



Do tracks yield reliable information on gaits?

– Part 1: The case of horses

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Abstract. During their lifetime animals leave many tracks and traces behind, which can provide insights into the animals' behaviour. Single footprints of extant vertebrates are frequently found in sediments all over the world, often arranged into trackways. The study of footprints and trackways lead to interpretations about the mode of locomotion of the trackmaker. Here we show an approach to identify gaits from tracks.

A series of experiments with horses was performed to determine whether gaits could be identified on the basis of fossil trackways, e.g. those left behind by sauropod dinosaurs of the Mesozoic era or Tertiary mammals, to unveil their locomotor abilities. The generally valid rules for quadrupedal locomotion were taken into consideration. Symmetrical gaits result in very similar trackways; a further differentiation can be made by application of statistics on step lengths, excursion angles and overstepping.

A clear difference exists between the trot and the pace. These rapid, symmetric gaits imply high ground reaction forces (GRF) because of their long phases of aerial suspension at higher speeds. The resulting GRF seem to be too high to be sustained by the limb bones of huge graviportal animals like sauropods. Unfortunately, most of these factors are rarely available in the case of fossil tracks. Likewise, the asymmetrical, springing gaits can be excluded for sauropods because of the enormous GRF. Provided that limb length as well as trunk length can be approximated, and left and right, as well as forefoot and hindfoot imprints can be discriminated, the symmetrical gaits (walk, amble, pace, trot) used when making a trackway can be discerned.

1 Introduction

Footprints of extinct animals are quite common in earth history and can be found in sedimentary rocks all over the world, often arranged into trackways of many metres in length. Apart from mostly descriptive approaches, the study of fossil footprints and trackways today raises two major questions: which animal was the trackmaker and what can we learn about the mode of its locomotion?

One aim of research on footprints and trackways is to apply and to verify a soil mechanical concept to predict the weight of the trackmaker and the direction and shifting of ground reaction forces (GRF) (Schanz et al., 2013), using footprint geometry and the soil mechanical properties of the subsoil by application of finite element analysis. Another aim is to apply our knowledge of the mode of locomotion of extant taxa on the footfall pattern in trackways of extinct taxa and to estimate gait as postulated by Thompson et al. (2007). The present study focuses on this second aspect, determining gaits with the aid of a thoroughly investigated living analogue.

Locomotion, in general, can be performed by cyclic or rhythmic repetition of the same sequence of movements, where the footfall sequences define the gaits (see below). Locomotion can also be acyclic, like in leaping. Large animals prefer cyclic locomotion because the available muscle force is limited and they require effective use of resources to save energy (Borelli, 1680; clearly shown and explained in Hildebrand and Goslow, 2003). In contrast, smaller masses permit and even favour acyclic locomotion (Günther, 1989; Günther et al., 1991) because they allow rapid bursts of speed, or more technically speaking, very high accelerations. Within limits,

at a given speed, the rhythm of the gait remains constant. This allows the use of pendulous movements to save energy.

One of the most obvious traits of trackways discriminates between “wide-gauge tracks” and “narrow-gauge tracks”, which means the distance of the imprints according to a middle line between right and left imprints (Farlow, 1992; Lockley et al., 1994; Henderson, 2006). In extant taxa, wide-gauge tracks can be found in lizards and in crocodiles, while narrow-gauge tracks, such as those of horses (with 15–20 cm), are usually less than the width of two imprints side by side (own observations; Gray, 1968). The width of the trackway is in part coupled with the posture of the limbs, which can either be sprawled, that is, abducted in the shoulder and hip joints by keeping the stylopodia more or less horizontal in a lateral direction (such as in many extant reptiles, newts and egg-laying mammals, e.g. Christian, 1995 and Preuschoft et al., 2007), or extended and moving more or less in a parasagittal plane (such as in quadrupedal, especially cursorial mammals).

Like track width, the gaits of extinct mammals or dinosaurs can hardly be deduced from single footprints, but may be derived from a trackway consisting of several footprints in sequence of one individual. A number of gait variants can be distinguished among living animals. The terminology used to describe gaits is mainly derived from horses which have been well investigated (Hildebrand, 1965). A basic characteristic of any cyclic locomotion is symmetry or asymmetry (Howell, 1944), the latter occurring in the “springing gaits”. Among the symmetrical gaits, “striding” gaits have duty factors of more than 50 % of cycle length. The cycle length, but not the foreswing period, is shortened in the pace-like walk. The walk may follow a “lateral sequence” (like in horses), or a “diagonal sequence” (like in crocodiles, lizards and primates; see Hildebrand, 1976; Hildebrand and Goslow, 2003). The diagonal footings make the latter similar to the trot, which, however, is characterized by phases of aerial suspension – like the pace – and duty factors of less than 50 % of cycle length and subsequent long steps. The amble is similar to the walk, but its frequency is greater. At higher speeds there may occur phases without ground contact of either the fore- or the hindlimbs.

