

Conclusion

Questions of scale in biology have a rich history, and an exciting future. The investigation of how life copes with changes in size has unquestionably advanced our understanding of basic biology. Nanotechnology, microfabrication, and microelectronics are providing new tools for biological investigation. They make it possible to sense and perturb previously inaccessible microscopic life in more and more sophisticated ways. Less appreciated but equally important is that for larger organisms they enable sensing and perturbation of multiple parts of intact, freely behaving animals, in complex or even native habitats. As we move towards integrated measurement of metabolism, biomechanics, and neural control in freely behaving animals, the future for questions of scale in biology looks extremely bright.

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Erroneous quadruped walking depictions in natural history museums

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Since the work of the photographer Eadweard Muybridge in the 1880s [1,2], experts know well how quadruped animals walk. All walking tetrapods advance their legs in the same sequence, and only the timing of supporting feet may differ [3–6]. Given the long time since Muybridge's work, one would assume that this knowledge should be reflected in the depictions of walking quadrupeds made by work of painters, taxidermists, anatomists and toy designers. The postures of legs of walking horses, however, are frequently erroneously illustrated in

the fine arts [7]. To see if this also applies to museums, veterinary books and toy shops, we collected hundreds of walking depictions and tested whether or not they correctly display limb positions. We found that almost half of the depictions are wrong. This high error rate in walking illustrations in natural history museums and veterinary anatomy books is particularly unexpected in a time where high-speed cameras and the internet offer ideal possibilities to obtain reliable quantitative information about tetrapod walking.

Although humans have observed walking quadrupeds for thousands of years, the exact characterization of the walking of tetrapods had to wait for the advent of photography [1,2]. The usual sequence by which the legs of walking quadrupeds contact the ground, the so-called 'foot-fall formula', is: left hind leg–left foreleg–right hind leg–right foreleg (LH–LF–RH–RF). The biophysical reason for this uniformity is that this gait confers maximal static stability to the body [6].

To study how correctly this foot-fall formula is represented in natural history museums, veterinary books

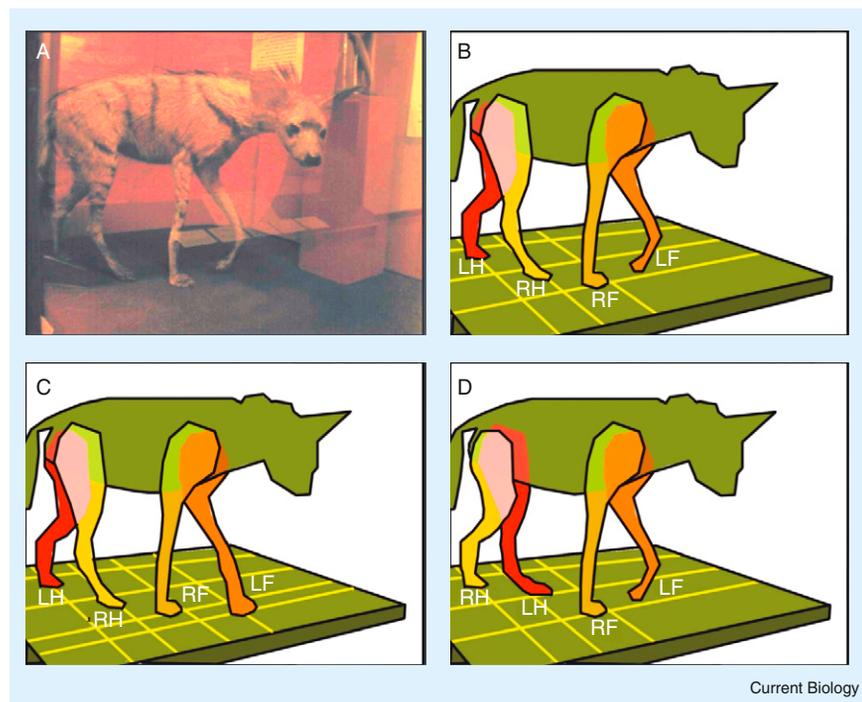


Figure 1. Erroneous three-foot-supported walking depiction of an aardwolf (*Proteles cristatus*). (A) Sample at the Natural History Museum, Florence, Italy (photo by Balázs Gerics) and its leg posture (B). (C,D) Two possible corrections. Erroneously, stepping by the right hind leg is followed by raising the left foreleg, which does not occur in quadruped walking. Instead, it should be followed by raising right foreleg (C), or raising left foreleg should be preceded by the step of left hind leg (D).

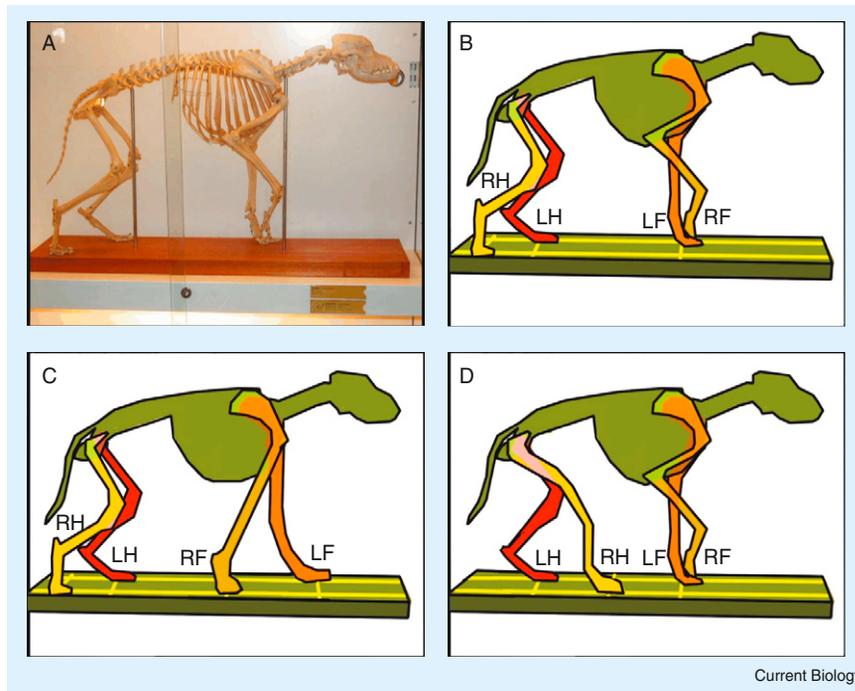


Figure 2. Erroneous three-foot-supported depiction of a domestic dog (*Canis familiaris*).

