manner. For this reason, it possesses a limb phasing value (limb phase in quadruped studies; lateral advanced placement in equestrian terminology) of around 0.25, representing timing of ipsilateral feet contacts in relation to stride duration. Some horse breeds, such as the Tennessee Walking Horse, can engage in a "running walk" which is a four-beat single-foot gaitperformed at a higher velocity with increased overstepping of hind over ipsilateral front feet.

The trot is an intermediate speeddiagonal-couplet gait. It commences with a hind foot (pes) followed by the contralateral front foot (manus), followed by the same sequence repeating on the opposite side of the animal. The trot possesses a limb phasing value (lateral advanced placement) of around 0.50, as diagonal limbs are highly coordinated and move forward together and land close together in time resulting in a two-beat gait. If the coordination of diagonal limbs is reduced somewhat (i.e. broken in equestrian terms) what results is the fox trot found in certain horse breeds such as the Missouri Fox Trotter.

The fastest gait of the horse is the transverse gallop, an asymmetrical gait wherein contralateral hind feet (pes) first hit the ground followed by the same sequence of contralateral front feet (manus). It is a fast four-beat gait but can become a slightly slower three-beat canter if the diagonal limbs land close together in time and space.

A few horse breeds can also perform intermediate to fast speed laterally coordinated gaits. These are valued by riders as there is less jolting in the saddle. If there is heavy coordination of ipsilateral limbs a two-beat pace occurs which possesses a limb phasing value (lateral advanced placement) approaching 0.0. Such a gait is found in Icelandic, Peruvian Paso, and Standardbred horses. If the coordination of ipsilateral limbs is slightly reduced (i.e. broken) a stepping pace results. Finally certain horse breeds including the Icelandic, Saddlebred, and Rocky Mountain, are capable of a rack (also called a tölt (especially in the Icelandic), saddle gait, or amble). A rack is an intermediate speed four-beat gait but has more coordination of ipsilateral limbs than the walk or running walk but less than the pace.

MATERIALS AND METHODS

Twenty-five horses were chosen for study, in particular those from breeds capable of a variety of gaits, including the Icelandic Horse, Peruvian Paso Horse, Mangalarga Marchador, Rocky Mountain Horse, Spotted Saddle Horse, and Tennessee Walking Horse, as well as smaller breeds including the Shetland Pony and Sicilian Donkey (see supplementary table S1 for particulars). Each horse originated from a farm with membership in a given breed association (with the exception of the Shetland ponies) and was ridden or led in a sandy arena by a trainer familiar with the horse breed (see acknowledgements) and able to get it to exhibit various gaits at a constant speed.

Based upon our previous work on modern horse gaits, linear kinematic parameters and ratios were identified that were useful for discriminating between horse gaits (Renders, 1984a,b; Vincelette, 2021; Renders and Vincelette, 2022). The key linear kinematic parameters and ratios are based upon the following definitions (modified from Leach et al., 1984; see figure 1):

Footprint width (FW): Greatest distance in centimeters across the middle portion of the hoof impression taken perpendicular to direction of travel (akin to greatest measurement across quarters, or central portion, of hoof).

Footprint length (FL): Distance in centimeters between anterior and posterior edges of hoof impression taken parallel to direction of travel (akin to measurement between toe and heel of hoof).

Stride length or cycle length (SL): Distance in meters between the anterior portion (i.e. toe of hoof) of successive footprints of the same foot parallel to the orientation of the trackway (ideally between left hind impressions if possible). The stride length tends to increase as a gait gets faster.

Stride length/Horse height ratio (SL/HT): Dimensionless speed ratio found by dividing stride length by horse height at the withers. As gaits get faster this number increases. In walking gaits this value is usually less than 1.0, between 1.0-2.0 in intermediate speed gaits, while in very fast gaits it can be above 2.0.

Distance between diagonal steps (DSD): Measurement in centimeters between anterior (i.e. corresponding to toe of hoof) and posterior (i.e. corresponding to heel of hoof) edges of contralateral front and hind hoofprints parallel to the orientation of the trackway. [As an alternative one might consider measuring from the posterior edges of contralateral front and hind hoofprints, as is often done; however, the method above encourages measuring and comparing individual hoof prints for consistency and to identify any sliding or discrepancies due to substrate].

Distance between ipsilateral steps (ISD): Measurement in centimeters between anterior (i.e. toe) and posterior (i.e. heel) edges of ipsilateral front and hind hoofprints parallel to the orientation of the trackway. Positive values indicate overstepping of ipsilateral hooves. Negative values indicate capping (overlapping or overstriking) of ipsilateral hooves when negative values are less than length of the foot and understepping when negative value exceeds foot length. [Alternatively one might set null value at alignment of ipsilateral posterior edges (i.e. at capping), as is sometimes done, and so negative values would represent understep; however, the above method is more consistent with equestrian practice].

Ipsilateral step distance [overstep, overstrike]/Stride length ratio (ISD/SL): Distance between ipsilateral steps divided by the stride length. The ipsilateral overstep [overstrike] can reach as high as 15-30% in fast ipsilaterally coordinated gaits.

Diagonal/Ipsilateral step distance ratio (DSD/ISD): Distance between diagonal steps divided by distance between ipsilateral steps. This value is above 0.5 in square gaits, but increasingly lower than 0.5 in laterally coordinated gaits, and exceeds 1.0 in diagonally coordinated gaits.

Step symmetry between diagonal and ipsilateral steps ([DSD1/DSD2+ISD1/ISD2]/2): ½ x (Diagonal step distance 1/Diagonal step distance 2)+(Ipsilateral step distance 1/Ipsilateral step distance 2). Make sure to place smaller of the two ISD and DSD values as the numerator on top.

Average interior straddle (IS) [trackway gauge]: Average distance in centimeters between quarters (center) of contralateral front (manus) and hind (pes) hoofprints measured perpendicular to the orientation of the trackway. In the walk and running walk this value is typically positive but in gaits with high-lateral coordination the hind limbs are free to come in or cross the centerline without interference and so this value is often negative.

Interior straddle/hind hoof width (IS/HW): Ratio of average interior straddle divided by average hind hoof width. This value is negative in fast laterally coordinated gaits such as the rack and pace, around zero in slow walks and trots, and positive in fast walks and trots.

Average foot pair lateral offset (LO): Average distance in centimeters between quarters of nearest hoofprint pairs whether formed by ipsilateral, diagonal, or contralateral front or contralateral hind measured perpendicular to the orientation of the trackway. This value is zero when ipsilateral limbs are in parallel alignment with regard to centerline, low when ipsilateral pairs of feet are close together, and higher when diagonal pairs are close together.

Foot pair lateral offset/footprint width (LO/FW): Ratio of average foot pair lateral offset divided by average width of hoofprint at quarters. This value is high for gaits with diagonal pairs landing close together in space but low for gaits with lateral pairs landing close together in space.

Angle between steps (SA): Though we did not take these measurements here it is worthwhile measuring the angle between different steps in relation to the centerline (direction of travel). Such angles are likely to be larger in certain gaits than others (i.e. angle between diagonal feet in fast rack as opposed to the trot) and further study may reveal their usefulness in discriminating between gaits.

Angle of hoof impression (HA): Though we did not incorporate this data here as more study is needed, we also recommend measuring the angle each hoof impression makes (line drawn between anterior (toe) center and anterior (heel) posterior margins of hoof impression) in relation to a line drawn parallel to the orientation of the trackway (i.e. centerline showing direction of travel). If 3D-image generating software is available 3D scans of the trackway would allow for additional study of depth of impressions, and angles hooves makes with horizontal and vertical planes in addition to angle of hoof with respect to centerline regarding direction of travel. This may yield important data allowing discrimination of gaits or feet in the future or showing aspects of conformation, slippage, hoof pressure, center of balance, or change of direction.

These linear parameters and ratios were then measured or calculated from trackways laid down in a raked sandy arena by the twenty-five horses performing a particular gait at a constant speed, including the walk, running walk, tölt or rack, fox trot, stepping pace, pace, trot, and gallop. Measurements from one stride cycle were recorded, but measurements were compared with two to three nearby stride cycles to make sure step distances and stride lengths were consistent. Basic measurements

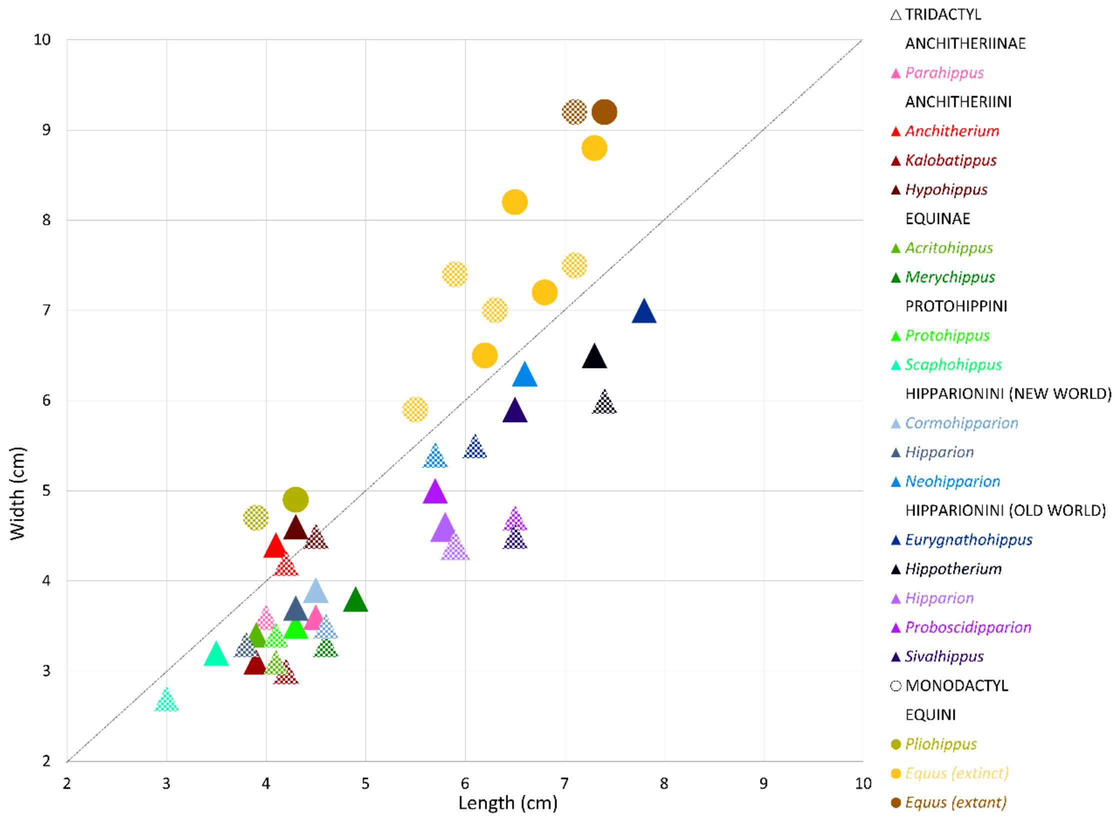

Figure 2. Bivariate plot of length versus width for central ungual phalanges (3PhIII) of fossil and modern equids with isometric line. Front phalanges (manus) are solid in color while hind phalanges (pes) are patterned with a crosshatch. Phalanges above line are wider than long (typical for monodactyl equids) while phalanges below the line are longer than wide (typical for tridactyl equids).

were also taken on the horses including height at the withers (HT), gleno-acetabular distance (GAD), 0hoof width (HW), and hoof length (HL). This new data was combined with data from our previous studies (Vincelette, 2021; Renders and Vincelette, 2022) to develop a dataset for principal component analysis of the key variables relating to each gait. Lastly, footprint patterns formed during these different gaits were photographed and sketched. All of the horses were videotaped performing the gaits at 60 hz (or 30 hz for gaits on European farms where horse speed was usually below 3.0 m/s) in order to determine whether any understep or overstep of ipsilateral feet occurred and to measure stride duration for use in velocity calculations.

We employed three methods of measuring horse speed with varied degrees of success. For the first few trials a speed gun was employed to measure the velocity of the horse throughout its gait. This allowed recording minor changes in speed. This method, however, was abandoned due to danger of the speed recorder as it required being stationed in the pathway of the oncoming horse, which was sometimes moving at high speeds. The speed of the first seven horses studied, in the end, was determined by two different methods. Horses were taken to an arena and brought to a constant speed appropriate for a given gait. In a first method, cones were set up or markers placed in the sand at a known distance (10 or 20 meters) and a stopwatch was used to determine the time it took the horse to traverse that distance. In a second method, the length covered by one stride cycle in a given gait (i.e. the distance between successive left hind limb impressions in the sand, see figure 1) was measured and divided by the time it took for a horse to complete that stride cycle (average of two strides). The latter was determined by a frame-by-frame analysis of the video recording as noted above.

These two methods of determining speed were found to give comparable results (average difference of 0.25 m/s) in ideal circumstances. The first method of determining horse speed, however, had greater margins of error due to the accuracy of the person operating the stopwatch and especially lack of optimal viewing angle regarding distance markers. The first method could be advantageous, however, if laser-based equipment were used as is done in track and field events with humans. The second method, in any case, was utilized exclusively to measure velocity for the remaining twelve horses, that is a stride length was physically measured and frame-by-frame video-tape analysis was used to determine how long it took for the horse to complete that particular stride cycle at a constant speed (averaging two stride cycles together).

RESULTS. METHOD FOR DETERMINATION OF TRACKWAY GAIT AND SPEED

Based upon our research on modern horse gaits, we identify the following protocol as most beneficial in determining the gait and velocity exhibited in a horse trackway. The protocol involves three stages. Stage one, a method for distinguishing front footprints (manus) from hind footprints (pes) in the trackway in order to determine the footfall pattern. Stage two, a method for determining the gait exhibited in a trackway (from trackway data alone and from combined trackway and osteological data) based upon six key ratios and footprint patterns. Stage three, and a method for estimating the velocity of the trackmaker gait (from trackway data alone and from combined trackway and osteological data).

Distinguishing front (manus) from hind (pes) hoofprints in fossil horse trackways

Knowing the footfall sequence is very important for determining gaits. In fact, our methodology for trackway measurement depends upon distinguishing front (manus) and hind (pes) hoofprints and identifying which prints are formed by ipsilateral foot pairs and which by diagonal foot pairs. Hence a necessary first step, before trackway measurements can be taken, is to determine the footfall sequence, which in turn requires distinguishing front from hind horse hoofprints.

Now it can be quite challenging to discriminate front hoofprints (manus) from hind hoofprints (pes) in fossil horse trackways. First, the detail found in the prints depends upon abiotic factors such as the substrate the print was made in and its moisture content, as well as upon gait velocity and horse behavior (Falkingham, 2014; Razzolini et al., 2014). Second, morphometric parameters for the hooves vary from species to species in fossil horses, and in some species the front hoof (manus) is longer, whereas in others the hind hoof (pes) is longer (see supplementary table S2, as well as S5-S6).

However, three key factors aid in the discrimination of front hooves (manus) from hind hooves (pes). First, from the Miocene onward the front ungual phalanges and hooves tend to be wider than the hind ungual phalanges and hooves (see tables S3, and S5-S6). Second, and more importantly, the front ungual phalanges and hooves tend to be more isometric (with a length/width ratio closer to 1.00) and circular in overall shape, whereas the hind ungual phalanges and hooves tend to be less isometric and more oval in shape (see figures 3 and 4, and tables S5-S6 in the supplemental section). This is generally true both for tridactyl fossil horses, wherein the length of the hoof is usually greater than the width, as well as for monodactyl fossil horses, wherein the hoof is often wider than long (Gromova, 1952; Sarjeant and Reynolds, 1999; Reynolds, 2006; see figure 2). However, for select fossil horse species, including *Miohippus intermedius*, *Kalobatippus avus*, *Pliohippus pernix*, and *Equus scotti*, the

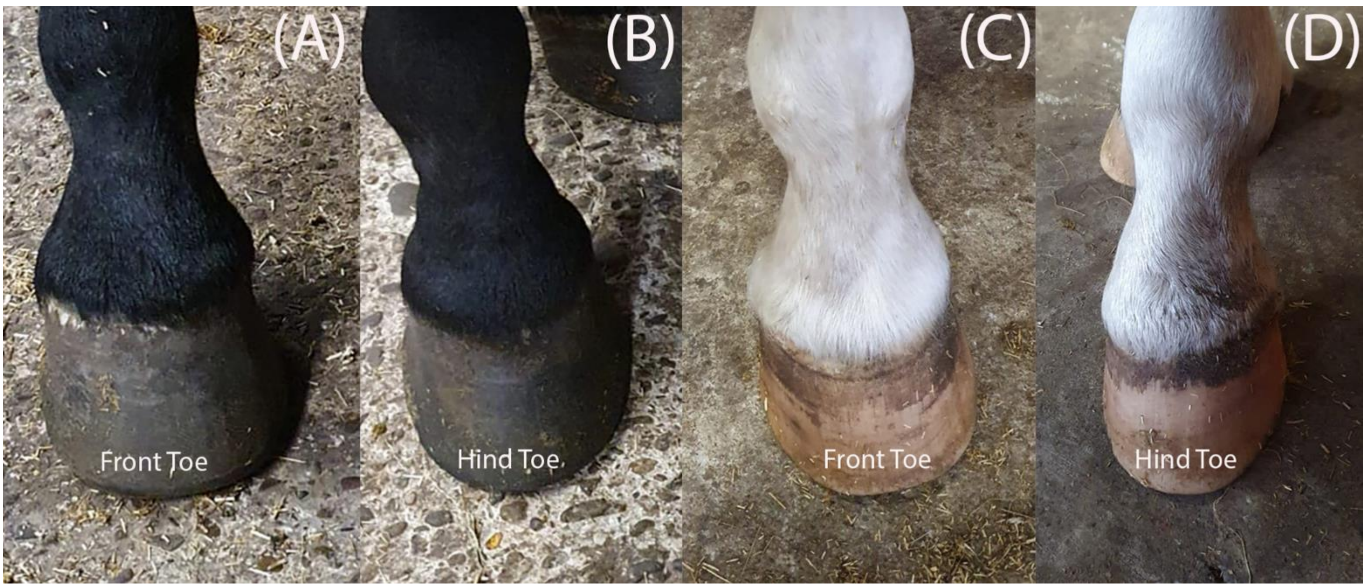

Figure 3. Difference in shape between front and hind hooves of modern horses. The front hooves are rounder in overall shape and have a more flattened and gently rounded anterior toe, whereas the hind hooves are more oval in shape and possess a more pointed anterior toe. A. Front hoof in horse 1 (width = 11.5 cm); B. Hind hoof in horse 1 (width = 11.5 cm); C. Front hoof in horse 19 (width = 12 cm); D. Hind hoof in horse 19 (width = 11 cm).

hind hoof is more isometric than the front hoof (see tables S5-S6). This brings us to the third, and in the end, most important criterion, the shape of the anterior toe of the hooves. Front hooves tend to have a gently curving anterior toe (tip) whereas hind hooves tend to have a more pointed anterior toe (see Inoue and Sagaguchi, 1997; see figures 3 and 4).

