

# Speeds of dinosaurs from the Albian–Cenomanian of Patagonia and sauropod stance and gait

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Estimates of locomotory speeds of small to large-sized Patagonian dinosaurs are presented for the first time. These estimates are inferred from trackways found on fine to coarse-grained brown sandstones located in the lower section of the Candeleros Member of the Río Limay Formation (Albian–Cenomanian), Neuquén Province, Argentina. The method used is based on the measurement of the stride length (distance between two successive prints of the same foot) and of the length of the hindfoot print, which in turn, allows us to estimate the height at the hip joint and, therefore, the approximate size of the animal. The hypothesis of dynamic similarity implies that the movements of geometrically similar animals, although of different sizes, are dynamically similar only when they move with the same Froude number. The dynamically similar movements (i.e., those with equal Froude number) require equal values of relative stride length (ratio between the stride length and the hip joint height). The relationship between the relative stride length and the Froude number allows us to estimate the speeds of dinosaurs. The dinosaurian ichnofauna studied reveals low speeds that range from 0.5 to 2.6 m s<sup>-1</sup>. Our analyses show that the sauropods responsible for these trackways were either walking very slowly in a bipedal stance or alternatively they were progressing quadrupedally on a slippery surface.

**Key words:** Dinosaur speeds, sauropod stance, palaeoichnology, Río Limay Formation, Albian–Cenomanian, Patagonia.

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## Introduction

The Albian–Cenomanian interval of Patagonia (southern South America) has yielded various dinosaurian taxa such as the titanosaurs *Argentinosaurus huinculensis* Bona-

parte & Coria, 1993 (one of the largest dinosaurs ever found), *Andesaurus delgadoi* Calvo & Bonaparte, 1991, *Epachtosaurus sciuttoii* Powell, 1986, and *Argyrosaurus superbus* Lydekker, 1893, the diplodocoid *Rebbachisaurus tessonei* Calvo & Salgado, 1995, the very large and basal tetanurine theropod *Giganotosaurus carolinii* Coria & Salgado, 1995 (the largest well-known carnivore in the Río Limay Formation and one of the largest carnivorous dinosaurs ever found), the abelisaur *Carnotaurus sastrei* Bonaparte, 1985, and *Xenotarsosaurus bonapartei* Martínez *et al.*, 1986, and some undetermined small to medium-sized basal iguanodontians of the clade Dryomorpha (Coria & Salgado 1993, 1996). The Albian–Cenomanian dinosaur fauna of Patagonia is also known through several polytypic assemblages of saurischian and ornithischian footprints (Calvo 1991). More dinosaur skeletal and ichnological material (e.g., eggs, eggshell fragments, and nests) has been discovered in this interval in the past few years and awaits formal description.

Up to the present, biomechanical studies of South American dinosaur trackways did not exist, except only for one estimation of speed based on the hindfoot prints of a theropod (Alonso & Marquillas 1986). In this study, estimates of the speed of Patagonian dinosaurs based on trackway measures are presented for the first time using an approach previously applied to some Laurasian and Australian dinosaurs (e.g., Alexander 1976; Farlow 1981; Thulborn 1990; Lockley 1991). Moreover, we tried to infer the most probable stance and locomotor behaviour in a pair of Patagonian sauropods.

**Institutional abbreviations.** — MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Paleontología de Vertebrados, Argentina.

## Material and methods

This study is based on a dinosaur tracksite located at Península Nueva, in the coastal surroundings of the artificial lake Ezequiel Ramos Mejía (15 km east of Picún Leufú village, Neuquén Province, Argentina). This palaeoichnological outcrop, where multiple track-bearing horizons occur in close stratigraphic proximity, was found in 1979 and originally described by Calvo (1991). Subsequently, some new dinosaur trackways were found in Isla Cerrito del Bote, located 600 m away from the main outcrop (Calvo 1989; Calvo & Mazzetta in preparation). This locality has been considered the main palaeoichnological outcrop in Argentina for its abundance, diversity and preservation of dinosaur footprints (Calvo 1991). The trackways were photographed and some were cast in plaster (replicas are on display at the Museo de Geología y Paleontología of the Universidad del Comahue) and mapped (see Calvo 1991) before most of the site was destroyed by the effects of erosion and weathering (Mazzetta personal observation).