In the literature, the description of gaits is primarily based on the variation of footfall sequence over time. Their variation in space, as can be seen in the footfall pattern available in trackways, is mostly ignored. One of the rare exceptions is Smith (1912, cited by Gray, 1968), who documented tracks similar to our results. Trackways document the distribution of footprints in space, and time is one of the unknown factors. One distinction between the gaits trot and pace is characterised by the pattern of footfalls in space.

Among the asymmetrical gaits, two variants can be discriminated. The relatively large cursorial mammals, as well as monkeys and apes (Arms et al., 2002; Preuschoft, 2002) prefer the canter, or gallop, with one phase of aerial suspension. A second phase of aerial floating (“extended”) oc-

curs in smaller cursorial mammals at higher speeds. Small-sized mammals, like cats, dogs or hares most often use the half bound. While the number of suspension phases depends on size and on speed, the canter offers somewhat elongated ground contacts; GRF are, therefore, moderate and in each cycle the animal has the chance to re-accelerate or to change direction.

Nearly all large hooved mammals, carnivores, even crocodiles and limbed squamates use very similar gaits. Notable exceptions are the graviportal elephants, as their repertoire of locomotion is confined to symmetrical gaits (Christian et al., 1999a; Hutchinson et al., 2003, 2006). With regard to their superior size (in the case of male African elephant up to 5.5 tons, in contrast to other heavyweights, e.g. rhino – 2.2 tons, hippo – 1.5 tons, giraffe – 1.2 tons, or crocodile – 1 ton; Fechner, 2009), it is unclear, whether this speciality depends on their size or on any other reason.

A simple theoretical consideration by Preuschoft et al. (2011) may help: the speed reached in any gait is defined by distance covered in one cycle multiplied by the frequency of the cycle. Since limb length as well as excursion angles are limited (see below), great step lengths can only be reached, if phases of suspension without ground contact are intercalated into each cycle. In combination with the given frequency, this leads to shortening of the ground contacts. The immediate consequences of phases of suspension are increased GRF, because the sum of impulses exchanged between the animal and the ground must be equal to the constantly acting body weight. Christian et al. (1999b) calculated the GRF, which are dependent on the intervals available for ground contacts. According to their calculations, the mass of large sauropods alone compels them to use elastic damping mechanisms to avoid dangerous stressing of limbs even while walking. This means that any further shortening of contact intervals must be excluded, which are, for example, typical for asymmetric gaits.

Some basic information about quadrupedal locomotion must be kept in mind: in all kinds of tetrapod locomotion (Preuschoft et al., 1994), the limbs are either swung forward (swing phase) or used for support (stance phase). The swing phase follows the law of the pendulum, and consequently sets limits to the frequency, since the time period (T) equals the product of the square root of the length (l) over the acceleration (g) and two times π :

$$T = 2\pi \sqrt{l/g}.$$

A marked flexion during foreswing, as well as the lightweight construction of the distal parts of the limbs, are means to reduce pendulum length and to increase frequency. In the stance phase, the limbs behave like an inverted pendulum. The distance (y) covered during each step depends on the excursion angle (α) and limb length (l):

$$y = l \sin \alpha.$$

Table 1. Horses (vertical) and gaits (horizontal) under investigation, including the speed of the run.