There is one further analysis possible from the direct observation of trackways, or photos and sketches of them, that may be useful for distinguishing manus from pes prints. It is known that during the swing phase of its stride, the horses' legs, especially the hind ones, move in an arc from outside to inside (even in horses with good conformation), and that the feet angle upward and outward before making ground contact. As a result, hooves, especially hind ones, land more on the posterior than the anterior portion of the hoof, and more on the outside than the inside wall of the hoof (Stan, 1964; Barrey, 1990; Ratzlaff et al., 1993; Schamhardt and Merkens, 1994; Crevier-Denoix et al., 2013). In addition, the movement of a horse hoof through a soft substrate likely parallels that of other vertebrates, and so continues in forward motion as the hoof sinks during the early phases of the stance after hoof impact (Turner et al., 2022). As a result, hooves, especially hind (pes), may leave a wider impression of the hoof wall anteriorly and a longer trace posteriorly on the outside edge of the hoof, potentially allowing one to distinguish hind from front hooves and left from right hooves (Stan, 1964; Lallensack et al., 2022). Horse hoofprints displaying such features occur on occasion, though usually as isolated prints (Sarjeant and Reynolds, 1999; Remeika, 2001; Reynolds, 2006; Herrero et al., 2022; Vincelette and Renders, 2023). More investigation and validation of this phenomenon in horses, however, is necessary, before it can be put to use. Indeed, the future use of technology for the 3D capturing of footprints, and its ability to capture impact angles of the hooves in great detail (Falkingham et al., 2018), should prove to be of great value in distinguish front (manus) from hind (pes) and left from right hooves, and unraveling whether gaits are more likely to be racking or trotting.

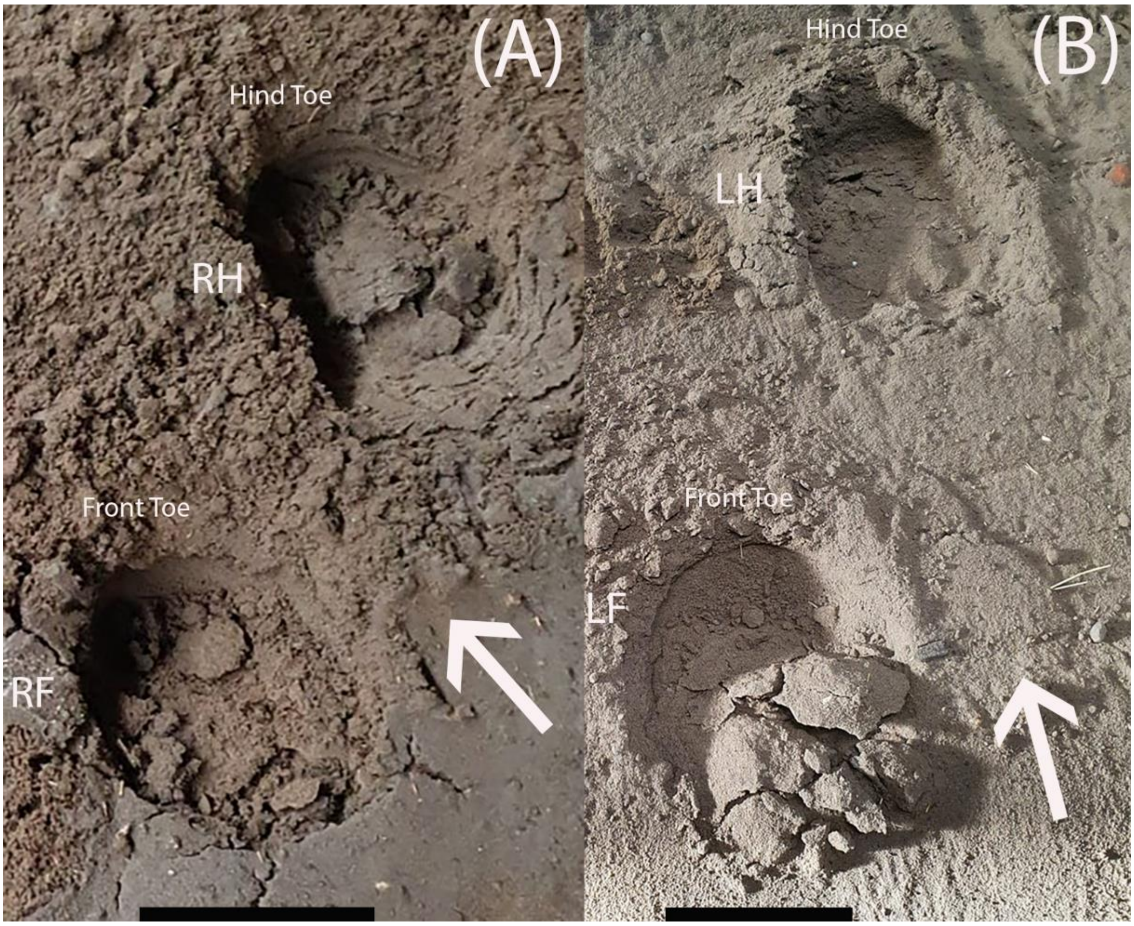

Figure 4. Difference in footprints made by front and hind hooves. The front hooves leave an impression that is more rounded overall and gently curved anteriorly (at the toe) whereas hind hooves leave an impression that is more oval overall and more pointed anteriorly. A. Front and hind hoof impressions in horse 1. Here the right hind foot, RH (width = 12.2 cm) oversteps the right front foot, RF (width = 11.8 cm). B. Front and hind hoof impressions in horse 19. Here the left hind foot, LH (width = 13.0 cm), oversteps the left front foot, LF (width = 12.0 cm). Arrows show direction of travel. Black bars are 10 cm long.

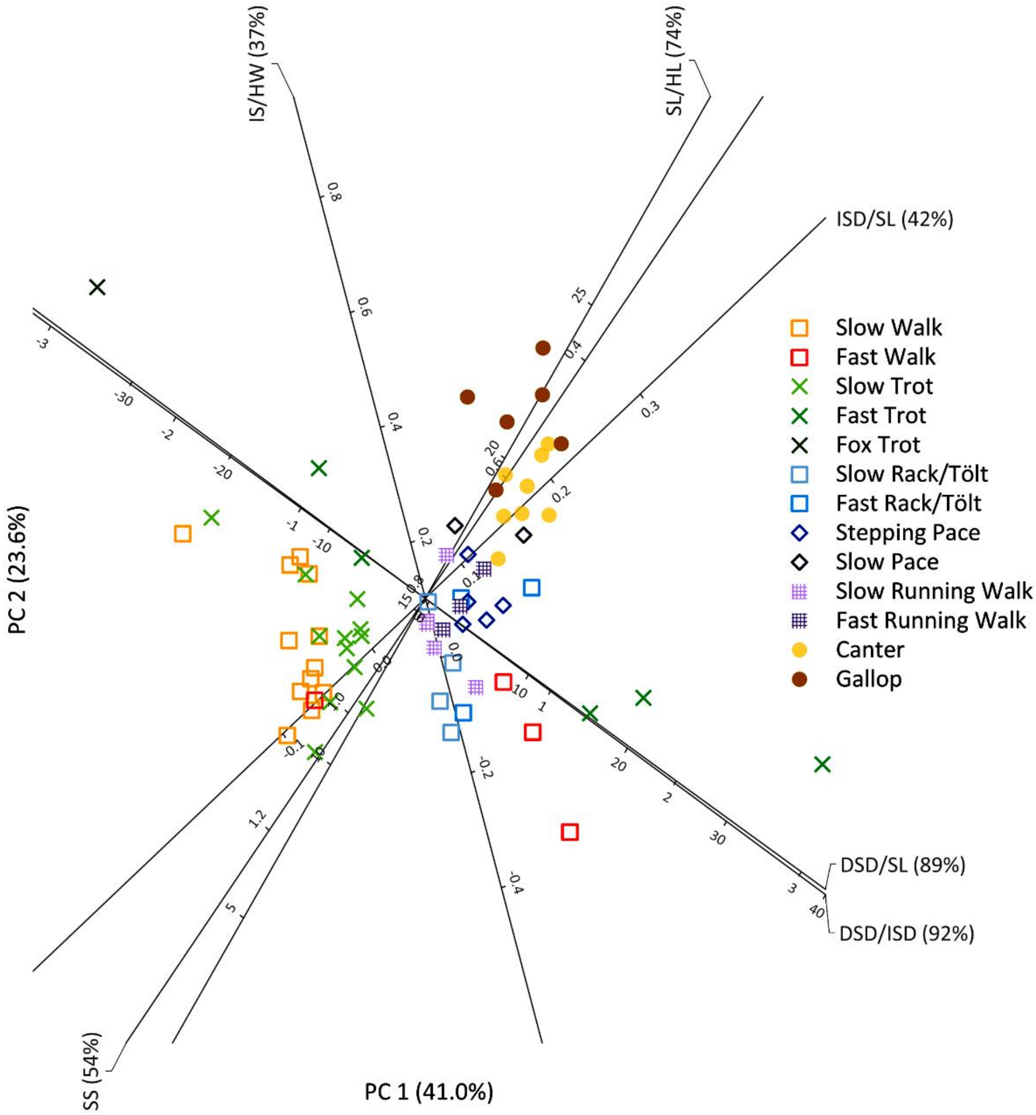

Figure 5. Footprint patterns of various gaits in modern horses. In the fast walk (A) there is a small stride length with a small overstep of ipsilateral hind feet resulting in distinct lateral pairs of prints in roughly parallel lines and a diagonal step distance much larger than the ipsilateral one. The fox trot, true fast trot, and slow rack (B) forms a trackway similar to that of the walk with lateral pairs of prints lining up more or less in parallel but possesses a greater stride length. In the running walk (C) there is a large overstep yielding no obvious pairs of prints as the ipsilateral step distance is nearly equivalent to the diagonal one but wherein the ipsilateral step distances and diagonal step distances are roughly equivalent with themselves. This should be contrasted with the gallop (D) which also lacks obvious footprint pairings but which has a much greater stride length and in which there is greater variance within the ipsilateral and diagonal step distances and a sequence of contralateral feet. In the fast rack or tölt (E) the ipsilateral step length is much greater than the diagonal one resulting in diagonal pairs of prints that form a bowed pattern with a large stride length and hind impressions that often cross over the centerline. In the stepping pace and true pace (F) there is an even greater stride length and the diagonal pairs of prints occur very close together as the ipsilateral step distance is much larger than the diagonal one. The scale is in centimeters

Determination of gait and velocity from trackway data alone

One can glean a lot of information from horse trackways themselves. Moreover, as fossil records can be incomplete, and species of trackmaker unknown, uncertain, or speculatively tied to a trackway, it is beneficial (at least initially) to use trackway data in isolation to estimate trackmaker size, gait, and gait velocity. This is done by taking the measurements on the trackway noted above and then following the methodology set forth below.

Determination of gait from trackway data alone

Once front and hind feet are able to be distinguished (see method given above), then the footfall sequence of the trackway can be determined. For example, one can determine that the order of prints

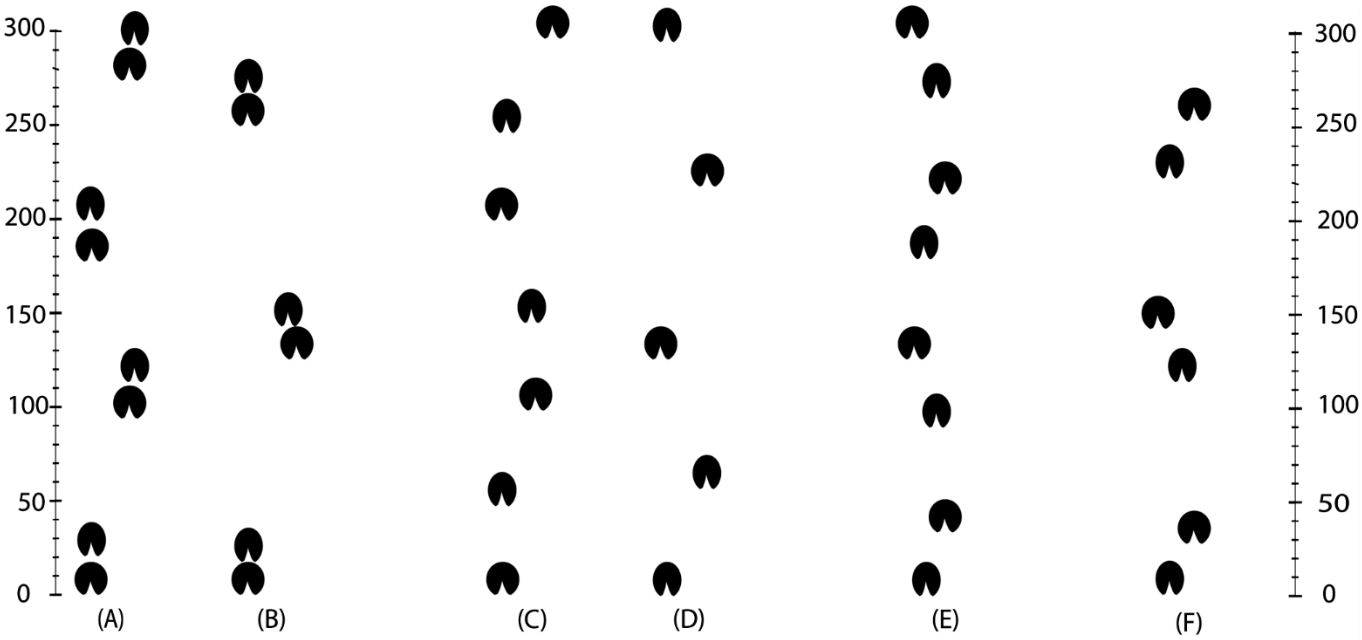

Figure 6. Photographs of modern horses in various gaits. A. Fast walk of a Tennessee Walking Horse (horse 12); B. Slow trot of a Shetland Pony (horse 24); C. Fast tölt (stepping pace) of an Icelandic Horse (horse 9); D. Right-lead gallop of a Shetland Pony (horse 24); E. Running walk of a Tennessee Walking Horse (horse 12). Arrows show direction of travel. Black bars indicate stride length in cm.

in a trackway is left hind (LH), left front (LF), right hind (RH), and right front (RF). Knowing the footfall sequence allows the various measurements described above to be taken, reveals the pattern of the trackway, and allows identification of likely gait of the horse trackmaker.