The footprints at this tracksite are preserved in fine to coarse-grained brown sandstones coming from the lower levels of the Candeleros Member of the Río Limay Formation (northwestern Patagonia), which are thought to be from the Albian–Cenomanian age (Calvo 1991). The sediments were deposited in a geomorphologically low, flat region with shallow water bodies and mudflats under a temperate climate with alternate rainy and dry periods (Calvo & Gazzera 1989).

A method proposed by Alexander (1976) was used for the estimation of the speed of the dinosaurian track-makers belonging to the Península Nueva site. This method is

based on the measurement of the stride length  $s$  (i.e., the distance between corresponding points on successive prints of the same foot) and the length of the hindfoot print  $FL$ . The latter measure allows to estimate the height (in normal standing) at the hip joint  $h$  and, therefore, the approximate size of the animal.

As suggested by Thulborn (1989), the dimension  $h$  was considered as approximately equivalent to  $4.5FL$  in small theropods ( $FL < 0.25$  m) and  $4.9FL$  in big theropods ( $FL > 0.25$  m). The same dimension was assumed as about 4.0 times  $FL$  in sauropods according to Alexander (1976). In large ornithopods,  $h$  was calculated as about  $5.9FL$  as proposed by Thulborn (1989), whereas in iguanodontian ornithopods, and according to the suggestion of Moratalla *et al.* (1988: p. 121), this dimension was estimated by means of the following regression equation:  $h = 3.91FL + 10.94$ , where  $FL$  and  $h$  are expressed in centimetres.

The physical principle underlying the above-mentioned method described by Alexander is accounted for by the hypothesis of dynamic similarity. According to this hypothesis, the movements of animals with geometrically similar shapes, even if they are different in size, are dynamically similar only when they move with equal values of a dimensionless parameter, the Froude number. This parameter is defined as  $v^2/gh$  (where  $v$  is the locomotory speed,  $g$  is the acceleration of free fall, and  $h$  is the height of the hip joint from the ground in normal standing). Dynamically similar movements (i.e., with equal Froude numbers) require equal values of relative stride length (ratio between the stride length  $s$  and the height at the hip joint  $h$ ). The relationship between the relative stride length ( $s/h$ ) and the Froude number allows us to estimate the speeds of dinosaurs. On this basis, Alexander (1976) proposed the following equation for estimating the speeds of dinosaurs from trackways:  $v = 0.25 g^{0.5} s^{1.67} h^{-1.17}$ , where the values of  $s$  and  $h$  are entered in metres and  $v$  is solved in metres per second. At present, this approach represents the best method for estimating the actual speeds implied by dinosaur trackways. However, the equation is limited to estimating the speed at which a particular trackway was made and cannot be used for estimating the top running speed of a dinosaur (Coombs 1978).

Alexander (1976) has pointed out that extant terrestrial mammals change from a walk to a run or trot when the ratio of stride length to hip height ( $s/h$ ) reaches a value of about 2.0, and suggests that the same was probably true for dinosaurs. In subsequent studies of dinosaur locomotion (Thulborn 1982; Thulborn & Wade 1984), Alexander's observations (1976) on the gait of extant vertebrates were extended to define three different gaits in dinosaurs: walk ( $s/h < 2.0$ ), trot ( $s/h$  between 2.0 and 2.9), and run ( $s/h > 2.9$ ). The same criterion was used in the present work in order to evaluate the locomotor performance in Patagonian dinosaurs.