Horse and height at withers	Slow walk	Fast walk	Slow trot	Rapid trot	Slow canter	Fast gallop	Slow amble	Rapid amble	Running pace	<i>Schweinepass</i>
German warmblood; 1.68 m	1.1 m s ⁻¹	1.6 m s ⁻¹	2.6 m s ⁻¹	4.6 m s ⁻¹		6.1 m s ⁻¹				
German saddle horse; 1.50 m	1.2 m s ⁻¹	1.5 m s ⁻¹	3.0 m s ⁻¹	4.3 m s ⁻¹	4.6 m s ⁻¹	6.9 m s ⁻¹				
German warmblood; ca. 1.64 m	1.45 m s ⁻¹			2.5 m s ⁻¹						
Icelandic horse; 1.35 m									6.3 m s ⁻¹	
Icelandic horse; 1.38 m									8.8 m s ⁻¹	
Icelandic horse; 1.38 m									10.2 m s ⁻¹	
Saddlebred; 1.65 m,							3.2 m s ⁻¹	4.4 m s ⁻¹		
Paso Fino; 1.65 m					3.3 m s ⁻¹		1.3 m s ⁻¹			
Icelandic horse; 1.37 m	1.7 m s ⁻¹						2.9 m s ⁻¹	3.6 m s ⁻¹		
Aegidienberger; 1.42 m							3.1 m s ⁻¹	4 m s ⁻¹		
Icelandic horse; 1.35 m										2.5 m s ⁻¹

In cursorial mammals the functional length of limbs is maximised by long metapodials (Preuschoft et al., 1994) and in hooved mammals by the inclusion of phalanges into the length of the limb. In the extreme case of horses, which are highly adapted to a cursorial lifestyle, only the tip of the distal phalanx transmits GRF between substrate and the animal's body and needs a local reinforcement in the form of a sturdy toe tip cover. In addition, the extended posture of the joints contributes to limb length.

During steady-state locomotion, the GRF follow a constant pattern in all quadrupeds as well as bipeds (e.g. Fischer and Lilje, 2011; Lee and Todhunter, 1999; Adachi et al., 1996; Li et al., 1996). The vertical force component follows a parabolic curve, while the horizontal force component decelerates in the first part of the stance and re-accelerates in the second. If horizontal and vertical force components are combined, the resulting GRF will change direction and size during each stance phase. The animals place their stance limbs close to this resultant GRF. Hence the carpal/tarsal, elbow/knee, and shoulder/hip joints are keeping the lever arms of the load short. Any deviation of the limbs from the GRF leads to greater torques particularly in the shoulder and hip joints and, therefore, requires more energy. This fact sets strict limits to the excursion angles of the limbs and step lengths, if limb lengths are given. It also explains why heavy animals prefer small excursion angles, and rather short steps, especially at slow speeds.

Considerable differences in movements may occur between steady-state locomotion at constant speed and phases of acceleration and deceleration. Because of the energy that is required for accelerating and decelerating, all extant large animals show a strong tendency to keep their speed at a constant level as well as changes of direction.

To infer the gait used from the observed tracks, we have analysed the trackways of horses moving in the most common gaits: walk (4-beat rhythm with intervals between footfalls of 25 % of cycle duration), trot (2-beat rhythm, in which hind hooves and contralateral fore hooves make ground contact nearly at the same time, amble (or *tölt*, a 4-beat rhythm with higher frequency than the walk), pace (2-beat rhythm, like the trot, but with lateral, instead of diagonal supports),

canter (German: *Galopp*, a 3-beat rhythm). Because of the demands of sport competitions, horse gaits (as well as body shapes) are highly standardised, and therefore a limited sample of horses can provide a reliable reference.

2 Methods and materials

A straight runway of 20 m, 25 m or 50 m (depending on the local facilities) in length and 1 m in width was prepared and marked. In the direction of movement, the starting line of the runway was used as a reference or zero line, as well as the limitation of the runway parallel to the direction of movement, in order to measure the distribution of the imprints like in a coordinate system. In total, 11 horses of different breeds and sizes (Table 1) were ridden along these runways. One difficulty in the analyses of tracks of horses and other cursorial animals is the similarity of the anterior (manus) and posterior (pes) hoofprints. The runs were recorded on video to identify the imprints from the footfall pattern, as well as to document the velocity and the gait used. Instead of measuring step and stride lengths, which are used as common indicators in track literature, the distribution of all hoofprints was measured in reference to the zero line, using the tips of the hoofprints as indicators (Figs. 1, 2).

3 Results

The pattern of hoofprints along the trackways includes step length and track width. This is applicable to all limb postures. Horses, like all cursorial mammals, move their limbs more or less in a parasagittal plane, and produce trackways, which are as narrow as one and a half hooves placed side by side.

In spite of their narrowness, no “crossing over” was observed; the left imprints were constantly placed further to the left than the right ones and vice versa. Rather than following a straight line, the horses sway from side to side forming a trackway with lateral deviations. The amplitudes of these fluctuations – against expectation – are independent of the speed of locomotion.