In terms of standard footfall patterns (see figures 6 and 7), as noted above, walking, trotting, and slow racking trackways have ipsilateral pairs of feet landing close together with slight understep, capping, or overstep. Fast racking and pacing gaits have diagonal pairs of feet landing close together, with hind feet often crossing over the centerline. Trackways made by walking and trotting gaits thus contain parallel rows of foot pairs, while trackways made by fast racks and pacing gaits do not but

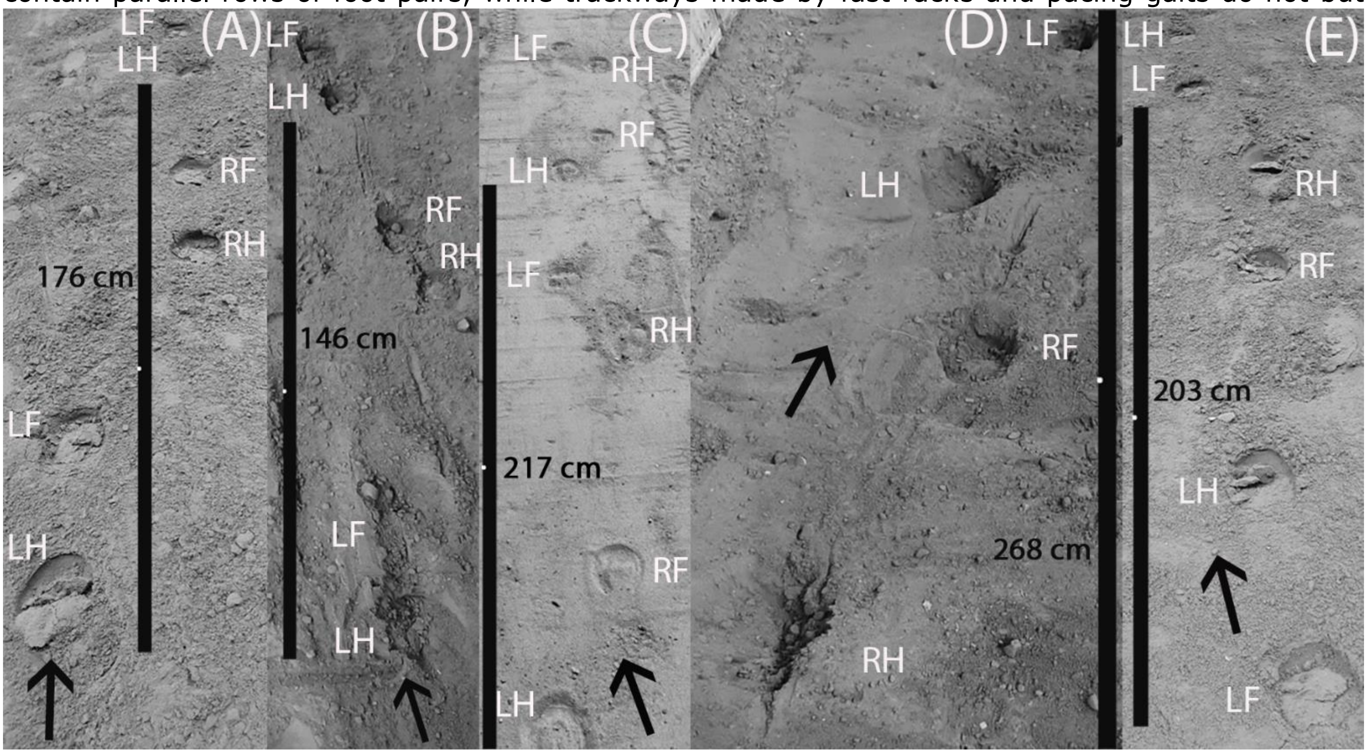

Figure 7. Photographs of modern horses in various gaits. A. Fast walk of a Tennessee Walking Horse (horse 12); B. Slow trot of a Shetland Pony (horse 24); C. Fast tölt (stepping pace) of an Icelandic Horse (horse 9); D. Right-lead gallop of a Shetland Pony (horse 24); E. Running walk of a Tennessee Walking Horse (horse 12). Arrows show direction of travel. Black bars indicate stride length in cm.

rather show a weaving pattern. Galloping gaits have contralateral pairs of feet landing close together with an asymmetrical trackway, and so will have a footfall sequence containing two contralateral hind limbs in succession, whereas the other gaits being symmetrical will contain ipsilateral and diagonal pairs of limbs in succession. Galloping gaits, and running walks, also lay down a pattern of isolated footprints 1-1-1-1 with no obvious foot pairings (as can a medium rack), or with the canter, just one pairing, an overstep of ipsilateral feet (1-2-1).

Moreover, once the above trackway measurements have been taken, the gait exhibited in the trackway can be determined with a fair amount of accuracy. This is because six trackway factors discriminate between modern horse gaits fairly well, namely: stride length/front foot length; interior straddle/hind foot width; ipsilateral step distance/stride length; diagonal step distance/stride length; diagonal step distance/ipsilateral step distance; and step symmetry calculation (table 1; figure 5).

Slow walks and slow trots tend to have a stride length/front hoof length ratio between 10 to 17, a diagonal/ipsilateral step distance ratio between -20 to 0, and a positive interior straddle/hind hoof width. Fast walks and fast trots are similar but have positive diagonal/ipsilateral step distance and ipsilateral step distance/stride length ratios. Racks and running walks tend to have a negative interior straddle/hind hoof width, and a positive diagonal/ipsilateral step distance ratio. Finally canters and gallops tend to have a stride length/front hoof length of 17 to 25. It is also important to look at the footfall patterns of the trackway as slow walks and slow trots tend to involve capping or understeps of ipsilateral feet, and slow racks, fast walks, and fast trots oversteps of ipsilateral feet. On the other hand, fast racks involve oversteps of ipsilateral feet (resulting in trackway displaying understeps of diagonal foot pairs) and running walks and gallops display isolated prints with the latter being asymmetrical (figure 6).

Still, it is hard using trackway data alone to distinguish certain gaits, such as slow walks from slow trots. In addition, horses smaller in height or shorter in body-length (gleno-acetabular distance) may have a fast walk or trot that matches more the data or footprint pattern of a slow walk or trot, since they have a greater tendency to understep. Moreover, the correlation between hoofprints and height is not as strong as that between ungual phalanges and height, as we will see. It is also important to note that footprint length and width is dependent upon factors other than hoof length and width, such as the speed of the gait (wherein fast gaits can leave prints 1-2 cm longer than those in slower gaits), substrate consistency (gaits in mud tend to be longer than those in sand), substrate collapse after hoof removal, and how clean the hoof is (Renders, 1982; Lallensack et al., 2022). Hence it is necessary to determine the hoof impressions and/or values most reflective of the hoof length and width, as opposed to those elongated by displaced dirt, toe drags, foot sliding, substrate collapse, or adhesion of mud to the back of the hoof. Hence, as we will argue for later it is good to make use of both trackway and osteological data if possible.

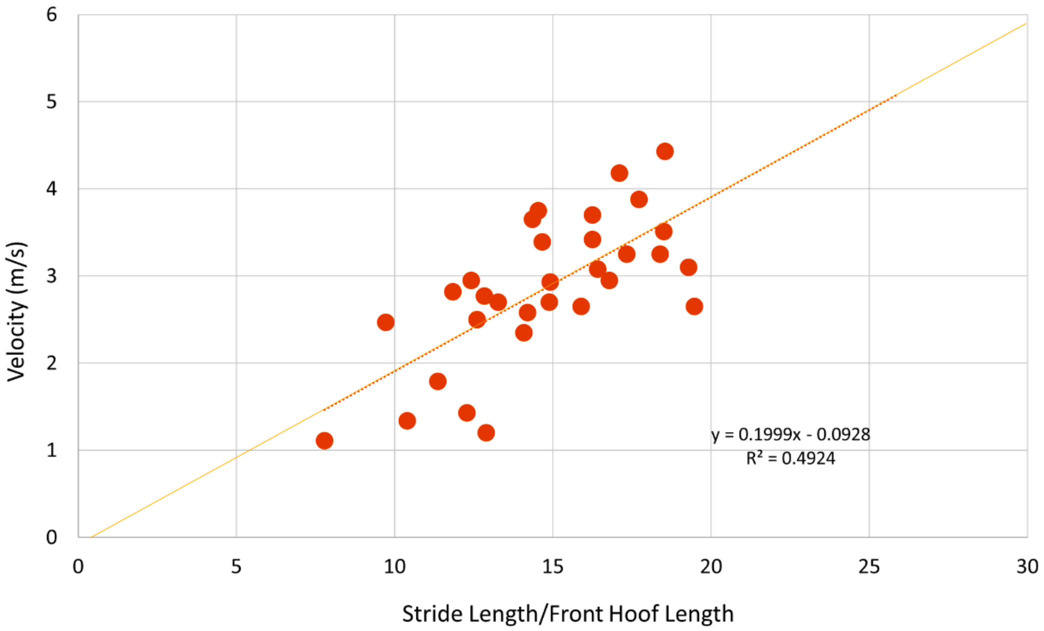

Figure 8. Bivariate plot of velocity (m/s) in relation to stride length/front hoof length with (extended) regression line.

Estimation of gait velocity from trackway data alone

We found some correlation of velocity of gait with stride length/front hoof length ratios in our study of modern horses (figure 8). On this basis one can get a rough estimate of trackmaker velocity using the following formula

$$(1) \quad V = (0.2 \times SL/HL) - 0.09$$

where V = velocity (m/s), and SL/HL = stride length/front hoof length ratio.

Estimation of trackmaker height from trackway data alone

It is also possible to estimate trackmaker height from trackway data alone. Hoof length does correlate with horse height at the withers to a fair extent in horses, as taller individuals tend to have longer hooves. Stachurska et al. (2011, tab. 3), in a study on 77 Polish horses of four breeds, found the correlation coefficient between front hoof length and height at the withers to be around 0.41 (see also Inoue and Sagaguchi (1997, fig. 14). Our own data from 19 horses of seven breeds (see supplementary table S1) yields a correlation coefficient of front hoof length to height at the withers of 0.66. There are also two fossil genera, *Hippotherium* and *Equus*, for which we possess nearly complete skeletons and fossilized hoofprints (see tables S3 and S5). By combining our modern horse data with the fossil data (albeit limited) a plot of the relationship between front hoof length and height at withers is found (figure 9), from which one can derive a formula for the estimation of the height of the equid trackmaker:

$$(2) \qquad HT = (6.5 \times HL) - 59.2,$$

where HT = height at withers (cm), and HL = front hoof length (cm).

In addition, one can use the ratio of diagonal/ipsilateral step distance (DSD/ISD) to get a rough estimate of the height of the equid trackmaker (see Renders and Sondaar, 1987; table S8 in the supplementary section). It would be good to compare these two values (estimations from front hoof length and from DSD/ISD) for consistency.

Determination of gait and velocity from trackway plus osteological data

Although trackway data alone can go a long way in identifying gait and estimating velocity, a more precise estimate of the height of trackmaker can help distinguish gaits even further and improve the estimation of velocity. For this, however, osteological data is necessary. Much stronger correlations with horse height at the withers occur with osteological elements than with footprint length (which we saw had values ranging from 0.41-0.66). For example, Chrószcz et al. (2014, tab. 2) found very high correlation coefficients between horse height at the withers and cranial (0.91), metacarpal (0.95), and metatarsal (0.91) bones. Hayashida and Yamauchi (1957, tab. 2) also found high correlation coefficients between horse height at the withers and cranial (0.83), metacarpal (0.90), metatarsal (0.87), phalanx I (0.81 and 0.91 for anterior and posterior), and phalanx III (0.85 and 0.89 for anterior and posterior) bones (see also Onar et al., 2018, tab. 3). Our own data from fossil horse species (table S3) yields similar correlation coefficients between equid height at the withers and cranial (0.96), metacarpal (0.96), metatarsal (0.96), phalanx I (0.92 for both anterior and posterior), and phalanx III (0.97 and 0.94 for anterior and posterior) bones.

It is important to note, however, that height can vary widely in modern horses of the same breed. This is due in part to sexual dimorphism (Pinto et al., 2008; Purzyc, 2009; Purzye et al., 2010; Asperen, 2013; Krebs et al., 2021), but more particularly to differences in age, diet, and genetics. Brooks et al. (2010) noted height variations between 130.0 cm and 180.0 cm in 221 adult Thoroughbreds. And Chrószcz et al. (2014) noted variations of height between 131.7 and 175.9 cm in seventeen mixed breed (Thoroughbred x Wielkopolski) horses (see also Staiger et al., 2016). Something similar presumably occurred with fossil equid species (see Gingerich, 1981), though we lack detailed knowledge of the height diversity found in extinct horse populations. It is especially difficult to estimate the age and gender of a fossil horse from trackways (though this is sometimes possible where several trackways occur at the same locality and one can see presence of adult and foals as well as maternal guarding behavior). For these reasons we believe the ideal method for determination of height should make use of a combination of trackway and osteological data as described below. Before this can happen, however, we need to identify the species of the trackmaker which has its own challenges.

Determination of species of trackmaker

To make use of osteological data in estimating trackmaker height, one first needs to determine the species of the trackmaker, and yet this presents several obstacles.

In the first place, it is not always clear what species of fossil equid left a set of tracks. Few trackway sites contain fossilized equid bones, since substrates ideal for the preservation of foot impressions are not always ideal for the preservation of fossilized bones. Hence one typically needs to associate horse

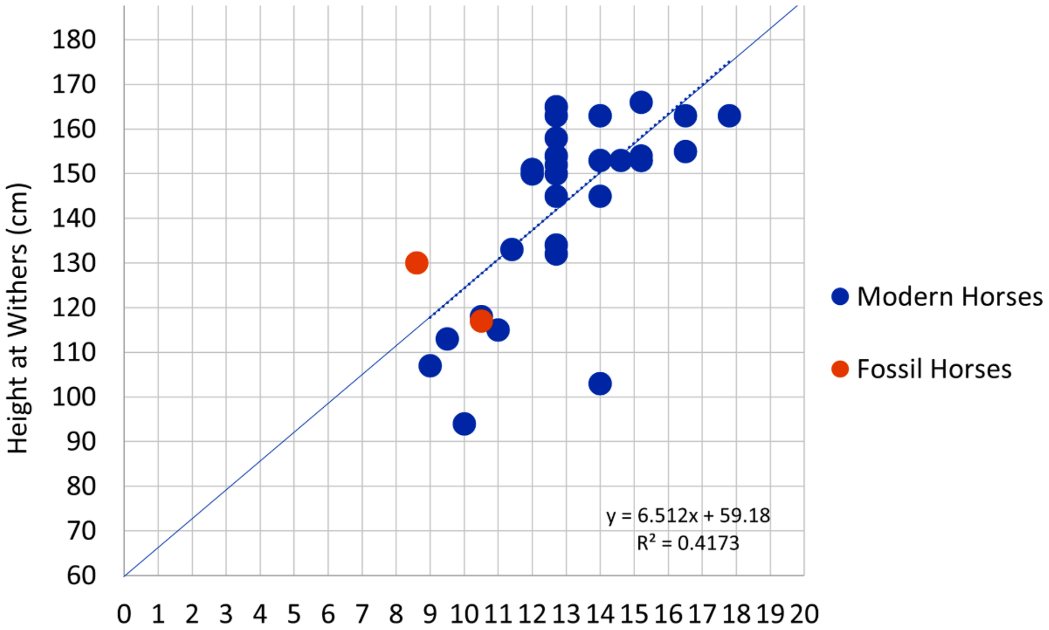

Figure 9. Bivariate plot of front hoof (print) length compared to height of equid at withers with (extended) regression line. Modern horse values were derived from measuring hoofprint lengths left by horse hooves during a slow walk in a sandy arena and are indicated in blue. Only two fossil horse genera have left tracks that can be tied to known skeletal heights (a shorter *Hippotherium* and a taller *Equus*) and these are indicated in orange.

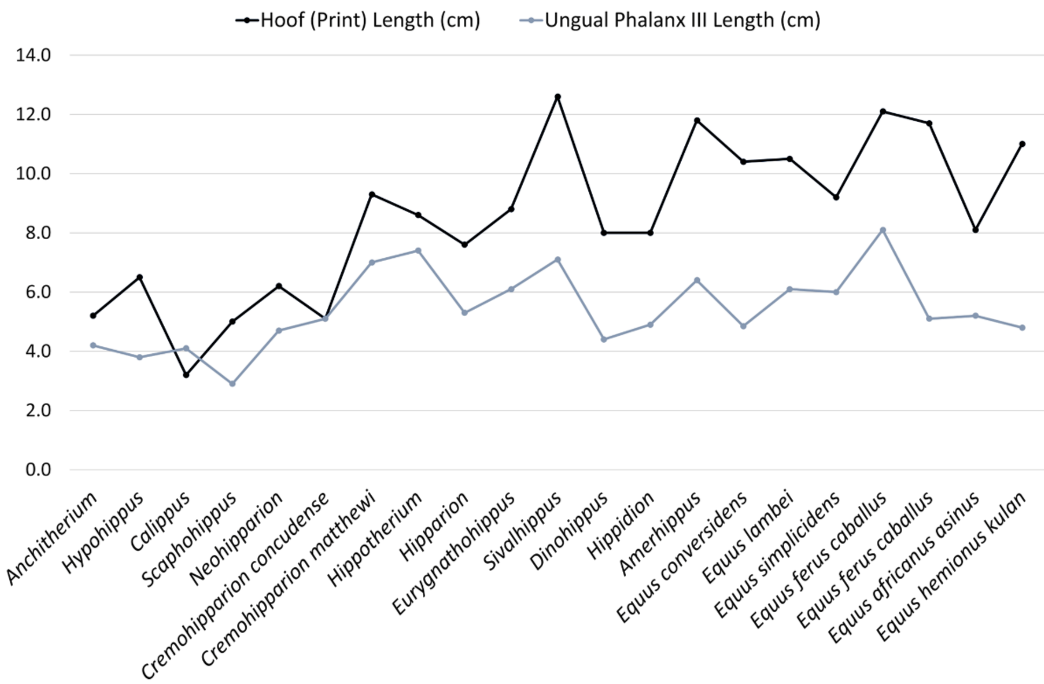

Figure 10. Plot of ungual phalanx length of digit III in relation to hoofprint size for fossil and modern equids.

trackways with equid osteological data found in nearby horizons of the same geological age. Ideally the same geological formation in which the trackway occurs, and at a nearby location, also bears fossil equid bones from which one can draw up a faunal list of potential trackmakers. Or alternatively strata immediately below or above the fossil trackway horizon can provide equid species that are possible trackmakers. However, in some cases the closest such fossilized bed of the same geological age may lie far away (such as in another state or country) forcing one to assume continuity of species size along with presence of species not yet revealed due to an incomplete fossil record. Hence correlations of horse fauna found strata of a similar geological age and close spatial proximity can provide trackmaker candidates. From this one can come up with a list of trackmaker candidates, prioritizing species present in nearby strata of the same geologic age, or found immediately above and/or below the strata. One must recognize, of course, that the data is often incomplete, and there is room for error and correction as future discoveries are made.

Still, there are ways of finding the most likely trackmaker and eliminating possible trackmakers. After a list of trackmaker candidates is developed, it is beneficial to look at which species of equids are the most common in the relevant strata (if such data is available). For the most common species are more likely than not to be the trackmaker. Of course, it is possible the track was made by a less common species (or that there is a bias in the fossil record), which brings us to the next criterion.