(A) Display at the Natural History Museum, Oulu, Finland (photo by Gábor Horváth) and its leg posture (B). (C,D) Two possible corrections. Erroneously, stepping by left hind leg is followed by raising right foreleg, which does not occur during walking. Instead, it should be followed by the step of left foreleg (C), or raising right foreleg has to be preceded by the step of right hind leg (D).

and quadruped toys, we gathered numerous walking depictions from various sources and analysed them with respect to the foot-fall formula. The postures of the fore- and hindfeet of these depictions were compared with the corresponding real positions of supporting and lifted feet for the eight typical stride phases of walking horses (see Supplemental Data published with this article online). We studied only illustrations in which the animals were on horizontal substrates and lifted one or two legs. Distinction of walking depictions from illustrations of other gaits/behaviours was made on the basis of leg postures and the attitudes of trunk, head, neck, mane, tail and hair. In total, we analysed 307 two- and three-foot supported depictions, which were collected randomly and representatively. Figures 1 and 2 show examples of incorrect walking depictions from museums. The error rates (r) of the investigated depictions were: $r_{\text{museum}} = 41.1\%$ in natural history museums; $r_{\text{taxidermy}} = 43.1\%$ in taxidermy catalogues; $r_{\text{book}} = 63.6\%$ in animal anatomy books; $r_{\text{toy}} = 50\%$ for quadruped toys; $r_{2\text{-foot}} = 70.2\%$ for two-foot-supported illustrations; $r_{3\text{-foot}} = 37.7\%$ for three-

foot-supported depictions; $r_{\text{total}} = 46.6\%$ for the total 307 walking illustrations.

Considering only the two- and three-foot supported illustrations of horses, or related quadrupeds (zebra, donkey, deer, elk, antelope, muntjac, kudu, dik-dik, impala, gazella, bongo, duiker, nyala, oribi, okapi), or both horses and related tetrapods, we obtained: $r_{\text{horse}} = 50.4\%$, $r_{\text{horsesrelated}} = 43.4\%$, $r_{\text{horse+horsesrelated}} = 48.2\%$. Hence, the error rate for horses and related quadrupeds is about the same as that for the total 307 depictions studied. Not surprisingly, the error rate $r_{\text{museum}} = 41.1\%$ is very similar to $r_{\text{taxidermy}} = 43.1\%$, because taxidermy companies provide museums with quadruped models. The small difference between $r_{\text{museum}} = 41.1\%$ and $r_{\text{toy}} = 50\%$, and in particular the relation $r_{\text{toy}} = 50\% < r_{\text{book}} = 63.6\%$ are, however, unexpected, because the quadruped toy models are intended for children where scientific correctness of walking representations seems not to be an important requirement, while in natural history museums and veterinary books scientific correctness should be expected.

Since the 1880s, knowledge of correct representations of quadruped walking is available from the publications of Muybridge [1,2] and others [3–7]. Our assumption, that the majority of the walking depictions may be correct, turned out to be wrong: 41.1–63.6% (on average 46.6%) of them are erroneous. Thus, there is almost 50% chance to come across an incorrect walking depiction in museums, anatomy books [8–10], or toy shops. Hence, taxidermists, book illustrators and toy designers are nowadays still not completely aware of the quadruped walking, despite the fact that numerous scientific tools are available to study the animal motion quantitatively, and to circulate the gathered information among communities concerned. As we show here, there are many erroneous depictions of quadruped walking even in the scientific world, and these errors can even be propagated given the ease of modern information exchange.

Supplemental data

Supplemental data are available at [http://www.current-biology.com/supplemental/S0960-9822\(08\)01633-3](http://www.current-biology.com/supplemental/S0960-9822(08)01633-3).

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Supplemental Data

Erroneous quadruped walking depictions in natural history museums

Acknowledgements

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Experimental Procedures*Collection of Quadruped Walking Depictions*

Although we collected about 1500 quadruped walking depictions, the majority of them were inappropriate for our goal: we analysed depictions only with 2 or 3 supporting feet. Illustrations with 4 supporting feet were not considered, because in these cases it cannot be usually decided unambiguously whether the animal is standing on all of its feet, or is represented in one of the possible 4-foot-support phases of its walking stride. We disregarded illustrations of other gaits (trot, pace, gallop, jump, etc.), or positions of the body displayed during scratching, grazing and prancing, for example. Finally, as total we analysed 307 two- and three-foot-supported walking depictions from the following sources:

- Photographs taken in the exhibitions and storerooms of natural history museums of Budapest (Hungary), Florence (Italy), Oslo (Norway), Oulu (Finland) and Vienna (Austria).
- Web sites of several natural history museums (e.g., www.bowlingsite.mcf.com, www.historical.library.cornell.edu, www.intermedia.c3.hu, www.maritimeheritage.org, www.sze.hu, www.temple.edu, www.amnh.org, www.wikipedia.com, www.worldcatlibraries.org).
- Home pages of quadruped toy model producers, and photographs taken from such toy models occurring in our private circles.
- Catalogues of Van Dyke Taxidermy, McKenzie Taxidermy and Jonas Taxidermy. These firms produce various real-scale animal models for taxidermists.
- Text-books of veterinary anatomy and drawing schools [8-10].

Table S1 shows the source types, number of sources N , number of samples M of the investigated walking illustrations, and the average $q = M / N$. For the sake of an easier analysis, we aligned (mirrored if necessary) all collected illustrations in order to make the animal walking from left to right. The names and numbers of the investigated quadruped species are listed in Table S2.