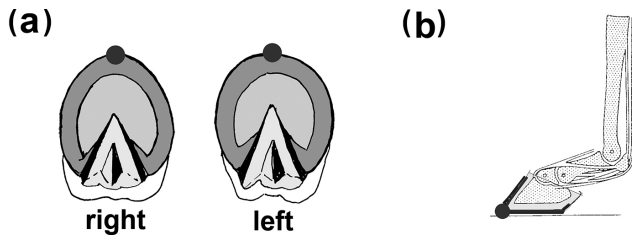


Figure 1. Horse hooves. (a) Hind hoof and fore hoof of a horse seen from below; (b) Longitudinal section through the mechanically relevant elements of the autopodium. The hoof is shown during the middle of the stance phase, while highest loads are acting. Dots at the tips of the hooves are indicating the points used for track measurement. The difference between the imprints of hind hoof and fore hooves is not obvious, so that both are hardly discernible in most tracks.

Table 2. Average number of gait cycles of horses with different wither heights in different gaits on a runway of 20 m.

	Height > 1.50 m; in cycles per 20 m	Height < 1.40 m; in cycles per 20 m
Walk	11	12
Amble	8.35	11.5
Trot	7.7	–
Canter	5.7	9
Running pace	–	6

As expected, the number of cycles on the runway becomes smaller with increasing speed and with the size of the horses (Table 2). The running pace of Icelandic ponies cannot be taken as an equivalent for trotting, because of its high speed, which is even faster than the canter of these small horses.

In the walk (Fig. 4), the placement of ipsilateral hoofprints shows three variants: first, the hind hooves touch the ground behind the spots where the fore hooves just have been. This is rarely practiced, especially in liming horses, or horses with very short legs in proportion to their body length. Second, hind hooves are put down at exactly the same place (capping, Thomson et al., 2007). This occurs at moderate speeds. If walking becomes more rapid, hind hooves are placed clearly in front of the prints of the fore hooves (overstepping; Fig. 2). Step length increases with walking speed and with size. As shown in Fig. 3, the longer the legs are in proportion to the distance between shoulder and hip joints (trunk length), the more often occurs overstepping.

In the *tölt* of Icelandic horses and in similar gaits (amble) of bigger horses (Fig. 5), step lengths are greater than in the walk, and the overstepping of hindlimbs is more apparent. At very high speeds, the hoofprints are no longer grouped in pairs of one fore and one hind, but evenly spaced along the whole trackway. Contralateral hooves may be placed closer together than the hoofprints of the same side (similar to the pace, see below).

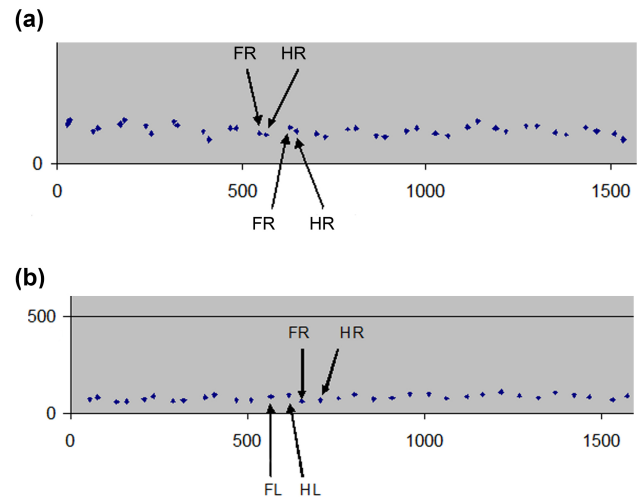


Figure 2. Raw data of two randomly chosen trackways; horizontal axis: distance covered in cm. (a) Slow *tölt* (i.e. amble); (b) Fast *tölt* of an Icelandic horse; FR – front right; HR – hind right; FL – front left; HL – hind left.