One can rule potential trackmaking species in or out by comparing postcranial (or other osteological) material with the trackway hoofprints (see Strickson et al., 2020). If there are ungual phalanges of digit III available from a possible trackmaking species, these can be compared with the hoofprints (of digit III) from the trackways in three significant ways: comparing lengths, widths, and length/width ratios. By plotting lengths, widths, and length/width ratios of the ungual phalanges of digit III in relation to those of the central hoofprints, for Miocene to extant equids (figures 10-12), we find that smaller tridactyl species from the Miocene to Pliocene tended to have ungual phalanges of digit III 1-2 cm shorter in both length and width than their hoofprints, while large tridactyl species (Anchitheriini) and monodactyl species tended to have ungual phalanges 3-4 cm shorter in both length and width than their hoofprints. If a potential trackmaker has ungual phalanges near or greater in size than the hoofprints (especially if it is an anchitheriin or monodactyl species) or quite a bit smaller than the hoofprints this suggests they are unlikely to be the trackmaker (though one must allow for the possibility a juvenile made the trackway or rule that out based upon other factors). There are also differences between particular genera that may be important (figures 10-12; tables S5-S6). Maximal length/maximal width ratios of the phalanges and hoofprints are also good to compare. If the length/width ratios of the phalanx and hoofprints are similar this supports a species being the trackmaker (see figure 12). A likely trackmaker then will have an ungual phalanx of digit III with dimensions (length, width, and length/width ratio) proportional to those of similar genera or taxa.

Studies on equid footprints have also suggested an increasing thickening of the hoof wall from 4-5 mm in equids living 17.5 to 12.5 Ma, increasing to 7-10 mm in equids living 10.3 to 2.6 Ma, and maxing out at 8-10 mm in horses living 0.85-0.40 Ma up to the present time (see Reynolds, 1999, 27, tab. 1; McNeil, 2008, 216; Oliva and Arregui, 2018, 434, tab. 4). If hoof walls are visible in the hoofprint this information may also be useful for the determination of the most likely trackmaker species.

If ungual phalanges are not available, one can estimate the size of possible trackmakers from other cranial and/or postcranial material (see table S3-S4). That is to say one can infer the size of the hoofprint likely to have been made by a given species based upon comparisons of skeletal elements with those of similar taxa with nearly complete skeletons (including ungual phalanges of digit III). For example, if a possible trackmaker from the genus *Hippotherium* has a metarsal III bone 10% shorter in length than that of *Hippotherium primogenium*, this would suggest it also has an ungual phalanx III 10% shorter (see tables S3 and S5), or around 6.6 cm long (see tables S3 and S5) and a hoofprint around 1 cm longer (figure 10), or 7.6 cm in length. Such a value can be compared with that found in the trackway to see how closely they match.

Finally, one can follow the procedure for estimating trackmaker height using various skeletal elements detailed below and see if these separate estimations match up with good consistency. If they do this supports identification of the species as the trackmaker, if they don't it lessens the likelihood (all things considered).

Nonetheless, determination of which horse species has made a trackway is difficult and involves much uncertainty. The age of the trackmaker is typically not knowable (unless there are several trackways of similar ichnomorphologies but different sizes), nor do we have a lot of knowledge about intraspecific variation (or sexual dimorphism) in fossil horses. Thus, tracks of young or small individuals might be wrongly identified as those of adults of a smaller species.

Estimation of height of the trackmaker from combined trackway and osteological data

In some situations, one can acquire a high degree of confidence that the print was made by an adult or near-adult. Such situations can occur where there are several trackways present of different sizes that reveal population structure, where trackways exhibit social behaviors indicative of adult or juvenile behavior (such as harem structures, protective encircling of a foal, or close following of a foal by a mare), or where there is a strong correlation of a trackway with a trackmaking species with the size of the adult ungual phalanx III matching the expected size given the hoof impression (see supplementary tables S5-S6). In populations of wild zebras and feral horses, adults tend to constitute 70-80% of the population (Georgiadis, 2003; Doku, 2007; Mendonça, 2022), and young foals are rarely far from their mares, and so the likelihood of an impression being formed by an isolated adult is much greater than that of it being formed by an isolated juvenile. Hence if the size of the print matches that expected based upon the size of the adult phalanx of the most likely species there is a strong likelihood that the print was made by an adult. Still one must use caution here and recognize a juvenile print is always a possibility.

That said, we believe that the best way to estimate trackmaker height (and determine gait and velocity) is by combining data from horse trackways and associated horse species osteology. As paleontologists have noted, the allometric ratios of the different bones comprising an equid limb can vary quite dramatically from one species to another (Gidley, 1903; Stock, 1951; Eisenmann, 1976; Eisenmann, 2000), and without a full limb bone set one may somewhat overestimate or underestimate horse height. This is why though in the past we replied upon height estimation multipliers developed from cranial or postcranial bones of modern horses (see table S2 in the supplemental section), we now prefer to use multipliers based upon fossil horse taxa possessing nearly complete skeletons from which height at the withers and bone lengths can be directly determined.

For though there are only a few complete or nearly complete horse skeletons (see supplementary table S3), and hopefully future findings will refine these measurements, what is available can yield knowledge of the ratios of skeletal material to horse size in different fossil taxa (figure 13), and provide height estimation multipliers for select genera and lineages. Table S4 in the supplemental section

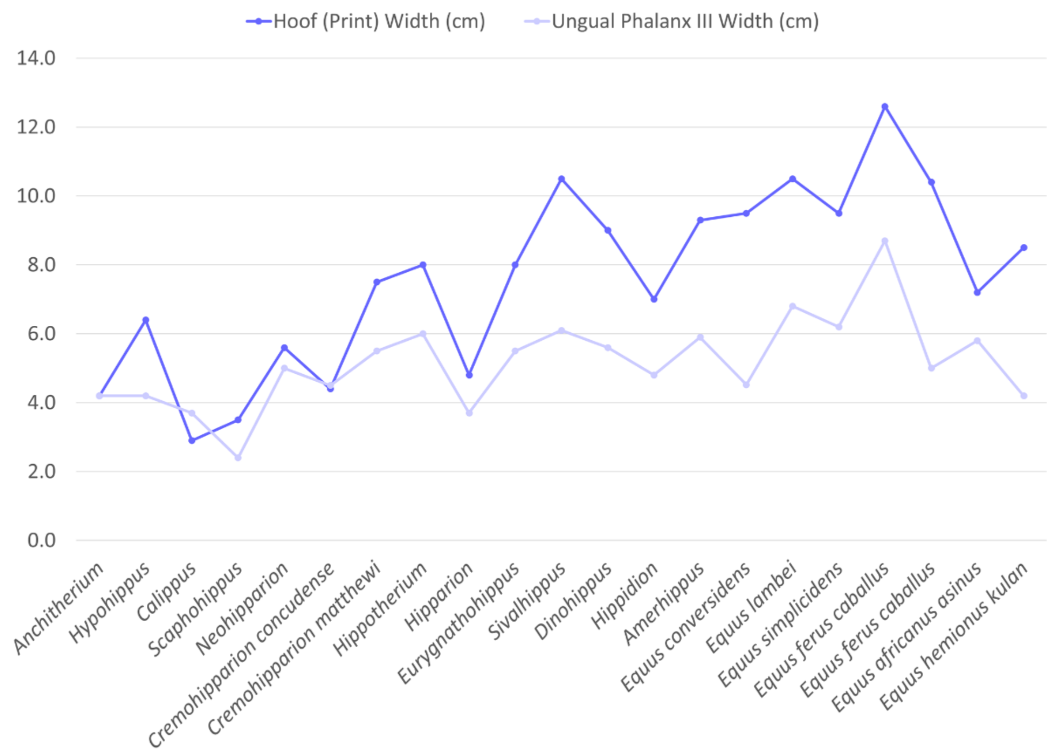

Figure 11. Plot of ungual phalanx width of digit III in relation to hoofprint size for fossil and modern horses.

contain these height estimation multipliers for the most commonly preserved (and highly correlatable) bones for the Eocene subfamilies Propalaeotheriinae and Hyracotheriinae, the Oligocene subfamily Anchitheriinae, the Miocene tribes Anchitheriini, Hipparionini, and Protohippini, and the Pliocene and Pleistocene monodactyl tribe Equini, as well as select genera in these groups. We also develop height estimation multipliers from hoofprint length based upon known values in modern and fossil horses. There are only two values available for fossil horse genera (figure 8), and here horse height at the withers averages 13.13 times hoofprint length. This matches closely with the study on modern horses done by Stachurska et al. (2011) who found height at withers to be 13.16 times the size of the front hoof (our own data in table S1 gives a lower value of height at withers being 10.9 times hoofprint length but our study relied upon hoof print versus morphological hoof data, our sample size was smaller, and our study included more ponies and hemiones which tend to have different ratios than other horse breeds; see Thieme et al., 2015). In any case, by taking the value of 13.16 and multiplying it by the ratio derived from dividing the fossil taxon phalanx multiplier by the modern horse phalanx multiplier (21.62), one gets scaled front hoof length multipliers for the fossil horse groups (table S4).

In light of this, our recommended height estimation method for fossil equid trackmakers is to make use of three independent lines of evidence where available (cranial, postcranial, and trackway data) to estimate trackmaker height. As we noted above trackway data is important given uncertainty about exact taxon or age or relative size of the trackmaker. Yet there are stronger correlations of height with osteology than with hoofprint length. Arguably then combining cranial and postcranial data will yield the best estimation of trackmaker height (assuming the taxon is correctly identified), with the osteological data relating to size at the species level and the trackway data to size at the individual level. In our formula we assign fifty percent of the weight to the hoofprint measurements as they are the primary known factor about the trackmaker, a trackmaker whose species is a matter of some inference and whose population height can be variable and whose age is unknown, 25% of the weight to the skull length (if available) which correlates well with the size of fossil horses and is a different line of evidence than the postcranial skeleton, and finally 25% weight to the postcranial elements that correlate closely with overall height and are commonly preserved, namely, the metacarpal, metatarsal, proximal phalanx, and distal phalanx lengths.

That is, estimated height of the trackmaker can be calculated from the following formula:

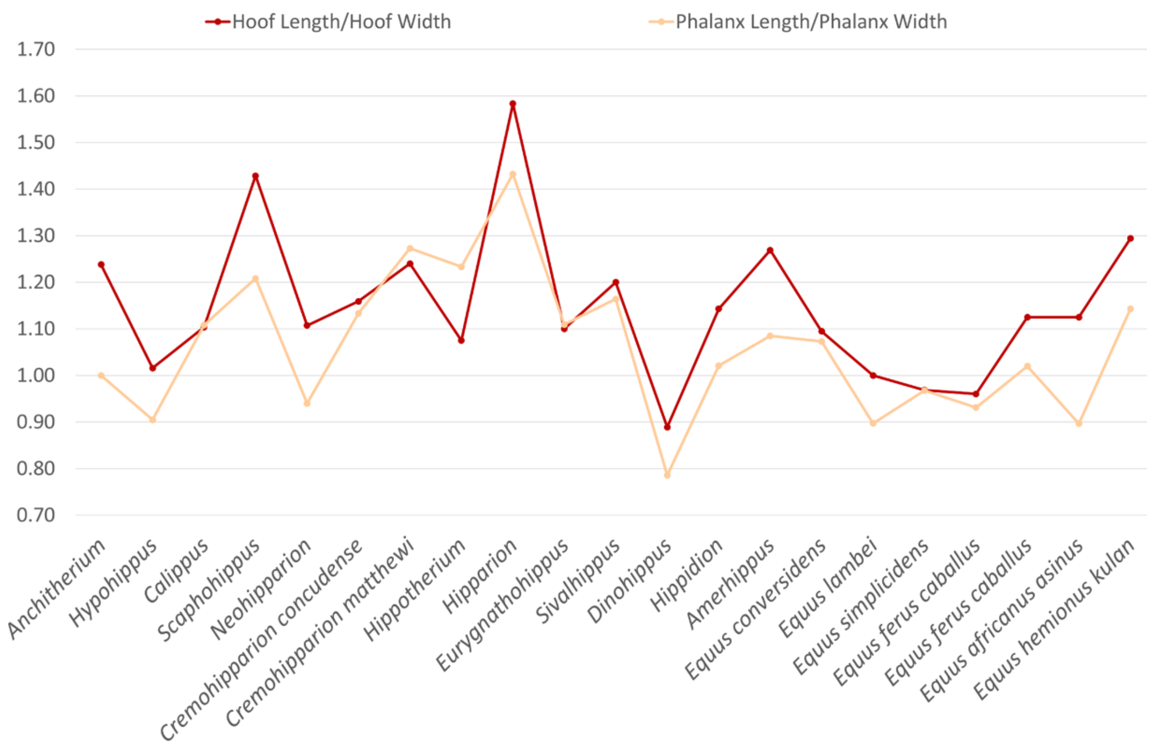

Figure 12. Plot of equid ungual phalanx versus hoofprint length/width ratios. The ratios of maximum length/maximum width of ungual phalanges of digit III and hoofprints tend to be similar. Smaller tridactyl species tend to have ungual phalanges and hooves longer than wide and so have a value larger than one, while larger tridactyl species and monodactyl species (excepting South American forms *Hippidion* and *Amerhippus* and hemiones) tend to be wider than long and so have values lower than one.

(3) 0.25(CLxCLMg)
x 0.25[(MTxMTMg)+(MCxMCMg)+(1P3x1P3Mg)+(3P3x3P3Mg)]/4
x 0.50(FFLxFFLMg),

where CL = maximal skull length measured from the tip of the incisive bone to the nuchal crest; MT = greatest metatarsal III length, MC = greatest metacarpal III length,1PIII = greatest proximal phalanx III length, 3PIII = greatest ungual phalanx III length; FFL = front footprint length, and CLM, MTM, MCM, 1P3M, 3P3M, and FFLM are the multipliers for the matching fossil horse groupings from table S4 (i.e. family, subfamily, tribe, or taxon)

The formula given above can be modified if particular skeletal elements are lacking, such as the skull or metatarsus. If no skeletal material can be linked to the tracks and a probable trackmaker identified, then one can resort to the previous methodology using trackway data alone.

Because specific identification of the trackmaker is difficult and the fossil record incomplete, the separate height estimations from each of the elements noted above (hoof, phalanges, metapodials, skull) should be compared for consistency. Such comparisons might suggest that the trackmaker has been incorrectly identified, the hoofprints misinterpreted, or that the species had different allometric skeletal ratios than other fossil horses of the same phylogenetic group.

Determination of gait from combined trackway and osteological data

As noted earlier, walking, trotting, and slow racking trackways have ipsilateral pairs of feet landing close together (whether with understep, capping, or overstep), fast racking and pacing gaits have diagonal pairs of feet landing close together, with hind feet often crossing over the centerline. Hence walking, trotting, and slow racking gaits display a pattern of prints with pairs lining up in parallel rows, whereas fast racking and pacing gaits display a weaving pattern of prints (see figures 6 and 7). Galloping gaits have contralateral pairs of feet landing close together with an asymmetrical trackway, and lay down a pattern of isolated footprints 1-1-1-1 with no obvious foot pairings (as do running walks and medium-speed racks at times), or with the canter, just one pairing, an overstep of ipsilateral feet (1-2-1).

Moreover, we can use refined versions of the six key factors noted above, to discriminate between gaits in modern horses even more distinctly (table 1), namely: step symmetry calculation (SS), stride length/trackmaker height at withers (SL/HT), interior straddle/hind hoof width (IS/HW), ipsilateral step distance/stride length (ISD/SL), diagonal step distance/stride length (DSD/SL), and diagonal/ipsilateral step distance (DSD/ISD).

Ipsilateral step distance/stride length is around -0.15 to 0.5 in walking and trotting gaits, but around 0.10-0.40 in the rack or pace. Slow walks and slow trots tend to have a negative diagonal step distance/stride length ratio (-20 to -3), with slow walks often having a height/stride length below 1.0 and slow trots between 1.0 and 1.2. Fast walks and trots tend to have a positive diagonal step distance/stride length ratio (3-20), with fast walks having a height/stride length ratio between 1.0 and 1.2 and fast trots between 1.2 and 1.7. The diagonal step distance/stride length hovers around zero for ipsilaterally coordinated gaits such as the rack, pace, and running walk (0.2-3.0). Racks tend to have an interior straddle/hind hoof width ratio that is negative or near zero (narrow gauge). This is because the lack of interference allows hind limbs to cross the centerline during the gait. Running walks most often have an interior straddle/hind hoof width ratio between 0.0 and 0.1, while walks and trots have a value above 0.1. Racks, running walks, and stepping paces also tend to have a height/stride length between 1.2 and 1.7.

All of the above gaits are symmetrical and so tend to have step symmetry (SS) between 0.80-1.00, while asymmetrical gaits of horses (canter and gallop) tend to have a lower step symmetry between 0.30-0.65. Galloping gaits are also noticeable in having a very high stride length/height ratio (SL/HT) of 1.5-2.5 or more, and being wide gauge, that is, having a large interior straddle/hind hoof width (IS/HW) above 0.15. For other variations in parameters between horse gaits see table 1.

These relations can be visualized and validated by subjecting the different gaits to Principal Component Analysis for each of the six key factors (figure 14). For such a purpose dimensionless speeds (figure S1; table S9) were used to separate walks into slow walks (SL/HT=0.78-1.09) and fast walks

(SL/HT=1.10-1.18); trots into slow trots (SL/HT=1.32-1.51) and fast trots (SL/HT=1.55-1.80); running walks into slow running walks (SL/HT=1.13-1.36) and fast running walks (SL/HT=1.59-1.60); and racks into slow racks (SL/HT=1.18-1.24) and fast racks (SL/HT=1.39-1.70). Such dimensionless speed values were coordinated with whether or not walks and trots had negative or positive ipsilateral step distance values, racks had ipsilateral or diagonal foot pairings, and running walks had an ipsilateral step distance/stride length above 0.2.