We analysed only such walking illustrations at which we were able to conclusively distinguish depictions of walking from depictions of another gait or behaviour. This distinction was relatively simple for such a well-studied animal as the horse, while in the many other quadrupeds investigated the distinction was more difficult. However, it was made easier by the great experience of some of the authors (G. Csorba, B. Gerics) gathered during their work in museums, veterinary universities and various field stations of the world in the last decades. We studied only such depictions in which the animals were on a horizontal substratum and lifted one or two legs. We disregarded the illustrations of other high-speed gaits (e.g., trot, pace, gallop, jump), or positions of the body displayed during scratching, grazing and prancing, for example. The speed during trot, pace, gallop and jump is higher than that characteristic to the walk. This higher motion speed could be guessed especially from the postures of the legs (e.g., the higher the speed, the wider the angle between the corresponding left/right and fore/hind legs), furthermore from the attitudes of the trunk, head, neck, mane, tail and hair (e.g., at higher speeds, the mane, tail and hair are streaming more intensely in the drag-induced wind).

Analysis of Quadruped Walking Depictions:

Since there are maximum 8 combinations of support in each locomotor cycle (or stride) of quadruped walking [6], we took the drawings of these 8 phases of the stride of walking horses [1-4] shown in Figure S1, and split them along a vertical axis into a fore and a hind half. Thus we obtained 8 fore halves designated *A, B, C, D, E, F, G, H*, and 8 hind halves designated *a, b, c, d, e, f, g, h* (Figure S2).

All fore halves were paired with all hind halves in all possible combinations, which resulted in the so-called **walking matrix**. A box of this matrix is designated by the capital letter of its row and the small letter of its column: box *Bb*, for example, represents a correct walking depiction, because it corresponds to phase *B* of walking (Figure S1), while box *Db* is an imaginable but incorrect depiction, because it never occurs during real quadruped walking (i.e., the fore feet attitudes of phase *D* in Figure S1 are never combined with the hind feet postures of phase *B* in Figure S1). In the boxes of the walking matrix (Figures. S2, S3) the positions of the supporting (weighted) and lifted (unweighted) feet are shown together with the number of supporting feet.

The boxes of the walking matrix (Figures. S2, S3) with black and grey background represent those phases of the stride of (very slow, slow, or rapid) walking, which are characteristic to almost all quadrupeds investigated until now [1-7], when the foot-fall formula is -LH-LF-RH-RF-. We considered a given two- and three-foot-supported walking illustration as correct only, if it correlates to the grey boxes of the walking matrix (Figures. S2, S3). Depictions in the boxes of the walking matrix with white background were considered as incorrect, because they do not correspond to the foot-fall formula -LH-LF-RH-RF- of walking, that is, do not occur in the stride during walking.

In order to analyse correctly the postures of the left and right legs of both the fore and hind leg pairs relative to each other, during the analysis of walking depictions we referred to three main phases of the stride: lifting, swinging and falling (Figure S4). On the basis of these three leg phases, we sought that box of the walking matrix, the leg attitudes of which approximate the best those of a given walking illustration. Thus, the position (row, column) of every illustration was determined in the walking matrix.

The walking matrix does not contain initial phases of walking, when only one leg is lifted and the fore or hind legs are nearly vertical and next to each other. The walking matrix neither shows the speed of walking and does not contain information about the attitudes of the trunk, head, neck, mane, tail and hair, more or less depending on the walking speed. If we disregarded from the postures of the trunk, head, neck, mane, tail and hair, and we took into account only the attitudes of the legs, then in the walking matrix the series of boxes *Ac-Bd-Df-Eg-Fh-Hb* and *Db-Ec-Fd-Hf-Ag-Bh* would correspond to the trot and pace, respectively. Note that in the walking matrix the diagonal grey boxes of walking run between the mentioned tilted lines of boxes of the trot and pace. Therefore, walking depictions with 2-foot-support needed a careful analysis, in which the postures of the trunk, head, neck, mane, tail and hair should have also been considered in order to distinguish walking from trot and pace. Apart from the latter problem, the walking matrix (Figures. S2, S3) makes it possible to decide easily, quickly and reliably whether a given 2- or 3-foot-supported depiction is correct (falling in a grey box of the matrix) or incorrect (falling in a white box).