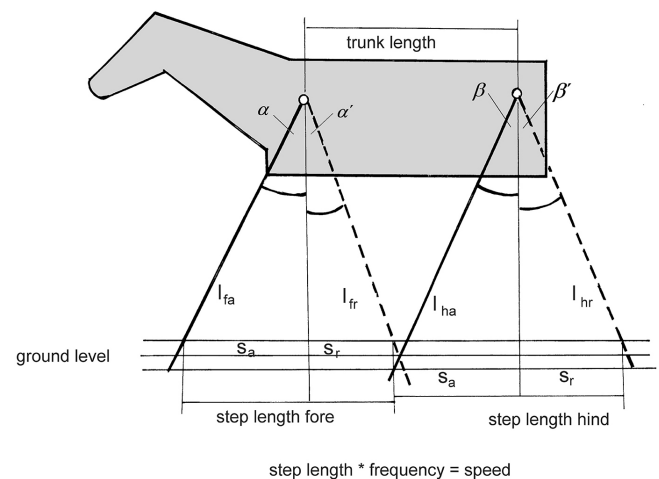


Figure 3. Relationship between trunk length and length of the limbs. The extremities are reduced to their “functional limb lengths”. Step length (s) is the product of excursion angles (α or β) and limb lengths (for example $s = \sin \alpha l_{fa} + \alpha' \sin \alpha' l_{fr}$). The longer the limbs, the lower the ground level below the animal, and the greater the distance (s) covered during each step, without any change of trunk length. The uppermost ground level indicates a lagging of the hind hoof behind the imprint of the fore hoof; the middle level indicates capping; the lowermost indicates overstepping. Excursion angles (α and β) are determined by the resultant GRF. Among living mammals, α usually is greater than α' , while β is commonly smaller than β' ; l_{fa} – left forelimb in anteversion; l_{fr} – left forelimb in retroversion; l_{ha} – left hind in anteversion; l_{hr} – left hind in retroversion.

In the trot (Fig. 6), the hoofprints are grouped in pairs, formed by ipsilateral limbs. Again three variants are possible: anterior imprints set in front of posterior imprints, capping

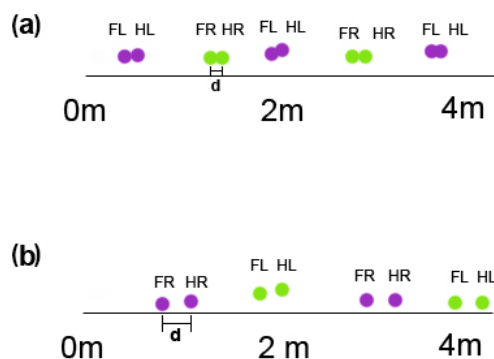


Figure 4. Typical tracks produced in the walk. The faster the walk (and the longer the limbs and the shorter the trunk), the greater is the distance (d) between the ipsilateral front- and hind hooves (i.e. the degree of overstepping increases); horizontal axis: distance covered in m. (a) Slow walk and (b) Fast walk of a German warmblood.

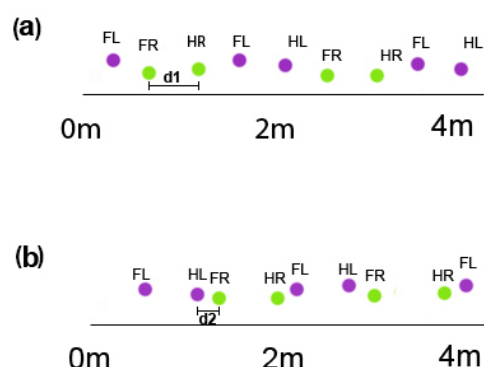


Figure 5. Typical track produced in the *tölt* (amble) of an Icelandic horse. In the amble the overstepping ($d1$) is greater than in the walk and the contralateral hoofprints are close to each other at fast speeds ($d2$). This is similar to the pace. (a) Slow *tölt*; (b) fast *tölt*.

and overstepping. The first can be observed rarely, especially at very slow speeds, and was not documented in this study. Capping can be observed in low and sometimes normal speeds (Fig. 6b). Overstepping is the result of great step lengths and becomes more marked at higher speeds (Fig. 6a). The really large step lengths are reached by intervals of aerial floating.

The running pace of Icelandic horses looks similar to the trot, but the paired prints are from contralateral sides, so that the seeming “overstepping” is performed by contralateral rather than ipsilateral hooves (Fig. 7).