## Results and discussion

All the data in Table 1 refer to trackways of fairly evenly spaced footprints (the step and stride lengths are relatively regular throughout the trackways), indicating progression at fairly constant speed. The studied ichnofauna reveals, in all cases, low speeds ranging from a maximum of  $2.6 \text{ m s}^{-1}$  for the trackway MUCPv-73 (ichnogenus *Limayichnus* Calvo, 1991) assignable to a large-sized iguanodont to a minimum of  $0.5 \text{ m s}^{-1}$  for the

Table 1. Estimates of dinosaur speeds at the Península Nueva site. For the iguanodontian ornithopods (see the last three trackways mentioned in the table),  $h$  was estimated by means of the equation proposed by Moratalla *et al.* (1988: p. 121), whereas for the sauropods,  $h$  was calculated as four times footprint length as suggested by Alexander (1976); in all other cases  $h$  was estimated by means of the ratios listed in Thulborn (1990: p. 251). ( $n$ , number of footprints;  $s$ , mean stride length;  $FL$ , mean footprint length;  $h$ , hip joint height; T, theropods; S, sauropods; O, ornithopods.)

Attributed taxon	Trackway	$n$	$s$ [m]	$FL$ [m]	$h$ [m]	Estimated speed		$s/h$
						[m s <sup>-1</sup> ]	[km h <sup>-1</sup> ]	
T	MUCPv-60	21	1.31	0.22	0.97	1.3	4.6	1.35
T	MUCPv-61	7	1.56	0.21	0.93	1.8	6.5	1.68
T	MUCPv-62	8	1.29	0.15	0.68	1.9	6.8	1.91
T	MUCPv-63	3	1.48	0.17	0.76	2.1	7.5	1.96
T	MUCPv-66	3	1.38	0.20	0.90	1.5	5.5	1.53
T	MUCPv-68	4	1.61	0.23	1.01	1.7	6.2	1.59
T	MUCPv-69	3	1.54	0.23	1.04	1.5	5.5	1.48
T	MUCPv-74	4	2.55	0.49	2.38	1.4	4.9	1.07
T	MUCPv-148	5	2.00	0.35	1.73	1.3	4.7	1.16
S	MUCPv-145	7	2.19	0.92	3.67	0.6	2.3	0.60
S	MUCPv-146	8	1.45	0.66	2.64	0.5	1.7	0.55
O	MUCPv-64	5	2.56	0.33	1.95	1.7	6.2	1.32
O	MUCPv-65	4	3.32	0.60	2.46	2.0	7.3	1.35
O	MUCPv-67	4	2.35	0.42	1.75	1.7	6.1	1.34
O	MUCPv-73	2	3.60	0.55	2.26	2.6	9.2	1.59

trackway MUCPv-146 (ichnogenus *Sauropodichnus* Calvo, 1991) attributed to a medium-sized sauropod.

The ratio of stride length to hip height is, in all cases, less than 2.0 (Table 1), which indicates that all dinosaurs in this location moved by walking. This is consistent with most of the known dinosaur trails distributed world-wide, and particularly those where, as in the palaeoichnological site here studied, the track-bearing beds were formed in a floodplain near shallow water bodies. On the other hand, it is remarkable the fact that the speeds attained by the sauropods in this tracksite are particularly low, less than a half of the speed reached by the slowest of the other dinosaurs studied (Table 1).

Fig. 1 show a plan of the sauropod trackways MUCPv-145 and MUCPv-146, consisting of seven and eight slightly elliptical hindfoot (pes) prints, respectively. These footprints, extremely poor in morphological details, have been assigned to the ichnospecies *Sauropodichnus giganteus* Calvo, 1991, and represent the first finding of sauropod imprints in Argentina. This assignment is supported by the overall shape of the footprints together with the absence of large quadrupedal dinosaurs belonging to any other clade during the Albian–Cenomanian times of South America. The pace angulation (angle between lines formed by two consecutive steps) of these sauropod

trackways varies from 60 to 80°, which is remarkably below the usual value in sauropods (where pace angulation values are often in the range 120 to 140°, according to Thulborn, 1990: p. 169). Moreover, the sauropod trackway gauges are wide, suggesting that their makers were titanosaurs as inferred from the analysis presented by Wilson & Carrano (1999).