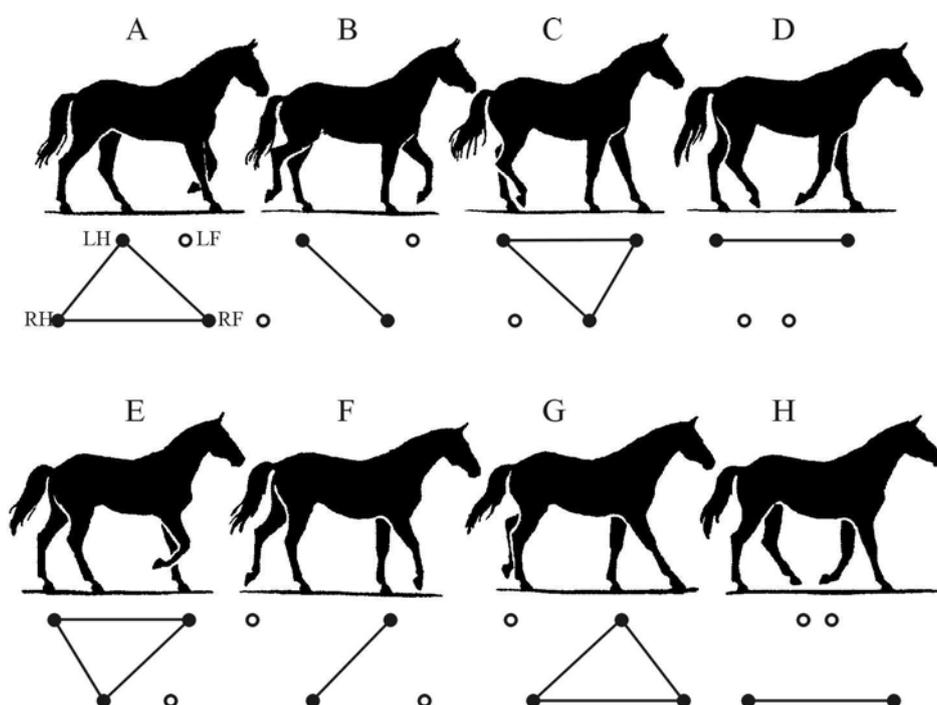


Figure S1: Eight phases of the stride of the rapid walking of horses indicating positions of supporting (black circles connected with lines) and lifted (open circles) feet, where L/R and H/F designate left/right and hind/fore, respectively. Certain quadrupeds do not use phases D and H, furthermore in the case of the slowest walking only phases A, C, E and G occur together with the 4-foot-support phases corresponding to them (not shown here) (adapted from Gambaryan, 1974).

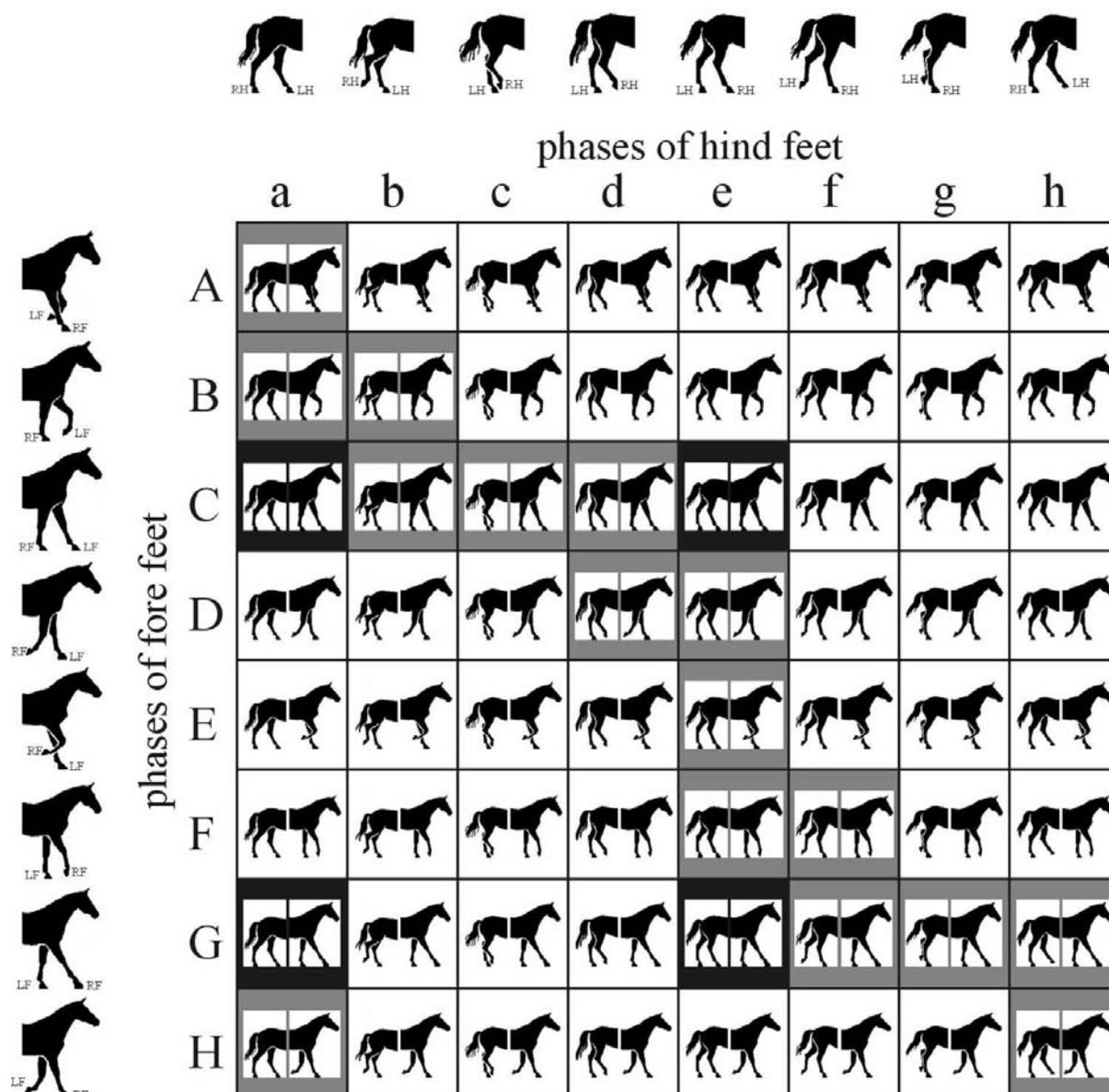


Figure S2: The 8x8 walking matrix of the stride of a horse walking from left to right. To each of the 8 columns and 8 rows belong given postures of the hind and fore feet pair, respectively, as shown by the black half horse contours on the top and left borders (see Figure S1). In a given box of the matrix the fore feet attitudes belonging to the row of the box are paired with the hind feet postures belonging to the column of the box. Black-shaded boxes represent 4-legged support, from which it cannot be decided if the animal is standing or walking. Black- and grey-shaded boxes contain correct walking depictions, while depictions in the white-shaded boxes are considered incorrect.