The pattern of hoofprints is completely different in the canter (German: *Galopp*; Fig. 8), which also comprises three variants. In all of them, groups of four evenly spaced imprints are separated by slightly longer distances (Fig. 8a). These longer distances correspond to support on the diagonal right hind hoof/left fore hoof, if the right limbs lead, and left hind hoof/right fore hoof if the left limbs lead. The track in Fig. 8a shows the slowest canter, in which the trailing hind

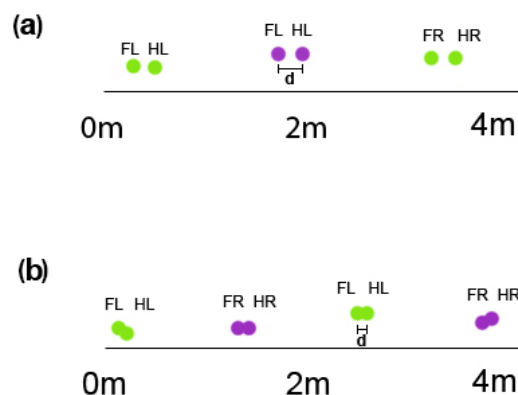


Figure 6. Typical tracks produced in the trot of a German warmblood. With higher speed, the overstepping (d) of the ipsilateral hind hoof is increasing. (b) Slow trot: the hind hoof is placed right on top of the fore hoof imprint (capping); (a) fast (extended) trot, which leads to marked overstepping. A third possibility is the placing of the hind hoof in front of the fore hoof at very slow speed (this is rarely done and not shown here).

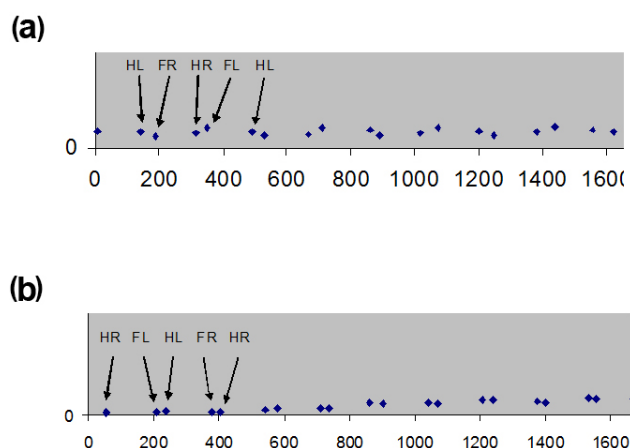


Figure 7. Part of the original tracks comparing fast running pace (a) and fast trot (b). In the running pace the contralateral hoofprints are grouped together with overstepping of the fore hoof over the contralateral hind hoof. In the trot the ipsilateral hoofprints are grouped with an overstepping of the front hoof over the ipsilateral hind hoof. The horizontal axis shows the distance covered in cm.

hoof does not reach the leading fore hoof (“understepping” in an atypical and not desired 4-beat rhythm). With growing speed, the distances between all imprints increase (Fig. 8b), and the imprint of the right hind hoof covers the left fore hoof imprint in the left lead (in the right lead, the left hind hoof imprint would cap the right fore hoof imprint). In rare cases, this usually longer distance can be the same as the other distances between hoofprints so that the imprints are distributed evenly along the trackway. The fastest canter is characterised by an overstepping of the trailing hind hoof over the leading fore hoof. The higher the speed, the greater the distance (d) between the hoofprints. In many cases the hind hooves are

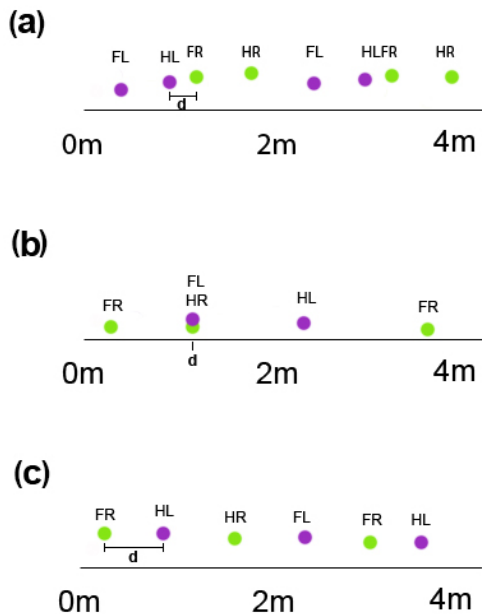


Figure 8. Typical footfall pattern of the canter (German: *Galopp*) in its three varieties. (a) Right lead of a Paso Fino at slow speed; (b) Left lead of a German warmblood horse at normal speed; (c) Right lead of a medium sized German saddle horse at fast speed. The stride length increases with increasing speed. The Paso Fino places the hind hooves between the imprints of the fore hooves, because of slow speed. The warmblood has the same limb length as the Paso Fino, but it is placing the hind hooves beneath the prints of the fore hooves, because of higher speed. The German saddle horse is medium sized and places the hind hooves in front of the fore hooves. With increasing speed in the canter, the separation between all four hoofprints becomes clearer (in the example of right lead the group HL, HR, FL, FR.).

placed slightly lateral to those of the forelimbs (“crabbing”). This obliquity is more pronounced than the distance between left and right limbs.