In neither of the two sauropod trackways of this outcrop were forefoot (manus) prints observed. With the aim of explaining this situation, several hypotheses were raised. One of them proposes an explanation based on the existence of prints (here considered as true prints or even underprints) of forefoot and hindfoot at different depths in the substrate, where subsequent erosive processes preserved only the hindfoot (pes) prints, for the simple reason that they were deeper than the forefoot prints.

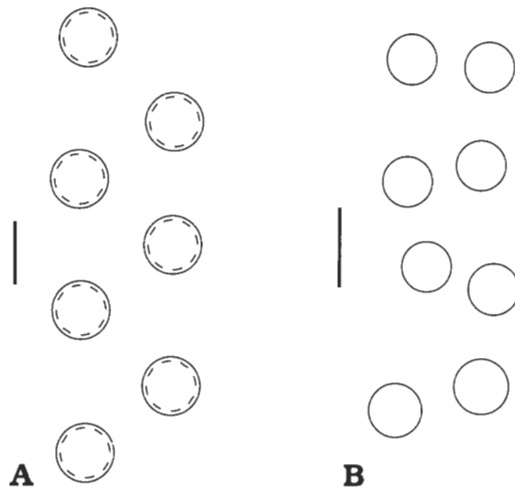


Fig. 1. Plan of the sauropod trackways MUCPv-145 (A) and MUCPv-146 (B) (ichnospecies *Sauropodichnus giganteus*) illustrating the basically circular outline of the pes prints. Scale bars 1 m. Redrawn from Calvo 1991.

In order to test this hypothesis, the size ratio between the areas of the forefoot (palm) and the hindfoot (sole) impressions was considered, and also the relationship of direct proportionality between the pressures exerted on the ground by the feet and the depths of their prints (i.e., the greater the pressure exerted by a foot, the deeper its print) in substrates with no significant frictional properties such as wet, fine-grained soils.

In *Sauropodichnus giganteus*, the horseshoe-shaped forefoot prints are somewhat smaller than one-half (i.e., about 40%) the size of the hindfoot prints, according to what can be observed for forefoot and hindfoot impressions of the same ichnospecies in another close tracksite of similar age studied by Calvo & Salgado (personal communication). Assuming this footprint size ratio for the sauropod trackways here studied, and then considering that (in standing pose) the pressure exerted on the ground by the hindfeet  $amg/A$  (where  $a$  is the fraction of body weight  $mg$  supported by the hindfeet, and  $A$  is the total area of the soles) was greater than the one generated by the forefeet  $(1-a)mg/0.4A$ , the percentage of sauropod's weight being supported by the hindfeet must be greater than 71% (in fact much greater, since hindfoot prints would be, at least, 8 cm deeper than forefoot prints as inferred from the depth of the pes prints of trackway MUCPv-145). This percentage probably eliminates any titanosaurian sauropod as responsible for the hindfoot prints since, in these dinosaurs, the percent-

age of body weight supported by the hindfeet would be about 60% according to calculations carried out on a composite mounted skeleton of the titanosaur *Neuquensaurus australis* (at the exhibition of the Museo de La Plata, Argentina) using a method of volumetric approximation in order to estimate its body mass (see Mazzetta 1999, for further details). The percentage would be even less if we consider the proposed phylogenetic affinity of *Brachiosaurus brancai* with the clade Titanosauria (Calvo & Salgado 1995; Salgado *et al.* 1997), in which animal this percentage is 52% (Alexander 1989: p. 55). Hence, the only way to accept this hypothesis is to consider that the sauropods responsible for these trackways had unusual body proportions, quite different from those of any known titanosaurian sauropod. This is unlikely. However, if the previously suggested titanosaurian origin of these trackways is ignored, the consideration of a value above 71% for the percentage of the weight held by the hindfeet might not completely rule out the Diplodocimorpha (*sensu* Calvo & Salgado 1995, a taxon created to include the Patagonian species *Rebbachisaurus tessonei* as a sister group of the Diplodocidae) as the track-makers. In this taxon, *Apatosaurus louisae* supported about 70% of their weight on their hindfeet, but an extreme case is observed in *Diplodocus carnegiei*, where this percentage reaches 83% (Alexander 1985).