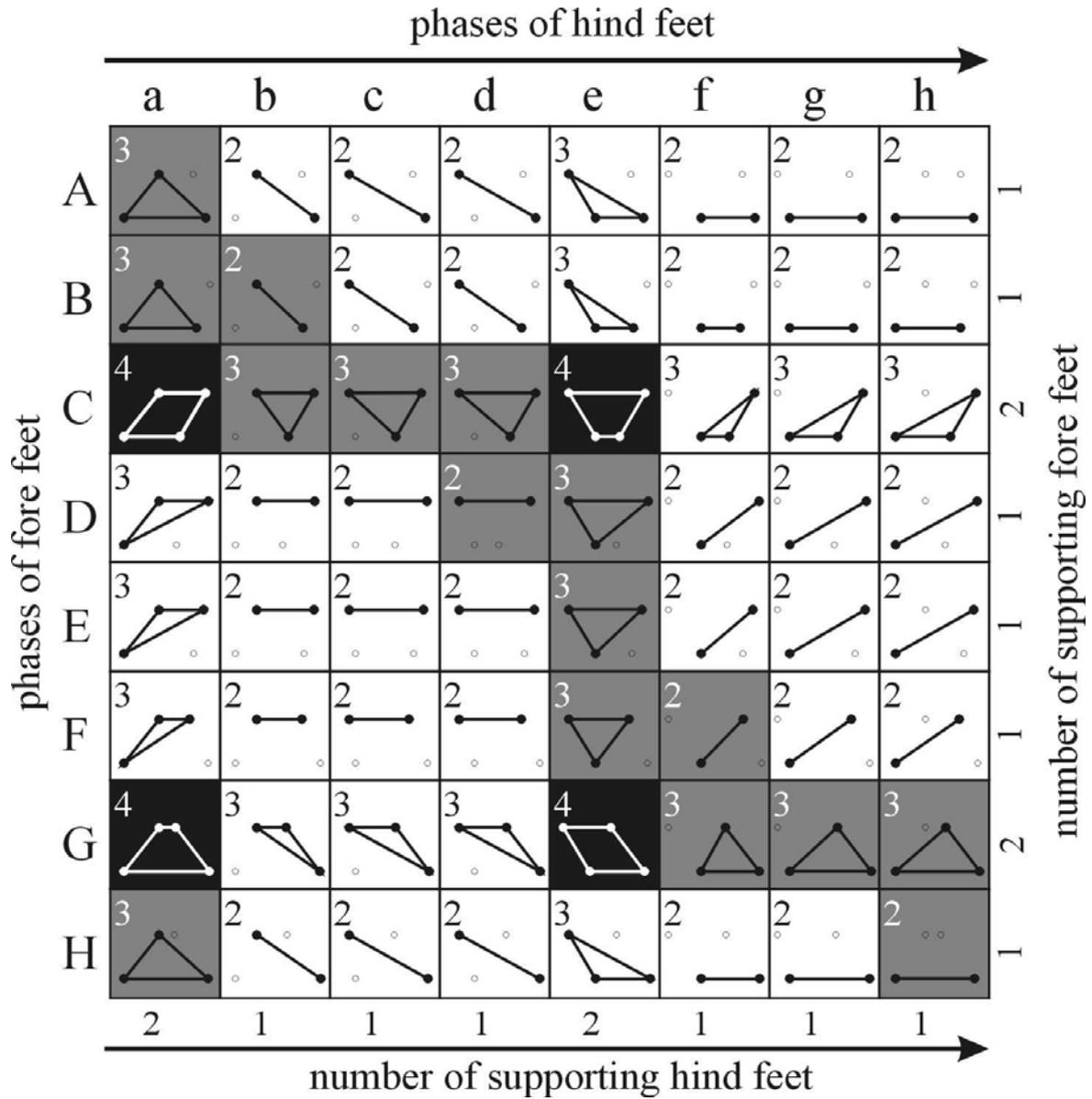


Figure S3: As Figure S2, but here in the boxes the positions of supporting (filled circles connected with lines) and lifted (open circles) feet are shown together with the number (2, 3 or 4) of supporting (weighted) feet. The arrows represent that the quadruped walks from left to right.

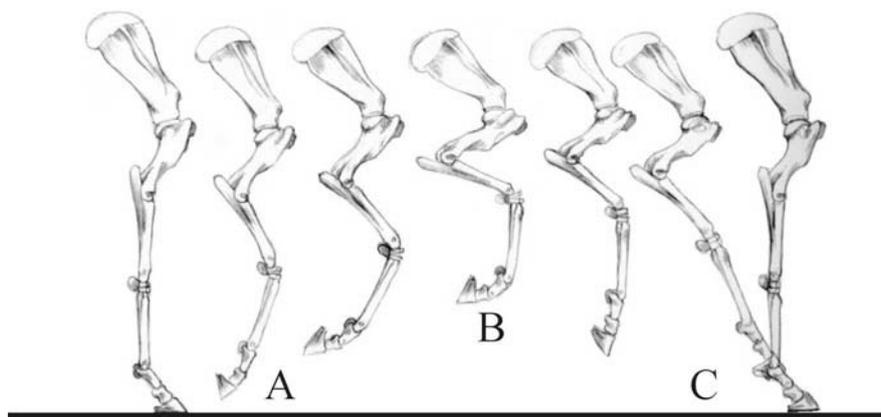


Figure S4: The three main phases of a stride of a horse: (A) lifting, (B) forward swinging, and (C) falling the leg (adapted from Szunyoghy and Fehér, 2004).

Supplemental Discussion

Figure S5 shows a typical example for correct 3-foot-supported walking depiction found in natural history museums. In this figure the left part is an original picture of the specimen and the right part is its schematic drawing (making the attitudes of legs easier to survey), respectively. Figures S6 and S7 show two representative examples for incorrect 2-foot-supported depiction occurring in animal anatomy text-books and among quadruped toy models. Here parts A and B are again the original pictures and their schematic drawings, while parts C and D are two possible corrections of the erroneous illustration. These corrections were performed in such a way that in figure C/D the postures of the hind/fore legs were kept, and those of the fore/hind legs were corrected, respectively. Of course, there are many further possibilities of corrections, but we indicated those two ones being closest to the original walking depiction.