4 Discussion

The small number of experimental animals is acceptable in view of the highly standardised locomotor patterns in the various breeds of horses. A dominating aim of horse breeding is performance with the same kinematic characteristics and the same sequence of footfalls. This is also the basis for any success in equine sports. In the following discussion, three aspects are emphasised: first the relation between mechanics and footprints in the case of horses, second the parallels to elephants and third the general conditions for the interpretation of tracks left by quadrupeds.

4.1 Footprint mechanics

The number of cycles on the runway (20 m) differs with gait, speed and body size (Table 2). As a whole, the hoofprints

are arranged evenly along the trackways, and so document a nearly continuous support of the body against gravity. Interruptions of support by phases of aerial floating entail enlarged GRF, but are not directly visible from the tracks. Distances (step lengths) between footings of the same limb depend on limb lengths and the excursion angles. Exceptionally long step lengths within a trackway can be derived from increased excursion angles. All symmetrical gaits produce very similar trackways.

The trackways are surprisingly narrow: 10–20 cm is less than the width of two hooves placed side by side. This of course has to do with the high level of motor coordination in cursorial mammals. Swaying (fluctuation) from one side to the other occurs, as well as crabbing. Both seem to be without relationship to speed or gaits – with exception of the canter, where crabbing occurs more often and more pronounced than in other gaits. We have not found any reduction of track width (“straddle”) with increasing speed, as postulated by Thompson et al. (2007).

The intervals between points, where support is given to the mass, are quite long in the trot and the pace, indicating long phases of aerial floating. The canter, by contrast, shows more continuous support of body mass. This may be one reason for changing from trot to canter in horses that have the choice and the preference of the canter over trot on slippery or rough ground. On this particular point, canter or gallop show clear differences to the commonly known half bound of, for example, hares, which contains long phases of aerial suspension.

Determining the arrangement of hoofprints in the case of horses is more difficult than in many other animals, because all four hooves are very similar to each other in shape. If left and right as well as fore and hind can be discriminated, the pace can be identified in contrast to the other symmetrical gaits. Alexander (2003) published “computer generated trackways” of a horse where the pace and trot were identical. The authors of several former studies concluded that gaits cannot be derived from tracks (e.g. Dagg, 1974). Thompson et al. (2007) studied fossil camelids and identified the pairs of imprints as ipsilateral. They used the distances between the first (fore) and the second (hind) imprints (that is the degree of overstepping) as a criterion for trot or pace. Doing so, they did not make full use of the available information about gaits in extant animals. According to our results, however, these pairs in the pace consist of contralateral, not ipsilateral hoofprints, in contrast to the trot. In the trackways of the same individual, the extent of overstepping seems to depend exclusively on its speed. To estimate gaits and speeds of the fossil camelids, an admittedly rough comparison can be drawn to our systematically collected data on horse gaits (Streitlein and Preuschoft, 1987). On a 60 m runway, three typical and successful German warmblood horses showed average stride lengths of 244 cm (speed 3.23 m s^{-1}) in the slow (“collected”) trot, and 348 cm (speed 4.91 m s^{-1}) in *Mitteltrab* (which can be translated as “extended trot”).

In the first gait, fore hooves are capped by the hind hooves, in the latter, faster gait, overstepping by 3–5 cm is essential. Obviously, the stride lengths of the fossil camelids, which varied from 101 cm (in the larger forms 168 cm) to 207 cm, are much shorter than those of our horses. Since the fore-foot imprints of the camelids varied from 9 cm \times 14 cm and from 17 cm \times 20 cm, the conclusion seems adequate, that these animals have been roughly of the same size class as our horses. This would imply, that the fossil camelids did neither trot nor pace, but rather used the comfortable and safe walk. This notion is confirmed by the results obtained by Van der Sluijs et al. (2010), on New World camels. Llama and alpaca clearly preferred a pace-like walk while moving at speeds of $1.13 \text{ m s}^{-1} \pm 0.12 \text{ m}$ or $0.97 \text{ m s}^{-1} \pm 0.15 \text{ m}$, respectively, and could by no means be induced to use a trot or true pace at all. Instead, they changed directly from walk into canter. The stride lengths of llama walking varied between 53 to $106 \pm 8 \text{ cm}$, depending on speed, that is near the lower border of the fossils.