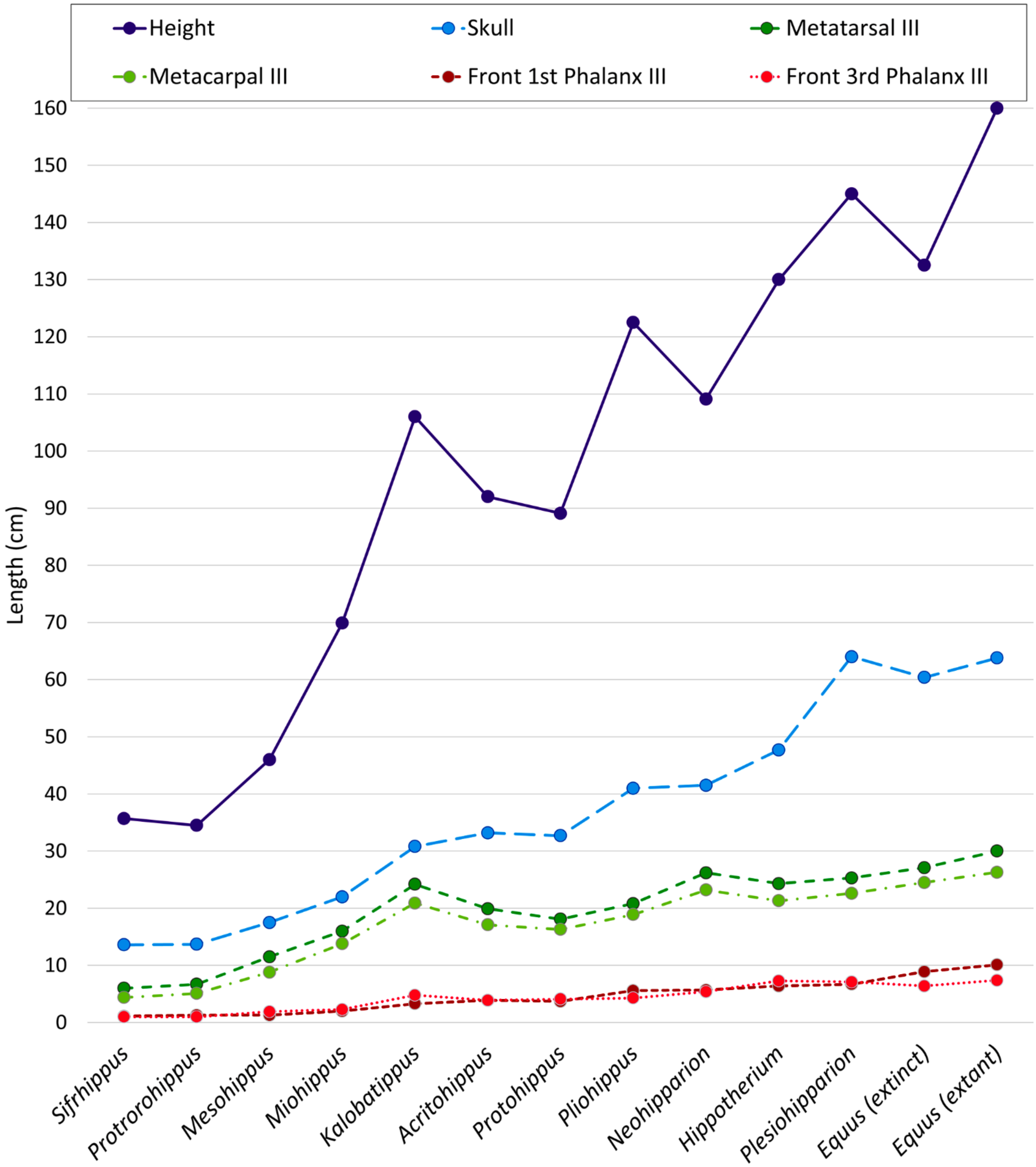

Figure 13. Plots of height at withers of fossil genera with nearly complete skeletons compared with dimensions of skeletal elements of same genera. Such a plot reveals the variability in allometric proportionality between the genera along with overall correlations of skeletal elements with height.

Table 1: Key Linear Measurements and Ratios of Modern Horse Trackways in Different Gaits; data from Vincelette (2021), and Renders and Vincelette (2022). and original data, 2022.

Gait	Average Stride Length (cm)	Average Dimensionless Speed (Stride Length/ Height)	Average Ipsilateral Step Distance/ Stride Length	Average Diagonal/ Ipsilateral Step Distance	Average Step Symmetry (for Ipsilateral and Diagonal Steps)	Average Interior Straddle/ Hind Hoof Width	Average Lateral Offset/ Hind Hoof Width
Slow Walk	145.4	1.02	-0.06	-7.96	0.92 (0.86, 0.97)	0.17	0.15
Fast Walk	159.7	1.13	-0.01	11.75	0.86 (0.79, 0.94)	0.04	0.23
Slow Trot	179.0	1.30	-0.11	-5.02	0.94 (0.92, 0.96)	0.15	0.29
Fast Trot	240.9	1.71	-0.01	11.70	0.88 (0.80, 0.96)	0.16	0.39
Running Walk	213.8	1.40	0.16	1.21	0.90 (0.93, 0.87)	0.00	---
Slow Rack	173.00	1.21	0.10	2.54	0.83 (0.78, 0.88)	-0.12	0.21
Fast Rack	215.7	1.51	0.28	0.37	0.83 (0.95, 0.71)	-0.37	0.58
Stepping Pace	240.0	1.59	0.31	0.26	0.89 (0.88, 0.90)	-0.15	0.59
Canter/ Gallop	241.7/ 303.6	1.59/ 1.89	---	---	0.38/ 0.55 (0.09, 0.68)/ (0.41, 0.69)	0.15/ 0.48	---

Determining the velocity of the gaits from combined trackway and osteological data

Previous work by the authors (Vincelette, 2021) noted that the formula developed by Alexander (1976) to determine the speed of extinct vertebrates from height and stride length tended to underestimate the velocity of horses especially in slower gaits.

Alexander (1976, fig. 1) notes that his horse data was gathered from Muybridge's *Animals in Motion* (1957). This work does give information about time and length of strides for fourteen horse gaits (five slow walks, four fast canters/gallops, and five intermediate speed gaits of amble, trot, and rack), from which velocity can be calculated. Yet it does not indicate height of the horses utilized, and so Alexander likely had to estimate this from the photographs and/or height averages for associated breeds (which were not typically indicated but could perhaps be reconstructed from the photos).

Accordingly, we here measured the velocity in twenty-four trials of twelve modern horses in various slow, intermediate, and fast speed gaits. As hypothesized, our data comparing the velocities of the horses in various gaits with horse height and stride length necessitated modification of the Alexander Formula, as our measured speeds for the horses were 1.38 times greater (averaging 1.84 m/s higher in velocity) than those given by the original Alexander formula. Alexander's original formula was:

$$(4)\ v=0.25g^{0.50}S^{1.67}H^{-1.17}$$

(5) where v is the velocity, g is the gravitational constant of 9.81 m/s^2, S is the stride length (in meters), and H is the height of the animal at the hip (in meters).

Our modified Alexander formula for intermediate speed gaits, based upon the new correlation coefficients comparing stride length, horse height, and measured velocity from twenty-four gait trials including the running walk, rack, stepping pace, fox trot, and pace (figure 15), is as follows:

$$(5)\ v=0.72g^{0.50}S^{0.81}H^{0.21}$$

where again v is the velocity in meters/second, g is the gravitational constant of 9.81 m/s^2, S is the stride length in meters, H is the height of the horse at the withers in meters, and 0.23 is the speed multiplier (see Vincelette, 2021 for a slightly different formula, based upon more limited information).

Taking into account the impact of trackmaker body height and length

Variations in body-dimensions of quadrupeds, including height and length (gleno-acetabular distance or GAD), can also impact footprint patterns (Kienapfel et al., 2014; Stevens et al., 2016). We investigated this for horses by looking at how height at the withers (HT) and gleno-acetabular distance (GAD) were correlated with ipsilateral step distance (ISD), and ipsilateral step distance/stride length, i.e. ISD/SL (see figure 16).

We found that increases in velocity of the gait, or in the height or gleno-acetabular distance (GAD) of the trackmaker, generally results in increased ipsilateral step distances (correlation coefficients of 0.83/0.53/0.53), i.e. overstep or overstrike, and increased ipsilateral step distances/stride lengths (correlation coefficients of 0.66/0.24/0.46; see figures 17-19, and tables S8-S9, as well as similar findings in Renders, 1982; Kienapfel et al., 2014). So, for example, ponies which are shorter in height

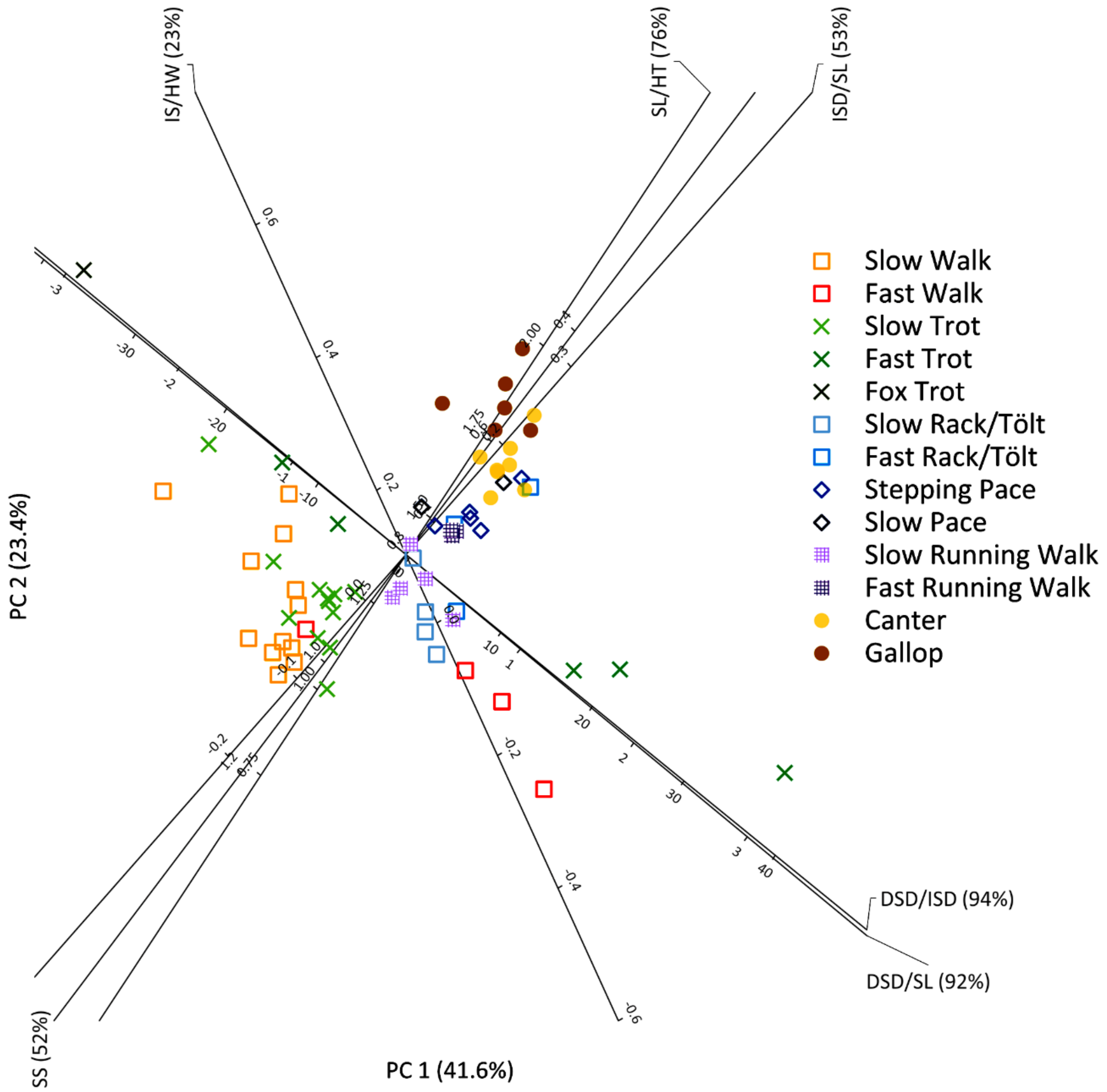

Figure 14. Principal component analysis for horse gaits involving six trackway factors where height of trackmaker can be estimated. These factors are SS (step symmetry); IS/HW (interior straddle/hind hoof width); SL/HT (stride length/height at withers); ISD/SL (ipsilateral step distance/stride length); DSD/SL (diagonal step distance/stride length); and DSD/ISD (diagonal/ipsilateral step distance).

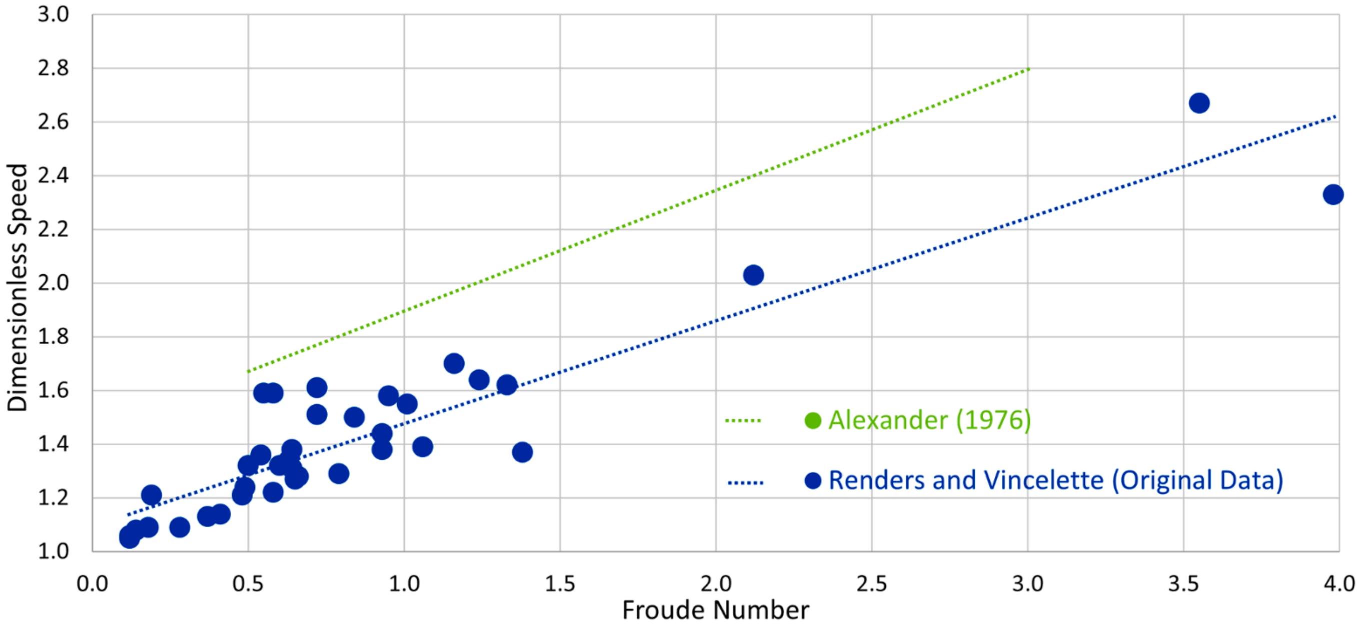

Figure 15. Dimensionless speed (stride length/height at withers) vs. Froude number (velocity^2/gravity x height at withers) for modern horses with regression lines. We found that Alexander's original formula (fig. 1), based upon limited data for horses, tended to underestimate dimensionless speed by almost 50%.

and have a smaller trunk length (gleno-acetabular distance or GAD), tended to have a greater understep in the walk and trot than did taller horses. Velocity and GAD had a particularly strong effect on increasing the overstep of the trotting gait, and velocity had a strong positive correlation with the overstep of the racking gait.

Importantly, these variations in the gait overstep (ipsilateral step distance) due to increasing velocity, height, or gleno-acetabular distance, did not affect the overall pattern of the footprints. This is because gaits form trackways with discrete ipsilateral pairs (walk, trot, slow rack), diagonal pairs (trot, fox trot, fast rack, stepping pace, pace), or isolated prints without visible pairings (medium rack, running walk, gallop). However, individuals of a smaller height or trunk length (GAD) may have gaits displaying an understep (pes landing behind manus of ipsilateral limbs) even at fast speeds in the walk and trot (figure 14). Our data is also for horses which are moderately sized and have a hip height similar to height at the withers. The impact of GAD on larger quadrupeds or those with quite different shoulder and hip heights may be greater.

Thus in classifying gaits as a slow or fast walk, or slow or fast trot, etc. (especially where velocity cannot be measured), it is good to estimate and take into account the height and body-length (gleno-acetabular distance or GAD) of the trackmaker. Methods for estimating height of trackmaker are given above. To estimate GAD for fossil trackways see Lallensack and Falkingham (2022) and Stevens et al. (2022).

CONCLUSIONS

We have identified a method of determining the gaits of modern and fossil horses from trackways based upon six variables: step symmetry, stride length/trackmaker height (or stride length/front hoof length), ipsilateral step distance/stride length, diagonal step-distance/stride length, interior straddle/hind hoof width, and diagonal step-distance/ipsilateral step distance. Based upon a study of twenty-five modern horses these six variables are able to discriminate between walking, trotting, racking, running walking, and galloping gaits, and even whether these are slower or faster versions of these gaits. It is possible to measure these variables for fossil horse trackways and use them to identify the probable gait exhibited in a trackway, and footprint patterns of trackways can also go a long way in identifying gaits. We have also identified ways of distinguishing front (manus) from hind (pes) feet in order to employ this method, and also ways of estimating the velocity of fossil horse gaits displayed in trackways.