According to the walking matrix (Figures. S2, S3), only 50% of the 24 possible 3-foot-supported illustrations can be correct (12 grey boxes with 3-foot-support of the matrix). Among the 36 boxes with 3-foot-support of the walking matrix only $4/36 = 1/9 \approx 11\%$ (4 grey boxes with 2-foot-support of the walking matrix) can represent correct depictions. Hence, if museum taxidermists, or veterinary anatomy book illustrators, for instance, do not know the correct ways of quadruped walking representation, they have a chance of 50% and 89% to illustrate incorrectly the quadruped walking with 3- and 2-foot-support, respectively.

The high error rates $41.1\% \leq r \leq 63.6\%$ of walking depictions demonstrate that these illustrations might be reproduced by copying: (i) During writing a new anatomy book the author(s) can reuse some depictions without any change from other books, or can illustrate the new depiction with the same leg attitudes as those of other books. (ii) In natural history museums the young generation of taxidermists can simply copy the walking illustrations of the elder generation, or taxidermists of different museums can adapt the walking depictions from each other. Thus the incorrect illustrations (passed on within the community of illustrators and taxidermists from generation to generation) make difficult, or even impossible the elimination of such errors.

Table S3 shows the distribution of the 307 investigated 2- and 3-foot-supported walking depictions in the walking matrix. 46.6% of the total 307 investigated depictions were incorrect. From Table S3 we can see that among these 307 cases many (44) of the possible 60 two- and three-foot-supported depictions occurred, and only $(60 - 44 =)$ 16 boxes of the walking matrix are empty. Among these 16 empty boxes there are 14 two-foot-supported and only 2 (Cg, Gc) three-foot-supported ones. In all probability, if the number of investigated cases were further increased, neither box would be empty. Among the studied 307 illustrations 84 (27.4%) and 223 (72.6%) are 2- and 3-foot-supported, respectively. Among the 143 incorrect depictions 59 (41.3%) are 2-foot-supported and 84 (58.7%) are 3-foot-supported.

From the studied 307 walking illustrations 84 are with 2-foot-support, 70.2% of which are incorrect, while only 37.7% of the 223 three-foot supported illustrations are erroneous. Hence the error rate of 2-foot-supported illustrations is almost twice (1.86) as high as that of the 3-foot-supported ones. This demonstrates well that it is more difficult to illustrate correctly the quadruped walking for 2-foot-support than for 3-foot-support.

Considering the production of quadruped models in natural history museums, the simplest cases with the largest static stability are 4-foot-supported models. Since the static stability decreases with the decreasing number of supporting feet, the production of a walking depiction with less supporting feet becomes more difficult. Among the investigated depictions in museums there were almost none having two feet on the same (left or right) side lifted. This is reasonable, since among the 2-foot-supported illustrations the latter represents the smallest static stability.

We would like to emphasize that our use of the word stability refers only to static stability. Dynamic stability does not depend on maintaining the body centre of mass within the base of foot support, and cannot be analysed based on a single pose of an animal. Static stability is more important in slower gaits such as walking, but note that this is not the only means of achieving stable gait.

We analysed 307 walking depictions from different, numerous sources. Table S1 contains the source types, number of sources N , number of samples M of the investigated walking depictions, and the average $q = M / N$. We sampled 18 natural history museums, 10 taxidermy catalogs, 4 anatomy books and 20 toy producers, partly from the internet. All the average numbers q of walking illustrations originating from these sources were (exactly or) nearly 6. Hence, in average there were taken only a few (~ 6) samples from the same source. It is concluded that a small number of samples taken from a relatively large number of museums constitutes nearly a random sampling. Consequently, the unexpectedly high error rate of $r_{\text{museum}} = 41.1\%$ represents small numbers of erroneous walking depictions from numerous museum curators, rather than many mistakes from the same curator (and those trained by that curator). Thus, the conclusion drawn from these data can be considered as correct, and a further increase of the number of museum samples would not result in considerably different results. Our sampling was approximately random and nearly representative of the entire international community. We admit that the relatively small number (22) of two-dimensional walking illustrations taken from a small number (4) of text-books may lead to the problem, that this sampling was not truly random and representative. However, we did not want to enhance further the number of these 2D illustrations, because our major aim was to focus on real 3D walking depictions, such as museum quadrupeds, taxidermy models and tetrapod toy models.

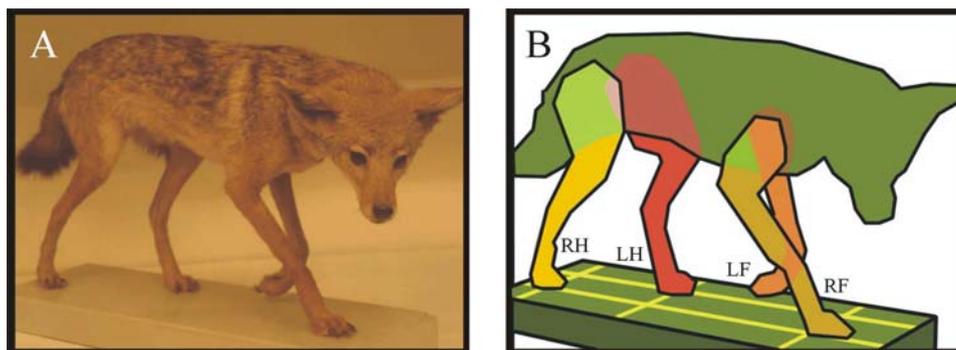


Figure S5: Correct 3-foot-supported walking depiction of a golden jackal (*Canis aureus*, Natural History Museum, Florence) fitting into the box *Ha* of the walking matrix (Figures. S2 and S3). In B the positions of ground contacts are the intersections of yellow lines on the green substratum.