Traits which are seen as important for horses, like overstepping, depend on the relation between trunk length and limb length. If both factors are unknown, the observation loses its value for characterizing the gait, unless independent information is available. Fechner (2009) discusses overstepping in the case of a probable trackmaker that definitely had long hind and shorter forelimbs.

4.2 Parallels to elephants

Elephants use the walk for slow locomotion. If not in a hurry, they extend the stance phases (Christian et al., 1999a). The foreswing of each limb follows the laws of the pendulum, and thus requires a given time interval. If this time interval is shorter than the animal needs, the least energy-consuming option is elongating the stance phase between the foreswings. The least energy-consuming speed is given by a continuous sequence of swing phases of each pair of limbs. For more rapid locomotion, elephants increase frequency and step length, but both factors reach narrow limits. To move even faster, elephants change to a gait very similar to the “amble” (Christian et al., 1999a; Hutchinson et al., 2003, 2006), by elongation of the steps. This is possible by intercalating a phase without ground contact first of the hindlimbs then of the forelimbs. This step elongation seems to be facilitated by marked elastic up and down-movements of the heavy head (Christian et al., 1999a). Gambaryan (1974) illustrated this gait, in his Fig. 11, but called it a “fast walk” without putting emphasis on the phases without ground contact of either the hindlimbs or the forelimbs.

The foot construction of the elephants is well known through a recent publication of Weissengruber et al. (2006) and the feet of sauropods seem to be similar to those of elephants, in having soft cushions for weight transmission parallel to the metapodials. The narrowness of hindfoot imprints

is often observed in relation to the broader forelimb imprints. This parallels hooves of horses and the feet of camels.

4.3 Conditions for the interpretation of tracks

Among the variables which influence the number of footprints per given distance (step length, aerial floating, excursion angle), the size, as indicator of limb and trunk length can be estimated, whereas speed and gait are the unknown values. The area of the imprints should be proportional to body size, provided that the construction of the foot, for example, hoof, paw with or without claws, soft cushion, such as in elephants (or camels), is known. This latter factor may well be visible from the footprints or from morphological analysis of the possible trackmaker's foot skeleton. In contrast to horses, the imprints of fore- and hindlimbs of quadrupedal dinosaurs can usually be identified; they differ markedly in shape, size and depth. Concerning these traits, the interpretation of a fossil trackway is fairly reliable.

The sequence of imprints along the trackway provides some information about the gait used (symmetrical, asymmetrical). Step length in relation to estimated limb length helps to find phases without ground contact. Identification of gaits like amble (i.e. *tölt*) from trackways is only possible, if limb length (height at withers, height of hip joint) as well as trunk length are known or can be approximated. If long trackways with at least 5 footprints are available, a discrimination between the symmetrical gaits may be possible from a trackway.

The narrow width of the trackways seems at a first glance to be characteristic for mammals, especially cursorials. However, it should not be overlooked that animals with sprawling limbs can also walk on a narrow track. The chameleons are outstanding examples of this locomotion type and use it especially when walking along branches. Their rather extended joints contribute to increasing functional limb lengths.

The next step of this investigation is the application of this knowledge to fossil tracks to reveal the mode of locomotion of extinct taxa (Läbe et al., 2013).

5 Conclusions

The arrangement of imprints along trackways provides valuable information about the gait (symmetrical versus asymmetrical) used by the trackmaker. Provided that the size of the trackmaker is known or can be approximated, in particular concerning lengths of limbs in relation to trunk length, the “symmetrical gaits” walk and amble can be discriminated from trot or pace. The bigger and heavier the trackmaker, the greater the vertical component of the ground reaction force and the narrower the excursion angle. If the limb lengths can be estimated or are known, step lengths greater than a reasonable estimate of the excursion angle indicate a phase of aerial suspension, which is typical of trot and pace, as well as fast

amble. If several characteristics of a trackway are combined with estimated body size and estimated limb lengths and excursion angles, and if at least 5 subsequent footprints of a trackway are available, an identification of the gait may be possible.

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