Other hypotheses that consider forefoot and hindfoot prints at the same depth, or forefoot prints deeper than hindfoot prints, are not supported by the palaeoichnological evidence since both types of prints would be observed, or at least the forefoot prints as observed in certain trackways of Laurasian sauropods described by Bird (1944) and Ishigaki (1989).

Occasionally, as observed in many living quadrupeds, some quadrupedal dinosaurs leave 'pseudo-bipedal' trackways in which these animals consistently planted their hindfeet over the impressions left by the forefeet (see, for example, the cases described by Huene 1931, and Lockley *et al.* 1986, or the *Gigantosauropus asturiensis* Mensink & Mertmann, 1984 track mentioned by Thulborn 1990: p. 171, which seems to comprise a sauropod manus print overtrodden by the pes). Hence, other hypotheses to be considered in order to explain the absence of forefoot prints in the *Sauropodichnus* trackways are those which propose a complete overprinting of the hindfeet on the forefoot prints (i.e., with the forefoot prints entirely overtrodden and obliterated by the prints of the hindfeet).

To test these hypotheses a different approach was used, considering that surviving sauropod trackways usually indicate symmetrical gaits (i.e., that the left foot of each pair moved half a cycle out of phase with its right counterpart) as shown by Alexander (1985) and also taking into account the distance from the midpoint between a pair of hindfoot impressions to the midpoint between the next pair of forefoot impressions. This measure can be used to estimate the distance between the shoulder joint (glenoid) and the hip joint (acetabulum) of the tetrapod that produced the tracks, and hence is commonly known as gleno-acetabular distance (*GAD*). The ratio of gleno-acetabular distance to hip joint height (*GAD/h*), when derived from measurements taken in or along the tracks, give an approximate idea of the actual proportions between the length of the animal's trunk and the height of their hindlimbs.

The ratio *GAD/h* was also obtained from measurements taken on drawings or photographs of several sauropod skeletons (see Table 2) in order to compare with the hypothetical values for the same ratio derived from sauropod tracks. For the sixteen sauropod

Table 2. Ratio of gleno-acetabular distance to hip joint height ( $GAD/h$ ) for various sauropod dinosaurs. The values shown for this ratio were obtained from data taken on drawings or photographs of the sauropod skeletons.

Taxon	$GAD/h$	Source of data
<i>Neuquensaurus</i>	0.97	Huene (1929)
<i>Pleurocoelus</i>	0.97	Langston (1974)
<i>Opisthocoelicaudia</i>	1.17	Wilson & Sereno (1998)
<i>Euhelopus</i>	1.07	McIntosh <i>et al.</i> (1997)
<i>Brachiosaurus</i>	1.04	Janensch (1950)
<i>Camarasaurus</i>	1.05	Gilmore (1925)
<i>Haplocanthosaurus</i>	1.07	McIntosh & Williams (1988)
<i>Barosaurus</i>	1.03	McIntosh <i>et al.</i> (1997)
<i>Diplodocus</i>	1.26	Hatcher (1901)
<i>Apatosaurus</i>	1.10	Gilmore (1936)
<i>Amargasaurus</i>	0.98	Salgado & Bonaparte (1991)
<i>Rebbachisaurus</i>	1.21	Calvo & Salgado (1995)
<i>Mamenchisaurus</i>	1.34	Dong (1997)
<i>Omeisaurus</i>	1.17	Dong <i>et al.</i> (1989)
<i>Shunosaurus</i>	0.98	Wilson & Sereno (1998)
<i>Patagosaurus</i>	1.00	McIntosh <i>et al.</i> (1997)

taxa included in Table 2 (conforming to a sample roughly representative of the overall skeletal variability within the clade), the ratio  $GAD/h$  showed values that range from 0.97 (as observed in the titanosaurs *Neuquensaurus* and *Pleurocoelus*) to 1.26 (in the more basal eusauropod *Mamenchisaurus*), with a sample mean ( $\pm$  SD) of  $1.09 \pm 0.11$ .