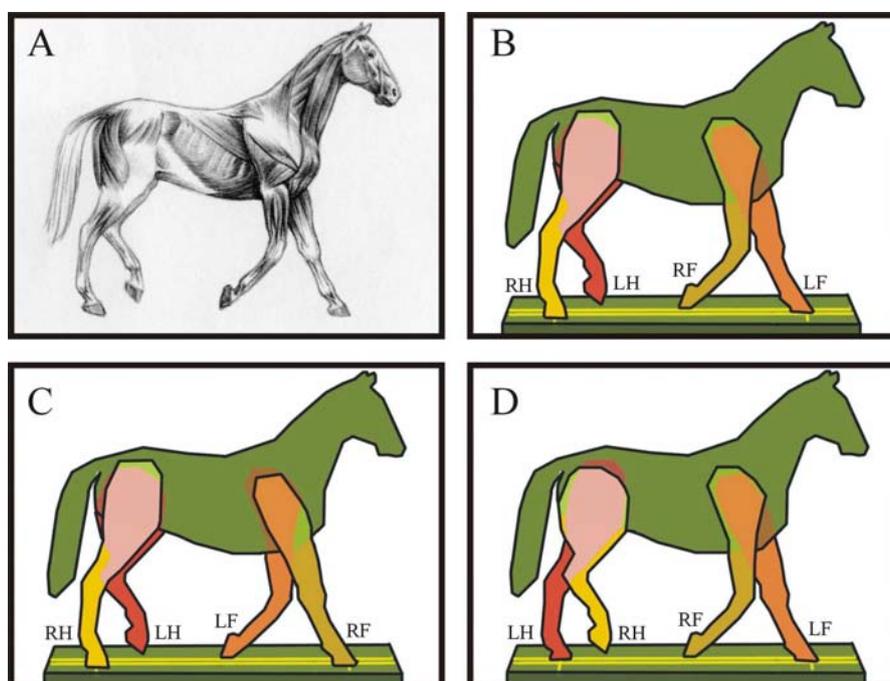


Figure S6: Erroneous 2-foot-supported walking illustration of a horse (*Equus caballus*, Callegari, 2003) fitting into the box *Dh* of the walking matrix (A, B), and its two possible corrections (C, D), where C and D belongs to the box *Hh* and *Dd* of the walking matrix, respectively.

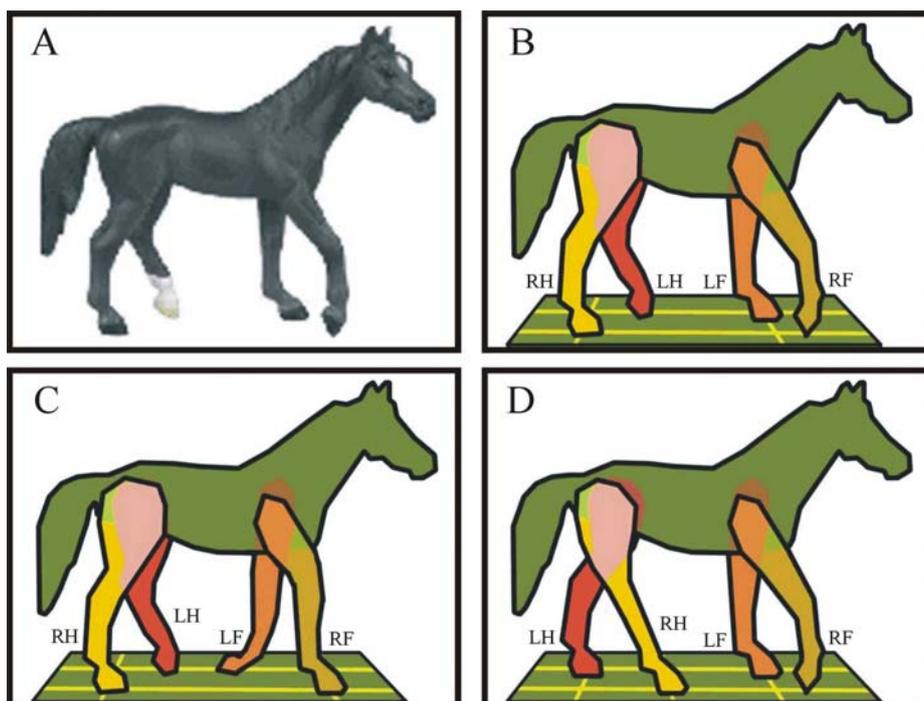


Figure S7: Erroneous 2-foot-supported walking depiction of a horse toy model (*Equus caballus*, http://www.healthstones.com/farm_life_store) fitting into the box *Fh* of the walking matrix (A, B), and its two possible corrections (C, D), where C and D belongs to the box *Hh* and *Fe* of the walking matrix, respectively.

Supplemental Tables

Table S1: Source types, number of sources *N*, number of samples *M* of the investigated walking depictions, and the average $q = M / N$.

source types	number of sources <i>N</i>	number of samples <i>M</i>	average $q = M / N$
natural history museums	18	107	$5.94 \approx 6$
taxidermy catalogues	10	58	$5.8 \approx 6$
veterinary anatomy and drawing school books	4	22	$5.5 \approx 6$
quadruped toy model producers	20	120	6
sum	52	307	$5.9 \approx 6$

Table S2: Names and numbers *n* of the investigated quadruped species.