It should be pointed out that some horses possess an imperfect constitution and so have limbs angled in unusual ways, and also that riderless horses often change direction during travel. Because of these factors, it is possible for unusual forms of a gait, such as a trot, to resemble other gaits, such as a rack, in footprint patterns and linear variables. It is also hard to distinguish slow walks from slow trots as the amount of overstep can differ from horse to horse, or to distinguish running walks from medium-speed racks. Moreover, horses with a shorter height or smaller body-length (gleno-acetabular distance) may have fast gaits that resemble slower ones.

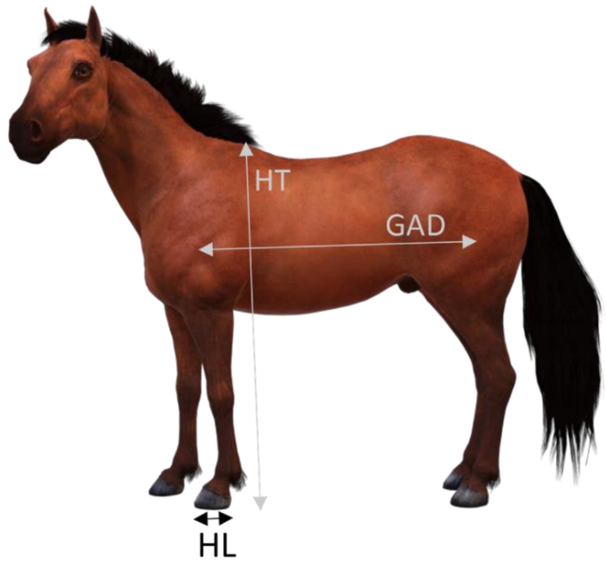

Figure 16. Key body dimensions of modern horses, namely: height at withers (HT), gleno-acetabular distance (GAD), and (front, manus) hoof length (HL).

Hence gait determination is a matter of greatest likelihood and not certainty. Still the methodology presented is, we believe, a reliable one for investigating the gaits and velocities exhibited by fossil equids in their trackways. Elsewhere we have applied this methodology to find the likely gait exhibited in several fossil horse trackways as well as their estimated speeds (Renders and Vincelette, 2023). In so doing it was found that trackways exist formed by extinct Miocene, Pliocene, and Pleistocene horse species (both tridactyl and monodactyl) likely engaged in intermediate-speed trots, intermediate speed racks and running walks, and fast gallops (see figure S1). That is, fossil horses, like modern horses, possessed the ability to perform a great variety of gaits, including both laterally coordinated (racks) and diagonally coordinated gaits (trots), as well as asymmetrical gaits (gallops).

In terms of future directions of study, research on modern horses in a riderless condition to analyze more natural horse locomotions would be quite useful. Most of our studies relied on horses with riders or on a lead with a horse traveling in a fairly straight line at a constant speed, whereas horses in the wild may weave back and forth or vary the speed of the gait. We have identified some of these gait variants in the past (Vincelette, 2021) but much more study is warranted. Such atypical gaits may

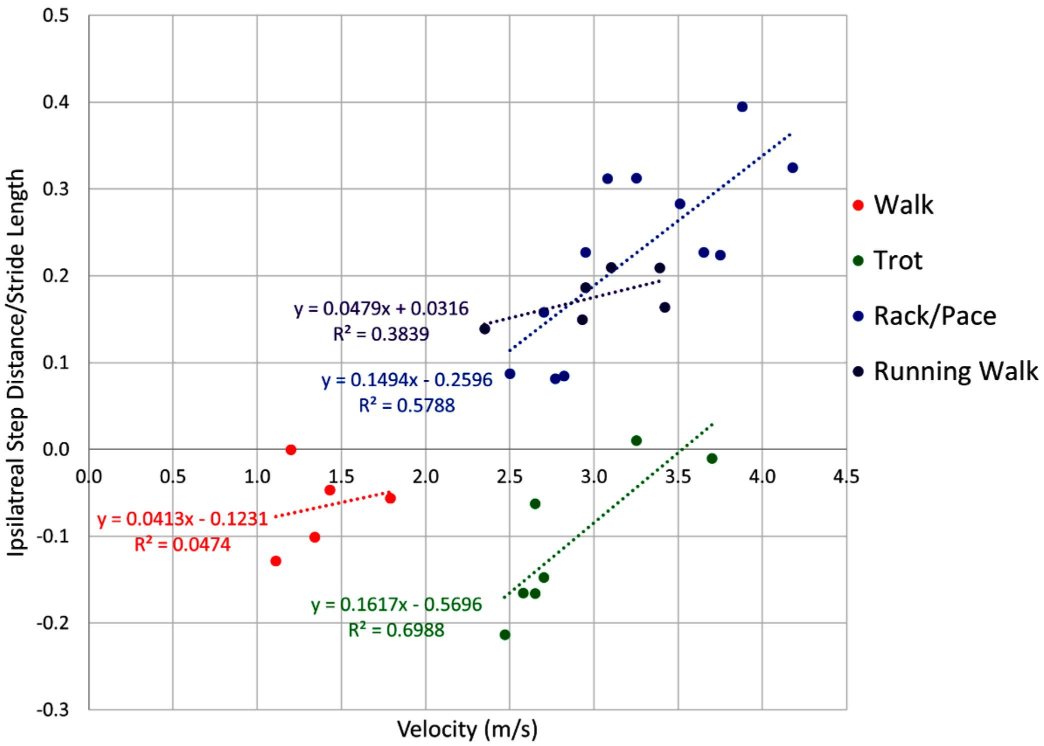

Figure 17. Bivariate plot of horse gait velocity in relation to ipsilateral step distance/stride length for gaits of walk, trot, rack or pace, and running walk. Increased velocity leads to increasing overstep, especially in trot and rack.

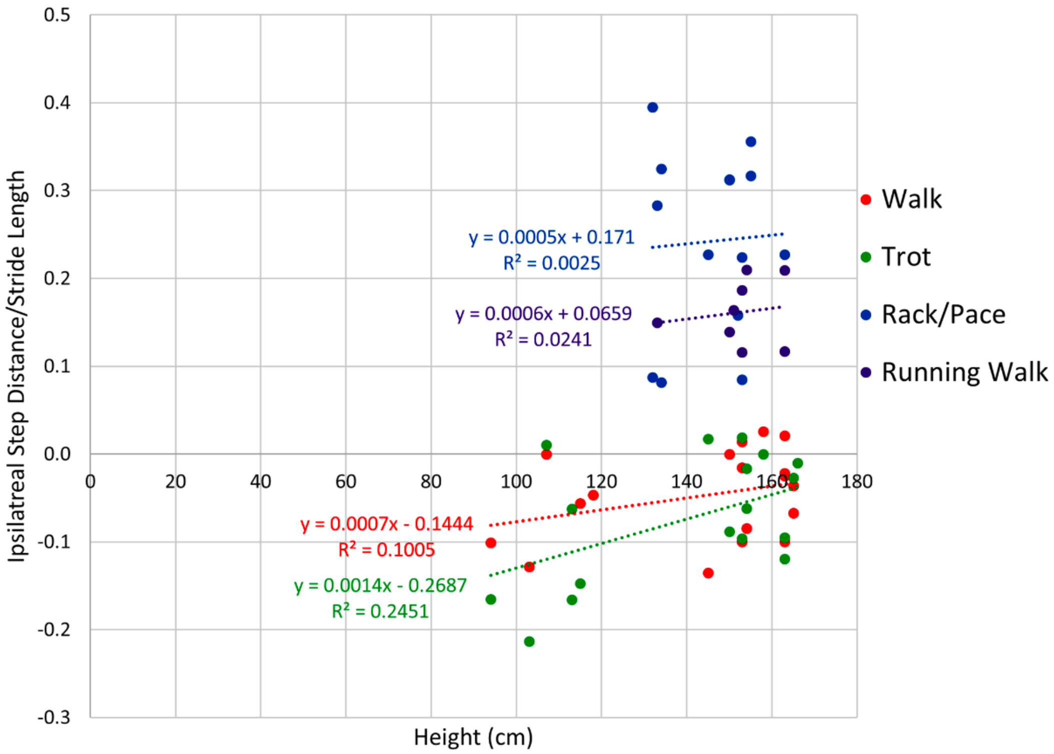

Figure 18. Bivariate plot of horse height at withers in relation to ipsilateral step distance/stride length for gaits of walk, trot, rack or pace, and running walk. Increased height leads to slightly increasing overstep in all gaits.

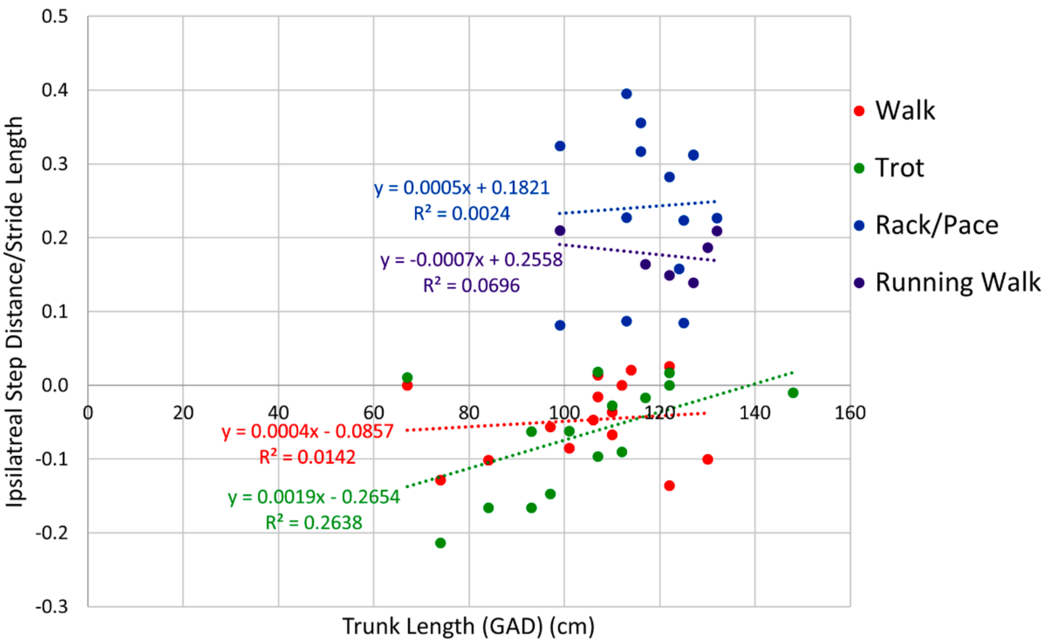

Figure 19. Horse trunk length or gleno-acetabular distance (GAD) in relation to ipsilateral step distance/stride length for gaits of walk, trot, rack or pace, and running walk. Longer bodied horses (higher GAD) leads to increased overstep in walk, trot (especially), and rack but not in running walk.

form trackways that blur the boundaries between the gaits identified here (or not). Study of wild mustang trackways in various gaits then might prove quite useful. More studies of modern horses in different gaits would also be useful to increase the dataset, as would further information on fossil horses. In general more data of modern horse gaits and their trackways, along with more discovery and study of fossil horse trackways and osteology would improve our ability to identify fossil equid gaits.

With advancing technology, 3D scans of modern and fossil horse trackways would also be beneficial, enabling detailed analysis of hoof angles at impact in relation to ground plane and direction of travel and varying depth of print and displacement of hoof in different substrates. This would enable interpretation of changes of hoof pressure, center of gravity, and travel direction, and likely enhance our ability to identify equid gaits. More quantification of how relative body size or limb length in horses and other quadrupeds affects trackways would also be desirable, as it appears that horses with smaller trunks (i.e. reduced gleno-acetabular distances between shoulder and hip) tend to understep more and those with elongated bodies (i.e. larger gleno-acetabular distances) tend to overstep more. Further work on how to estimate gleno-acetabular distance from fossil horse trackways and what impact it can have on trackways would be beneficial. Finally, further investigation of velocities of gaits in modern horses and how this relates to horse height and stride length would be desirable in order to develop refined formulae for the calculation of the velocities of fossil horse gaits.

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Original raw images at full resolution and animated material can be downloaded at
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SUPPLEMENTARY MATERIAL

Table S1: Basic Information Regarding Modern Horses Utilized in This Study

Number	Breed	Gender	Height at withers (m)	GAD (m)	Hoof (Print) Length (cm)	Hoof (Print) Width (cm)
1	Tennessee Walker	Female	1.50	1.27	12.0	12.5
2	Peruvian Paso Horse	Male	1.51	ca. 1.17	12.0	11.5
3	Tennessee Walker	Male	1.53	ca 1.30	14.6	ca. 14.9
4	Tennessee Walker	Male	1.63	ca 1.32	17.8	ca. 17.1
5	Spotted Saddle Horse	Female	1.52	ca. 1.24	12.7	ca. 12.7
6	Peruvian Paso Horse	Male	1.33	ca. 1.22	11.4	ca. 11.9
7	Tennessee Walker	Female	1.66	ca. 1.48	15.2	ca. 14.8
8	Icelandic Horse	Male	1.35	1.13	12.7	ca. 13.2
9	Icelandic Horse	Female	1.34	0.99	12.7	ca. 12.1
10	Rocky Mountain Horse	Male	1.53	ca. 1.25	15.2	ca. 15.2
11	Rocky Mountain Horse	Male	1.45	ca. 1.13	14.0	ca. 14.5
12	Tennessee Walker	Male	1.54	ca. 0.99	12.7	ca. 13.4
13	Tennessee Walker	Male	---	---	---	---
14	Icelandic Horse	Female	1.48	---	---	---
15	Mangalarga Marchador	Male	1.50	---	---	---
16	Mangalarga Marchador	Male	1.48	---	---	---
17	Icelandic Horse	Female	ca. 1.27	---	---	---
18	Peruvian Paso Horse	Female	ca. 1.44	---	---	---
19	Tennessee Walker	Male	1.59	---	13.3	12.8
20	Shetland Pony	Female	1.03	0.74	14.0	12.7
21	Shetland Pony	Male	1.07	0.67	9.0	8.5
22	Shetland Pony	Male	1.18	1.06	10.5	10.5
23	Shetland Pony	Female	1.13	0.90	9.5	9.7
24	Shetland Pony	Male	1.15	0.97	11.0	11.0
25	Sicilian Donkey	Female	0.94	0.84	10.0	7.5

Table S2: Height Estimation Ratios for Modern Horses and Related Species

Species (Breed)	**Height/Cranium**	**Height/ Metacarpal III**	**Height/ Metatarsal III**	**Height/Front Hoof Length**	**Source**
Equus ferus caballus	---	6.49	---	---	Koudelka, 1885
Equus ferus caballus	2.7 (total length) 10.16 (interior cavity)	6.41	5.33	---	Kiesewalter, 1888; Chrószcz, 2014
Equus ferus caballus	---	6.10	---	---	Vitt, 1952
Equus ferus caballus (Draft horses) *Equus grevyi* (Greby's Zebra)	---	7.0 6.25	6.0 5.43	---	Eisenmann, 2000
Equus ferus caballus (Arabian) (Draft) (Pony) *Equus africanus asinus* (Donkey) *Equus ferus przewalski* (Przewalski's horse) *Equus africanus somaliensis* (Somali Wild Ass) *Equus grevyi*	---	 5.81 6.48 6.24 5.78 5.77 5.90 5.84	 4.90 5.57 5.09 4.88 4.85 5.00 5.08	---	Eisenmann and Beckouche, 1986; Eisenmann, 1991; Eisenmann, 2009

(Grevy's Zebra) *Equus quagga quagga* (Cape Quagga) *Equus quagga boehmi* (Broehm's Zebra) *Equus hemionus onager* (Asian Wild Ass) *Equus hemionus hemionus* (Mongolian Wild Ass) *Equus hemionus hemippus* (Syrian Wild Ass) *Equus kiang* (Kiang)		 5.88 5.78 5.47 5.37 5.35 6.04	 5.11 5.15 4.67 4.61 4.62 5.34		
Equus ferus caballus (Arabian) (Anglo-Arabian) (Polish Konick) (Polish Coldblood)				[ca. 11.80] 13.16 12.84 11.11 9.89	Stachurska et al., 2011
Equus ferus caballus (Polish Arabian)	---	---	3.65	---	Sobczuk and Komosa, 2012
Equus ferus caballus	2.62	5.95	4.98	---	Hayashida and Yamauchi, 1957

(Japanese breeds)				(16.21 for Phalanx I; 32.90 for Phalanx III)	
Equus ferus caballus (Various breeds)	---	5.66	---	---	Onar et al., 2018
Equus ferus caballus (Various breeds)	---	---	---	11.13	Table S1 data (above)
Other Perissodactyla					
Tapirus terrestris	2.55	7.86	7.86	7.73	Sellards, 1918; Ferrero et al., 2014; Moreira et al., 2018

Table S3: Key Morphometric Parameters of Complete or Nearly Complete Fossil Horse Skeletons (Useful for Estimating Height of Related Species)

Species	**Geological Age (Ma)**	**Height at withers from skeleton (cm)**	**Cranial length (cm)**	**Metacarpal III length (cm)**	**Metatarsal III length (cm)**	**Proximal (1st) Phalanx III length Front/Hind (cm)**	**Distal (3rd) Phalanx III length Front/Hind (cm)**	**Specimen and Source**
Subfamily Propalaeotheriinae (equoid; tetradactyl manus; tridactyl pes; Eocene)								
Eurohippus messelensis	47.9-47.4	30.0	15.2	ca. 4.8	5.4	ca. 1.0/1.1	ca. 0.8, 1.0	SFM ME-11034; Franzen and Habersetzer, 2017
AVERAGE	47.7	30.0	15.2	4.8	5.4	1.0/1.1	0.8/1.0	---
Subfamily Hyracotheriinae (tetradactyl manus; tridactyl pes; Eocene)								
Sifrhippus grangeri	55.7	ca. 35.7	ca. 13.6	4.4	6.0	1.1/1.5	1.0/1.4	UM 115547; Wood et al., 2011
Protrorohippus venticolum	55.5-51.0	34.5	13.7	5.1	6.7	ca. 1.3/---	ca. 1.0/---	AMNH 4832; USNM 336126; USNM 22-72363; Cope, 1884; Granger, 1908; Simpson, 1932; Robb, 1936; Kitts, 1956; Solounias, et al., 2018
Orohippus pumilus	50.3-46.2	ca. 35.0	14.0	4.7	6.7	---/---	1.3/1.4	AMNH 12648;

								Cope, 1884; Granger, 1908; Robb, 1936
AVERAGE	52.4	35.1	13,8	4.7	6.5	1.2/1.5	1.1/1.4	---
Subfamily Anchitheriinae, basal (tridactyl manus and pes; Oligocene)								
Mesohippus bairdi	33.9-33.3	46.0	17.5	8.8	11.5	1.3/ca. 1.5	1.9/ca. 2.0	AMNH 1477 and 1492; AMNH 12456; AMNH 74063; Gidley, 1903; Robb, 1936; Scott and Jepsen, 1941; Hussain, 1975
Miohippus intermedius	33.3-30.8	64.8	22.6	12.8	15.0	1.9/2.2	ca. 2.3/3.4	AMNH 1196; Osborn and Wortman, 1895; Sinclair, 1925; Robb, 1936; O'Sullivan, 2008
Miohippus gidleyi	33.3-30.8	74.9	21.3	14.8	16.9	2.0/2.3	2.3/3.0	YPM 10729; AMNH 680; AMNH 1192; Osborn, 1918 Sinclair, 1925
AVERAGE	32.6	61.9	20.5	12.1	14.5	2.0/2.0	2.2/2.8	---

Paraphyletic Merychippine Group (tridactyl manus and pes; early to middle Miocene)								
Acritohippus isonesus	16.5-16.0	89.5	32.8	ca. 15.9	17.5	ca. 3.3/3.6	3.9/4.1	AMNH 8174-8175; AMNH 14185; Cope, 1889; Osborn 1918; Simpson, 1932
Acritohippus stylodontus	14.4	ca. 94.5	33.6	18.3	22.3	4.4/ca. 4.3	ca. 3.8/3.5	UCR 14057; UCMP 21386; Merriam, 1919; Vincelette, 1992
AVERAGE	15.3	92.0	33.0	17.1	19.9	3.9/4.0	3.9/3.8	---
Tribe Protohippini (tridactyl manus and pes; early Miocene)								
Protohippus sejunctus	16.0-13.7	ca. 89.1	32.7	16.3	18.1	ca. 3.7/3.8	ca. 4.1/3.4	AMNH 8291; AMNH 8383; AMNH 9378; AMNH 9389-9390; Cope, 1874; Gidley, 1907; Osborn 1918; Robb, 1935-6
AVERAGE	14.9	89.1	32.7	16.3	18.1	3.7/3.8	4.1/3.4	---
Tribe Anchitheriini (tridactyl manus and pes; Miocene)								
Kalobatippus agatensis	ca. 24.8-20.4	ca. 106.0	30.8	20.9	24.2	3.3/3.6	ca. 4.8/ 5.2	AMNH 12147; Romer, 1926
Hypohippus osborni	ca. 15.0-14.0	ca. 110.0	37.1	20.3	ca. 21.8	ca. 4.2/4.2	---/ca. 4.4	AMNH 9407; Gidley, 1907; Gregory, 1912;

								Matthew, 1926; Robb, 1936
AVERAGE	22.6	18.6	34.0	20.6	23.0	3.8/3.9	4.8/4.8	---
Tribe Hipparionini, New World (tridactyl; late Miocene-Pliocene)								
Neohipparion affine (New World)	13.6-10.3	ca. 102.6	37.8	21.2	24.5	4.6/4.4	4.1/4.1	AMNH 9815; Cope, 1889; Gidley, 1903; Osborn, 1918
Neohipparion leptode (New World)	5.3-4.8	115.6	45.1	25.1	27.9	ca. 6.8/ 6.2	ca. 6.6/ 5.7	CIT 54; Stock, 1951
AVERAGE	8.5	109.1	41.5	23.2	26.2	5.7/5.3	5.4/4.9	---
Tribe Hipparionini, Old World (tridactyl; late Miocene-Pliocene)								
Hippotherium primogenium (Old World)	10.3	130.0	47.7	21.3	24.3	6.4/6.4	7.3/7.4	SMNK HoA; Bernor et al., 1997
Plesiohipparion zandaense (Old World)	4.6	145.0	ca. 64.0	22.6	25.3	6.7/6.3	ca. 7.1/ ---	IVPP V18189; Deng et al., 2012
AVERAGE	7.5	137.5	55.9	22.0	24.8	6.6/6.4	7.2/7.4	---
Tribe Equini, basal (monodactyl manus and pes; late Miocene-Pliocene)								
Pliohippus pernix	16.0-10.3	122.5	41.0	18.9	20.8	5.6/ ca. 5.1	4.3/3.9	YMP 13007; AMNH 60803; AMNH 17225; Marsh, 1874; Troxell, 1916; Osborn, 1918; Robb, 1936
AVERAGE	13.2	122.5	41.0	18.9	20.8	5.6/5.1	4.3/3.9	---
Tribe Equini, caballoid, extinct (Pliocene to Pleistocene)								
Equus simplicidens	3.4-3.2	130.0	60.8	25.2	27.6	8.6/7.8	6.2/5.5	USNM 12567, 13792-

								13795, 13826; AMNH 20076-20077; Gazin, 1936; Robb, 1936
Equus scotti	1.8-0.3	135.0	60.0	23.8	26.6	9.2/8.8	6.5/ ca. 7.1	AMNH 10606; Troxell, 1916; Gazin, 1936; Robb, 1936; Hussain, 1975
AVERAGE	2.2	132.5	60.4	24.5	27.1	8.9/8.3	6.4/6.3	---
Equus ferus caballus	Current	160.0	63.8	26.3	30.0	10.1/10.1	7.4/ca. 7.1	Robb, 1935-1936; Gidley, 1903; Vincelette, 1992; Thomason et al., 2001
Other Perissodactyla								
Palaeotherium magnum	47.8-41.2	137.0	54.0	14.0	11.7	ca. 2.9/---	---/---	Déparet, 1917; Abel, 1924
Superfamily Tapiroidea								
Family Helaletidae								
Helaletes nanus	50.3-48.5	44.2	15.6	7.4	9.8	2.4/1.9	2.0/1.6	USNM V12584; YPM 11807; Peterson, 1919; Schoch, 1984
Superfamily Rhinocerotoidea								

Family Hyrachidae								
Hyrachus modestus	48.5-47.0	53.8	20.8	7.9	11.2	1.9/---	---/---	AMNH FM12664; AMNY FM1612; YPM 11170; Troxell, 1922; Bai et al., 2017
Hyrachus eximius	47.0-46.2	87.2	34.0	ca. 9.9	10.7	---/2.5	---/2.9	AMNH FM5065 and FM5065A; Cope, 1884; Stilson et al., 2016; Bai et al., 2017
Family Tapiridae								
Tapirus terrestris	Current	93.5	36.6	11.9	11.9	ca. 6.3	ca. 3.2	Sellards, 1918; Piper, 2009; Ferrero et al., 2014; Moreira et al., 2018

Table S4: Height/Skeletal Element Ratios (Multipliers) for Fossil Horses

Equine Group	**Height/ Cranium**	**Height/ Metacarpal III**	**Height/ Metatarsal III**	**Height/ Proximal (1st) Phalanx III (Front)**	**(Hind)**	**Height/ Distal (3rd) Phalanx III (Front)**	**(Hind)**	**Height/Front Hoof Length (Print)**
Propalaeotheriinae	1.97	6.25	5.56	30.00	27.27	37.5	30.00	22.83
Eurohippus	1.97	6.25	5.56	30.00	27.27	37.5	30.00	22.83
Hyracotheriinae	2.55	7.44	5.44	29.50	23.80	32.37	25.25	19.70
Sifrhippus	2.62	8.11	5.95	32.45	23.80	35.70	25.50	21.73
Protrorohippus	2.52	6.76	5.15	26.54	---	34.50	---	21.00
Orohippus	2.50	7.45	5.22	---	---	26.92	25.00	16.39
Anchitheriinae, basal	2.92	5.15	4.19	35.58	30.84	27.29	22.51	16.61
Mesohippus	2.63	5.23	4.00	35.38	30.67	24.21	23.00	14.74
Miohippus	3.20	5.06	4.38	35.78	31.01	30.37	22.02	18.49
Merychippines	2.77	5.40	4.68	24.30	23.42	23.91	24.42	14.55
Acritohippus	2.77	5.40	4.68	24.30	23.42	23.91	24.42	14.55
Protohippini	2.72	5.47	4.92	24.08	23.45	21.73	26.21	13.23
Protohippus	2.72	5.47	4.92	24.08	23.45	21.73	26.21	13.23
Anchitheriini	3.20	5.25	4.72	29.61	27.82	22.08	22.69	13.44
Kalobatippus	3.44	5.07	4.38	33.03	29.44	22.08	20.38	13.44
Hypohippus	2.96	5.42	5.05	26.19	26.19	---	25.00	13.16
Hipparionini	2.55	5.75	5.08	20.53	20.87	19.83	20.11	12.07
Hipparionini, New World	2.64	4.73	4.17	19.65	20.98	21.27	22.65	12.95
Neohipparion	2.64	4.73	4.17	19.65	20.98	21.27	22.65	12.95
Hipparionini, Old World	2.50	6.26	5.54	20.98	21.67	19.11	17.57	11.63
Hippotherium	2.73	6.10	5.35	20.31	20.31	17.80	17.57	10.83
Plesiohipparion	2.27	6.42	5.73	21.64	23.02	20.42	---	12.43
Equini, basal	2.99	6.48	5.89	21.88	24.02	28.49	31.41	17.34
Pliohippus	2.99	6.48	5.89	21.88	24.02	28.49	31.41	17.34
Equini, caballoid, extinct	2.20	5.42	4.90	14.90	16.01	20.88	21.33	12.71
Equus	2.20	5.42	4.90	14.90	16.01	20.88	21.33	12.71
Equini, extant (*Equus ferus caballus*)	2.51	6.08	5.33	15.84	15.84	21.62	22.54	13.16
Other Perisssodactyla								
Tapiroidea, *Helatelidae*	2.83	5.97	4.51	18.41	23.26	22.10	27.63	7.73

Rhinocerotoidea, *Hyrachus*	2.58	7.81	6.48	28.32	34.88	---	30.07	---
Palaeotheriidae, *Palaeotherium*	2.53	9.79	11.71	47.24	---	---	---	---

Table S5: Measurements of fossil horse distal phalanx III and hoofprints (data from references in table S6)

Horse Species	**Geologic age (Ma)**	**Front hoof length and width (prints) (cm)**	**Rear hoof length and width (prints) (cm)**	**Front distal phalanx III length and width (cm)**	**Rear distal phalanx III length and width (cm)**
Subfamily Propalaeotheriinae (equoid; tetradactyl; Eocene)					
Eurohippus messelensis	47.9-47.4	---/---	---/---	0.8, 0.6	1.0, 0.9
Subfamily Hyracotheriinae (tetradactyl; Eocene)					
Sifrhippus grangeri	55.7	---/---	---/---	1.0, 0.7	1.4, 0.9
Protrorohippus venticolum	55.5-51.0	---/---	---/---	1.0, 0.9	---/---
Arenahippus pernix	55.8-48.6	---/---	---/---	1.1, 0.8	1.2, 0.8
Orohippus pumilus	50.0-48.0	---/---	---/---	1.3, 0.6	1.4, 0.8
Orohippus agilis	46.2	---/---	---/---	1.3, 0.9	1.5, 0.9
Subfamily Anchitheriinae, basal (tridactyl; Oligocene)					
Mesohippus celer	38.0-34.0	---/---	---/---	2.2, 1.7	1.9, 1.5
Miohippus intermedius	33.3-30.8	---/---	---/---	2.3, 2.3	3.4, 2.4
Miohippus anceps	30.8-20.4	---/---	---/---	3.1, 2.5	3.4, 2.8
Subfamily Anchitheriinae, stem Equinae (tridactyl; middle Oligocene to early Miocene)					
Parahippus tyleri	30.8-24.8	---/---	---/---	4.5, 3.6	4.0, 3.6
Parahippus pristinus	20.4	---/---	---/---	---/---	3.0, 2.0
Parahippus coloradensis	ca. 16.0	---/---	---/---	---/---	3.5, 3.3
Tribe Anchitheriini (tridactyl; early Miocene)					
Anchitherium clarencei	20.4-13.6	---/---	---/---	---/---	4.6, 4.0
Anchitherium aurelianense	20.5-16.9	3.6-4-4/2.5-3.7	---/---	4.1, 4.4	4.2, 4.2

Kalobatippus avus	16.0-13.6	---/---	---/---	3.9, 3.1	4.2, 3.0
Hypohippus equinus	20.4-16.0	---/---	---/---	4.3, 4.6	4.5, 4.5
Kalobatippus agatenses	24.8-20.4	---/---	---/---	4.8, 4.5	5.2, 5.5
Paraphyletic Merychippine Grouping (tridactyl; early Miocene)					
Acritohippus isonesus	16.5-16.0	---/---	---/---	3.9, 3.4	4.1, 3.1
Merychippus eohipparion	15.0-14.0	---/---	---/---	4.9, 3.8	4.6, 3.3
Merychippus eoplacidus	15.0-14.0	---/---	---/---	3.8, 3.3	4.1, 3.0
Acritohippus stylodontus	14.4	---/---	---/---	3.8, 3.3	3.5, 3.2
Tribe Protohippini (early Miocene)					
Protohippus sejunctus	16.0-13.6	---/---	---/---	4.3, 3.5	4.1, 3.4
Scaphohippus sumani	14.5	5.0, 3.5	5.2, 3.5	3.5, 3.2	3.0, 2.7
Tribe Hipparionini (tridactyl; early to late Miocene)					
New World Hipparionini					
Cormohipparion sphenodus	16.0-13.6	---/---	---/---	4.5, 3.9	4.6, 3.5
Hipparion insignis	16.0-10.3	---/---	---/---	4.3, 3.7	3.8, 3.3
Neohipparion affine	13.6-10.3	---/---	---/---	4.1, 4.1	4.1, 4.5
Neohipparion leptode	5.4-4.8	---/---	---/---	6.6, 6.3	5.7, 5.4
Old World Hipparionini					
Hippotherium primogenium	10.3	---/---	---/---	7.3, 6.5	7.4, 6.0
Sivalhippus theobaldi	10.0-9.0	---/---	---/---	6.5, 5.9	6.5, 4.9
Cremohipparion moldavicum	9.9-6.8	---/---	---/---	6.0, 5.4	---, 4.3
“Hipparion” laromae	9.7-8.7	---/---	---/---	---/---	6.5, 6.2
“Hipparion” elegans	9.0-5.3	---/---	---/---	5.8, 4.6	5.9, 4.4
Cremohipparion matthewi	8.7-7.5	9.3, 7.5	---/---	---/---	---/---
Hippotherium malpassii	6.0-5.3	8.6, 8.0	---/---	---/---	---/---
“Hipparion” fissurae	4.9-4.2	ca. 6.5, 4.4	ca. 7.7, 4.4	---/---	---/---
Plesiohipparion zandaense	4.6	---/---	---/---	7.1, 6.9	---/---
Proboscidipparion heintzi	4.0	---/---	---/---	5.7, 5.0	6.5, 4.7
Eurygnathohippus hasumense A and B	3.7	8.8, 8.0 (A) 9.1, 8.0 (B)	7.5, 6.5 (A) 7.6, 6.7 (B)	---/---	---/---
Eurygnatohippus pomeli	2.5	---/---	---/---	7.8, 7.0	6.1, 5.5
Family Equinae, Tribe Equini, basal (Middle Miocene to Pliocene)					
Pliohippus pernix	16.0-10.3	---/---	---/---	4.3, 4.9	3.9, 4.7
Neohipparion sp.		---/---		---/---	---/---
Hippidion principale or *devillei*	16-12k	8.0, 7.0	6.0, 5.0	---/---	---/---

Tribe Equini, caballoid, extinct					
Equus simplicidens	4.9-2.6	---/---	---/---	6.2, 6.5	5.5, 5.9
Equus scotti	1.8-0.3	---/---	---/---	6.5, 8.2	7.1, 7.5
Equus ferus antunesi	29-6k	---/---	---/---	6.8, 7.2	6.3, 7.0
Equus ferus gallicus	28-13k	---/---	---/---	7.3, 8.8	5.9, 7.4
Amerhippus insulatus	16k-12k	15.0, 12.0	11.8, 9.3	---/---	---/---
Equus conversidens	13-11k	---	---/---	5.5, 6.0	4.8, 4.9
Equus lambei	13-11k	10.5, 10.5	---/---	---/---	5.7, 7.1
Tribe Equini, caballoid, extant (Anthropocene)					
Equus ferus caballus	Current	12.5, 13.0 (hoof)	11.5, 13.0 (hoof)	7.4, 9.2	7.1, 9.2
Other Perissodactyla					
Homogalax protapirinus	55.2-52.9	---/---	---/---	---/---	1.4, 0.8
Heptodon brownorum	53.0-51.0	---/---	---/---	---/---	1.4, 0.8
Helalites nanus	50.3-46.2	---/---	---/---	2.0, 1.2	1.6, 1.2
Hyrachus modestus	47.0-46.2	---/---	---/---	1.9, 1.6	---/---
Tapirus terrestris	Current	---/---	ca. 5.7, 3.6	3.1, 3.9	---/---

Table S6: Morphometric Ratios of the Distal Phalanx III or Hoofprints of Fossil and Modern Horses