English name (<i>Latin name</i>)	<i>n</i>
MARSUPIAL	
tasmanian tiger (<i>Thylacinus cynocephalus</i>)	1
ANTEATER	
giant anteater (<i>Myrmecophaga tridactyla</i>)	2
HORSES	
horse (<i>Equus caballus</i>)	111
Burchell's zebra (<i>Equus burchelli</i>)	1
donkey (<i>Equus asinus</i>)	2
fossil horse species (Equidae)	3
DEERS	
red deer (<i>Cervus elaphus</i>)	2
white-tailed deer (<i>Odocoileus virginianus</i>)	2
reindeer (<i>Rangifer tarandus</i>)	7
hog deer (<i>Axis porcinus</i>)	1
sambar deer (<i>Rusa unicolor</i>)	1
mule deer (<i>Odocoileus hemionus</i>)	2
roe deer (<i>Capreolus capreolus</i>)	3
elk (<i>Alces alces</i>)	3
muntjac (<i>Muntiacus sp.</i>)	1
BOVIDS	
domestic cattle (<i>Bos taurus</i>)	1
african buffalo (<i>Syncerus caffer</i>)	1
bison (<i>Bison sp.</i>)	1
eland (<i>Taurotragus sp.</i>)	1
blackbuck (<i>Antilope cervicapra</i>)	1
beisa oryx (<i>Oryx beisa</i>)	1
bontebok (<i>Damaliscus pygargus</i>)	1
sunì (<i>Neotragus moschatus</i>)	2
nilgai (<i>Boselaphus tragocamelus</i>)	1
common duiker (<i>Sylvicapra grimmia</i>)	2
red forest duiker (<i>Cephalophus natalensis</i>)	1
Harvey's duiker (<i>Cephalophus harveyi</i>)	1
impala (<i>Aepyceros melampus</i>)	1
dama gazella (<i>Nanger dama</i>)	1
dibatag (<i>Ammodorcas clarkei</i>)	1
nyala (<i>Tragelaphus angasi</i>)	2
mountain nyala (<i>Tragelaphus buxtoni</i>)	1
Salt's dik-dik (<i>Madoqua saltiana</i>)	3
sitatunga (<i>Tragelaphus spekii</i>)	1
bongo (<i>Tragelaphus eurycerus</i>)	1
lesser kudu (<i>Tragelaphus imberbis</i>)	2
greater kudu (<i>Tragelaphus strepsiceros</i>)	1
oribi (<i>Ourebia ourebi</i>)	1
GOATS	
goat (<i>Capra hircus</i>)	6
sheep (<i>Ovis aries</i>)	1
bighorn sheep (<i>Ovis canadensis</i>)	3
mountain goat (<i>Oreamnos americanus</i>)	1
chamois (<i>Rupicapra sp.</i>)	2
iberian ibex (<i>Capra pyrenaica</i>)	1

PIGs	
domestic pig (<i>Sus domesticus</i>)	3
wild boar (<i>Sus scrofa</i>)	3
bushpig (<i>Potamochoerus</i> sp.)	1
warthog (<i>Phacochoerus africanus</i>)	2
OTHER UNGULATES	
collared peccary (<i>Pecari tajacu</i>)	2
okapi (<i>Okapia johnstoni</i>)	1
pronghorn antelope (<i>Antilocapra americana</i>)	1
lesser malay chevrotain (<i>Tragulus javanicus</i>)	1
ELEPHANTS	
african elephant (<i>Loxodonta africana</i>)	4
deinotherium (<i>Deinotherium</i> sp.)	2
RHINOCEROSes	
black rhinoceros (<i>Diceros bicornis</i>)	3
white rhinoceros (<i>Ceratotherium simum</i>)	2
DOGS	
domestic dog (<i>Canis familiaris</i>)	1
red fox (<i>Vulpes vulpes</i>)	13
golden jackal (<i>Canis aureus</i>)	1
african wild dog (<i>Lycaon pictus</i>)	1
fennec fox (<i>Vulpes zerda</i>)	1
arctic fox (<i>Alopex lagopus</i>)	3
grey wolf (<i>Canis lupus</i>)	4
grey fox (<i>Urocyon cinereoargenteus</i>)	2
coyote (<i>Canis latrans</i>)	1
CATs	
domestic cat (<i>Felis catus</i>)	4
mountain lion (<i>Puma pconcolor</i>)	5
cave lion (<i>Panthera spelaea</i>)	1
african lion (<i>Panthera leo</i>)	6
tiger (<i>Panthera tigris</i>)	3
serval (<i>Leptailurus serval</i>)	1
jaguar (<i>Panthera onca</i>)	1
lynx (<i>Lynx lynx</i>)	2
saber-toothed tiger (<i>Smilodon fatalis</i>)	1
jaguarundi (<i>Puma yaguarondi</i>)	1
wild cat (<i>Felis silvestris</i>)	2
bobcat (<i>Lynx rufus</i>)	1
leopard (<i>Panthera pardus</i>)	2
BEARS	
cave bear (<i>Ursus spelaeus</i>)	1
polar bear (<i>Ursus maritimus</i>)	3
grizzly bear (<i>Ursus arctos</i>)	3
black bear (<i>Ursus americanus</i>)	6
OTHER CARNIVORES	
raccoon (<i>Procyon lotor</i>)	1
ring-tailed coati (<i>Nasua nasua</i>)	1
spotted hyena (<i>Crocuta crocuta</i>)	4
aardwolf (<i>Proteles cristatus</i>)	1

large-spotted genet (<i>Genetta tigrina</i>)	1
african civet (<i>Viverra civetta</i>)	1
small-spotted genet (<i>Genetta genetta</i>)	1
small asian mongoose (<i>Herpestes javanicus</i>)	1
american marten (<i>Martes americana</i>)	1
volverine (<i>Gulo gulo</i>)	1
CAMELS	
dromedar (<i>Camelus dromedarius</i>)	1
bactrian camel (<i>Camelus bactrianus</i>)	3
RODENTS	
black rat (<i>Rattus rattus</i>)	1
agouti (<i>Dasyprocta</i> sp.)	1
FOSSIL REPTILES	
apatosaurus (<i>Apatosaurus</i> sp.)	2
triceratops (<i>Triceratops</i> sp.)	1
stegosaurus (<i>Stegosaurus</i> sp.)	1
other fossil reptile secies	4
total	307

Table S3: The numbers of correct (grey boxes) and incorrect (white boxes) 2- and 3-foot-supported walking depictions in the walking matrix. $N_{\text{correct}} = 164$, $N_{\text{incorrect}} = 143$, total $N = N_{\text{correct}} + N_{\text{incorrect}} = 307$. The rate of incorrect depictions is $r = N_{\text{incorrect}} / N = 46.6\%$.

		phases of hind feet							
		a	b	c	d	e	f	g	h
phases of fore feet	A	19	3		1	6		1	
	B	20	13	10	2	19	3		1
	C		11	1	9		14		4
	D	7			2	23	5		5
	E	14	1		1	26	3	2	7
	F	13	4		2	5	6		6
	G		4		2		3	1	9
	H	12	2			1			4