Species (Breed)	**Front Length/ Width**	**Hind Length/ Width**	**Front Length/ Hind Length**	**Front Width/ Hind Width**	**Source**
Fossil Horses					
Subfamily Propalaeotheriinae (equoid; tetradactyl; Eocene)					
Eurohippus messelensis	1.33	1.11	0.80	0.67	Franzen and Habersetzer, 2017
Subfamily Hyracotheriinae (tetradactyl; Eocene)					
Sifrhippus grangeri	1.43	1.55	0.71	0.78	Wood et al., 2011
Arenahippus pernix	1.38	1.50	0.92	1.00	Lull, 1907
Orohippus agilis	1.44	1.67	0.87	1.00	Marsh, 1874; Lull, 1907
Orohippus pumilus	2.17	1.75	0.93	0.75	Granger, 1908; Robb, 1936
Subfamily Anchitheriinae, basal (tridactyl; Oligocene)					
Mesohippus celer	1.29	1.27	1.16	1.13	Lull, 1907
Miohippus intermedius	1.00	1.42	0.68	0.96	Osborn and Wortman, 1895; Sinclair, 1925; Robb, 1936
Miohippus anceps	1.24	1.21	0.91	0.89	Lull, 1907
Subfamily Anchitheriinae, stem Equidae (tridactyl; middle Oligocene to early Miocene)					
Parahippus tyleri	1.25	1.11	1.13	1.00	Osborn, 1918
Tribe Anchitheriini (tridactyl; early Miocene)					
Anchitherium aurelianense	0.93	1.00	0.98	1.05	Kovalevsky, 1873
Anchitherium aurelianense (footprints, 20.5-16.9 Ma)	1.44	---	---	---	Díaz-Martínez, 2011
Kalobatippus avus	1.25	1.40	0.93	1.03	Osborn, 1918
Hypohippus equinus	0.93	1.00	0.96	1.02	Lull, 1907
Kalobatippus agatensis	1.07	0.95	0.92	0.82	Romer, 1986
Paraphyletic Merychippine Grouping (tridactyl; early Miocene)					
Acritohippus isonesus	1.15	1.32	0.95	1.10	Cope, 1889; Osborn 1918
Merychippus eohipparion	1.29	1.30	1.07	1.15	Osborn, 1918
Merychippus eoplacidus	1.15	1.37	0.93	1.10	Osborn, 1918
Acritohippus stylodontus	1.15	1.09	1.09	1.03	Vincelette, 1992
Tribe Protohippini (early Miocene)					
Protohippus sejunctus	1.23	1.21	1.05	1.03	Cope, 1874; Osborn 1918

Scaphohippus sumani	1.09	1.11	1.17	1.19	Merriam, 1919; Sarjeant and Reynolds, 1999
Scaphohippus sumani (footprints, 14.5 Ma)	1.43	1.49	0.96	1.00	Sarjeant and Reynolds, 1999; Reynolds, 2006; Vincelette, 2021
Tribe Hipparionini (tridactyl; late Miocene)					
New World Hipparionini					
Cormohipparion sphenodus (New World)	1.15	1.31	0.98	1.11	Osborn, 1918
Hipparion insignis (New World)	1.13	1.15	1.13	1.12	Osborn, 1918
Neohipparion affine (New World)	1.00	0.91	1.00	0.91	Gidley 1903; Lull, 1907
Neohipparion leptode	1.05	1.06	1.18	1.17	Stock, 1951
Hipparion sp. [?] (footprints, 4.1 Ma)	1.16	1.19	1.07	1.09	Santucci and Nyborg, 1999; Sarjeant and Reynolds, 1999; Reynolds, 2006
Neohipparion sp. [?] (footprints, 4.1 Ma)	0.97	1.09	0.93	1.04	Santucci and Nyborg, 1999; Sarjeant and Reynolds, 1999; Reynolds, 2006
Old World Hipparionini					
Hippotherium primogenium	1.12	1.23	0.99	1.08	Bernor at al., 1997
Sivalhippus theobaldi	1.10	1.53	1.00	1.31	Colbert, 1935
"Hipparion" elegans	1.26	1.34	0.98	1.05	Gromova, 1952
"Hipparion" fissurae	1.48	1.75	0.84	1.00	Lancis and Estevéz, 1992
Proboscidipparion heintzi	1.14	1.38	0.88	1.06	Bernor and Sen, 2017
Eurygnathohippus hasuymense A and B (footprints, 3.7 Ma)	1.10 (A) 1.14 (B)	1.15 (A) 1.13 (B)	1.17 (A) 1.20 (B)	1.23 (A) 1.19 (B)	Renders, 1984; Renders and Sondaar, 1987
Eugygnathohippus pomeli	1.11	1.11	1.28	1.27	Eisenmann and Geraads, 2007
Tribe Equini, basal (monodactyl; middle Miocene-Pliocene)					
Pliohippus pernix	0.88	0.83	1.10	1.04	Troxell, 1916
Dinohippus interpolates [?]; *Neohipparion eurostyle* [?]	---	1.12	---	---	Johnston, 1937
Dinohippus sp. [?] (footprints, 4.1 Ma)	0.97	0.94	0.99	0.96	Santucci and Nyborg, 1999; Sarjeant and Reynolds, 1999; Reynolds, 2006
Hippidion principale or *devillei* (footprints ca. 16-12 ka)	1.14	1.20	1.33	1.40	Oliva and Arregui, 2018
Tribe Equini, caballoid, extinct (Pliocene to Pleistocene)					
Equus simplicidens	0.95	0.93	1.13	1.10	Gazin, 1936
Equus scotti	0.80	0.94	0.92	1.08	Gazin, 1936

Equus ferus antunesi	0.94	0.90	1.08	1.03	Cardoso and Eisenmann, 1989
Equus ferus gallicus	0.83	0.80	1.24	1.19	Eisenmann, 2009
Amerhippus insulatus (footprints, ca. 16-12 ka)	1.25	1.27	1.27	1.29	Oliva and Arregui, 2018
Equus conversidens	0.92	0.98	1.15	1.22	Dalquest and Hughes, 1965
Tribe Equini, caballoid and hemione, extant (Anthropocene)					
Equus ferus caballus (footprint)	1.04	1.04	1.00	1.00	Vincelette, 1992
Equus ferus caballus (hoof) (Tennessee Walker)	0.96	0.88	1.09	1.00	Renders and Vincelette data (Horse 19)
Equus ferus caballus (hoof) (Arabian)	1.04	1.05	1.02	1.03	Stachurska et al., 2008
Equus ferus caballus (hoof) (Anglo-Arabian)	1.01	1.04	1.02	1.06	Stachurska et al., 2008
Equus ferus caballus (hoof) (Polish Konicks)	1.09	1.08	1.05	1.04	Stachurska et al., 2008
Equus ferus caballus (hoof) (Polish Cold Bloods)	0.97	1.03	0.99	1.04	Stachurska et al., 2008
Equus ferus caballus (hoof) (Criollo)	1.10	1.14	1.01	1.04	Souza et al., 2016
Equus ferus caballus (hoof) (Various breeds)	1.11	1.04	1.09	1.02	Kawareti et al., 2017a
Equus ferus caballus (hoof) (Thoroughbred)	1.03	1.09	1.04	1.10	Kawareti, et al., 2017b
Equus africanus asinus (hoof) (Working donkey)	1.12	1.21	1.06	1.14	Mostafa et al., 2020
Equus ferus caballus (Thoroughbreds and Standardbreds)	0.71-0.89 (distal phalanx) 0.96-1.06 (hoof)				Thomason et al., 2001; Cruz et al., 2006; Thomason et al., 2008
Other Perissodactyla					
Superorder Tapiroidea, Family Helaletes					
Helaletes nanus	1.67	1.45	1.25	1.09	Peterson, 1919; Schoch, 1984

Table S7: Correlation of horse height and stride length with speed in various gaits

Horse	**Breed**	**Gait**	**Velocity (m/s)**	**Stride Length (m)**	**Height at Withers (m)**
20	Shetland Pony	Walk	1.11	1.09	1.03
21	Shetland Pony	Walk	1.20	1.16	1.07
25	Sicilian Donkey	Walk	1.34	1.04	0.94
19	Tennessee Walker	Walk	1.35	1.67	1.59
22	Shetland Pony	Walk	1.43	1.29	1.18
24	Shetland Pony	Walk	1.79	1.25	1.15
1	Tennessee Walker	Running Walk	2.35	1.69	1.50
11	Rocky Mountain	Rack (Show)	2.43	1.65	1.45
20	Shetland Pony	Trot	2.47	1.36	1.03
8	Icelandic	Tölt	2.50	1.60	1.32
25	Sicilian Donkey	Trot	2.58	1.42	0.94
23	Shetland Pony	Trot	2.65	1.51	1.13
24	Shetland Pony	Trot	2.70	1.46	1.15
5	Spotted Saddle	Running Walk	2.70	1.89	1.52
9	Icelandic	Tölt	2.77	1.63	1.34
10	Rocky Mountain	Rack (Show)	2.82	1.80	1.53
6	Peruvian Paso	Paso Llano	2.93	1.70	1.33
3	Tennessee Walker	Running Walk	2.95	2.45	1.53
4	Tennessee Walker	Stepping Pace	2.95	2.21	1.63
1	Tennessee Walker	Stepping Pace	3.08	1.97	1.50
5	Spotted Saddle	Stepping Pace	3.10	2.11	1.52
12	Tennessee Walker	Running Walk	3.10	2.45	1.54
21	Shetland Pony	Trot	3.25	1.66	1.07
1	Tennessee Walker	Pace	3.25	2.08	1.50
4	Tennessee Walker	Running Walk	3.39	2.61	1.63
2	Peruvian Paso	Paso Llano	3.42	1.95	1.51
6	Peruvian Paso	Sobreandando	3.51	2.11	1.33
11	Rocky Mountain	Rack (Pleasure)	3.65	2.01	1.45
23	Shetland Pony	Trot	3.70	1.85	1.13
7	Tennessee Walker	Fox Trot	3.70	2.48	1.66
10	Rocky Mountain	Rack (Pleasure)	3.75	2.21	1.53
8	Icelandic	Tölt	3.88	2.25	1.32
24	Shetland Pony	Canter	3.95	1.58	1.15
9	Icelandic	Stepping Pace	4.18	2.17	1.34
21	Shetland Pony	Canter	4.72	2.17	1.07
24	Shetland Pony	Transverse Gallop	6.70	2.68	1.15
19	Tennessee Walker	Transverse Gallop	7.44	4.24	1.59

Table S8: Average linear stride ratios for various gaits (data from Vincelette, 2021; Renders and Vincelette, 2022; original data, 2022)

Gait	**Diagonal/ Ipsilateral Step Distance**	**Ipsilateral Step Distance/ Stride Length**	**Interior Straddle/ Hoof Width**	**Lateral Offset/ Hoof Width**	**Average Stride Length/Height**	**Diagonal/Ipsilateral Step Distance Multiplier for SL/H**
Slow Walk (n=14)	-7.96	-0.06	0.17	0.15	1.02	-0.13
Fast Walk (n=4)	11.75	-0.01	0.04	0.23	1.13	0.10
Slow Trot (n=11)	-5.02	-0.11	0.15	0.29	1.30	-0.25
Fast Trot (n=6)	11.70	-0.01	0.16	0.39	1.71	0.15
Running Walk (n=8)	1.21	0.16	0.00	---	1.40	1.16
Slow Rack/Tölt (n=4)	2.54	0.10	-0.12	0.21	1.21	0.48
Fast Rack/ Tölt (n=3)	0.37	0.28	-0.37	0.58	1.51	4.08
Stepping Pace (n=5)	0.26	0.31	-0.15	0.59	1.59	6.12
Slow Pace (n=2)	0.26	0.30	0.10	1.12	1.49	5.73
Canter (n=8)	---	---	0.15	---	1.59	---
Gallop (n=6)	---	---	0.48	---	1.89	---

Table S9: Correlation coefficients between physical parameters of horses and linear symmetrical gait parameters.

	Height	**Gleno-acetabular distance (GAD)**	**Velocity**
Stride length	0.82	0.76	0.89
Diagonal step distance	-0.23	-0.19	-0.28
Ipsilateral step distance	0.65	0.59	0.68
Diagonal/ipsilateral step distance	-0.24	-0.45	0.07
Ipsilateral step distance/stride length	0.70	0.63	0.68
Interior straddle	0.16	0.24	-0.07
Interior straddle/hoof width	0.13	0.20	-0.08
Lateral offset	0.47	0.43	0.63
Lateral offset/hoof width	0.25	0.24	0.56

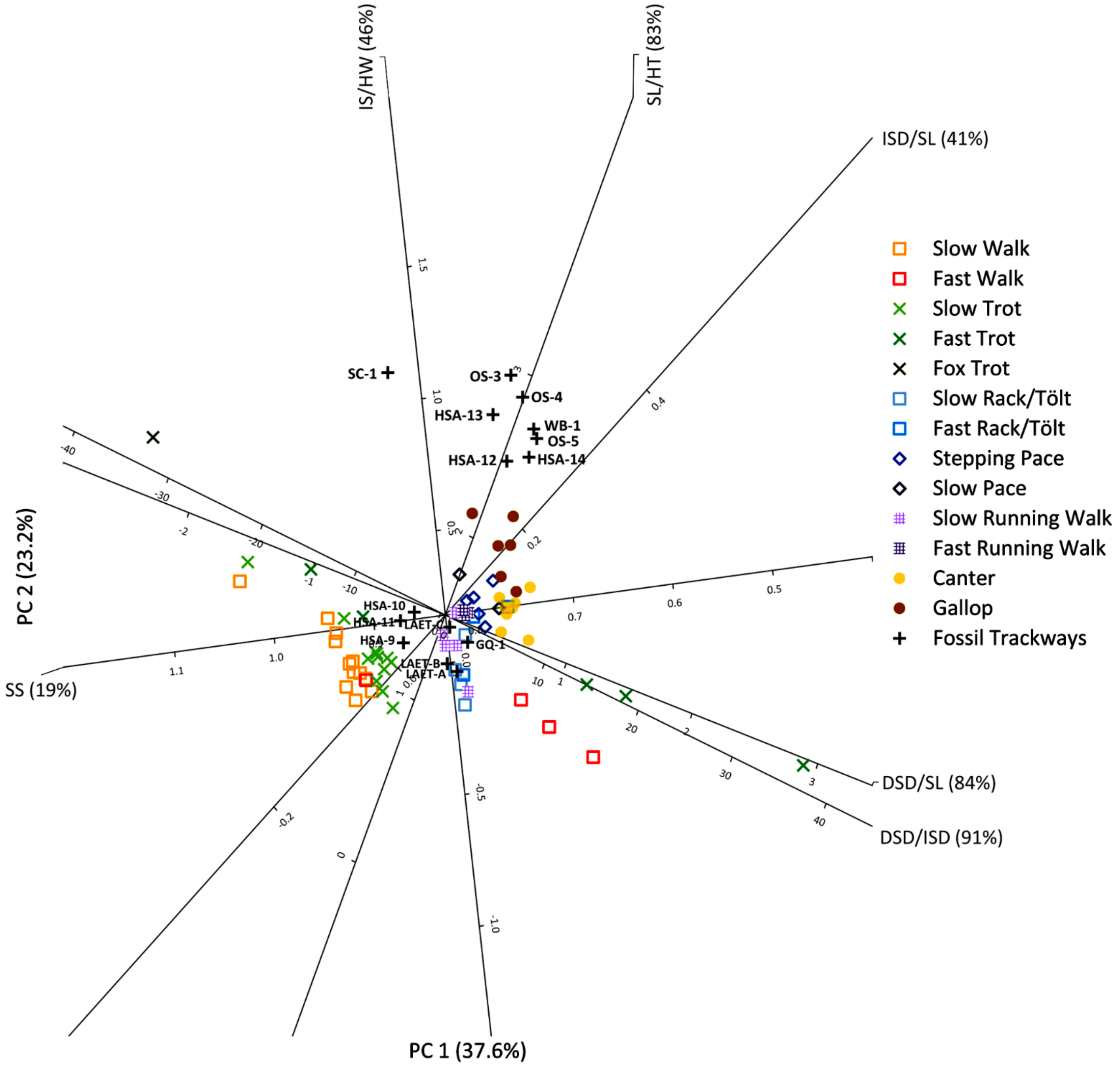

Figure S1. Six-factor principal component analysis for fossil horse trackways plotted against values for modern horse trackways: Step symmetry (SS); Interior straddle/hind hoof width (IS/HW); Stride length/height at withers (SL/HT); Ipsilateral step distance/stride length (ISD/SL); Diagonal step distance/stride length (DSD/SL); Diagonal/ipsilateral step distance (DSD/ISD). Seven fossil horse trackways align well with galloping gaits (HSA-12, HSA-13, HSA-14, OS-3, OS-4, OS-5, WB-1), four with trotting gaits (HSA-9, HSA-10, HSA-11, SC-1 with a large interior straddle), and four with lateral gaits of rack or running walk (GQ-1, LAET-A, LAET-B, LAET-C).

COLLECTION ABBREVIATIONS

AMNH: American Museum of Natural History, New York, U.S.A.

CIT: California Institute of Technology, Paleontology Collection, Pasadena, California, U.S.A.

IGF: Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze, Firenze, Italy

IVVP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

LACM: Los Angeles County Museum, Los Angeles, California, U.S.A.

NHMB: Basel Naturhistorisches Museum, Basel, Switzerland

SBCM: San Bernadino County Museum, Redlands, California, U.S.A.

SMF: Senckenberg Forschungsinstitut, Frankfurt am Main, Germany

SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany

UCMP: University of California, Berkeley, Museum of Paleontology, Berkeley, California, U.S.A.

UCR: University of California, Riverside, Paleontology Collections, Riverside, California, U.S.A.

UF: University of Florida, Paleontology Collections, Gainsville, Florida, U.S.A.

UM: University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, U.S.A

USNM: Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A.

YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

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