According to Alexander (1985), sauropod progression could be implied either a lateral sequence single-foot walk (in the terminology of Hildebrand 1976) or a walking pace. However, as noted by Hildebrand (1985) for living tetrapods, the pace is relatively unstable at low speeds (it is usually used at the run or near run) and consequently, this gait is quite unlikely for very slow walking sauropods such as the ones here considered.

Hence, assuming a lateral sequence single-foot walk for the sauropods that printed the *Sauropodichnus* trackways (i.e., a gait where each fore footfall follows that of the hind on the same side of the body), two extreme situations of overprinting may be hypothesised in which the obliterated forefoot prints are positioned against the anterior or against the posterior edge of the hindfoot prints (see Fig. 2). In both situations the ratio  $GAD/h$  is very low (0.35 or 0.27, for the maker of trackway MUCPv-145, and 0.44 or 0.34, for the maker of trackway MUCPv-146) in comparison with the values observed for the sauropods considered in Table 2.

On the other hand, assuming (in spite of its unlikelihood) a walking pace for the sauropods that made the *Sauropodichnus* trackways (i.e., a gait involving a synchronous movement of ipsilateral limbs, as sometimes observed in long-legged animals such as camels), also the same two extreme hypothetical situations of overprinting above mentioned should be considered (see Fig. 3). In both situations the ratio  $GAD/h$  would be also low for each of the makers (0.63 or 0.56, and 0.66 or 0.56, respectively) when compared with the values obtained from sauropod skeletons (see Table 2).

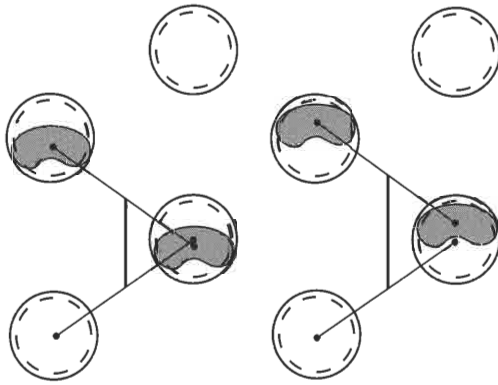


Fig. 2. Sauropod pes prints with hypothetical extreme positions of missing manus prints (shaded area). The track-maker is represented using a lateral sequence single-foot gait (*sensu* Hildebrand 1976) while their manus prints are entirely obliterated by the pes prints. The vertical straight line indicates the gleno-acetabular distance inferred for the track-maker.

Summing up, and considering the hypotheses involving the overprinting phenomenon, the highest ratio  $GAD/h$  estimated for the makers of the *Sauropodichnus* trackways (i.e., 0.66) represents a population whose mean is significantly lower ( $P < 0.005$ ) than that from which the sample included in Table 2 has been drawn. Consequently, all these hypotheses must be rejected because would result in animals with a ridiculously short trunk and/or ridiculously long legs. In addition, there is also another argument which would rule out complete overprinting in the *Sauropodichnus* trackways. In effect, if it is taken into account the fact that the relative placement of manus and pes prints usually varies a great deal within a single trackway, as noted by Thulborn (1990), the consistent obliteration of manus prints by pes prints should be highly unlikely, especially in the trackway MUCPv-146. In this case, it seems quite unlikely that the track-maker always planted completely their hindfeet over the imprints made by the forefeet due to the sinuous path revealed by the trackway (see Fig. 1B). Moreover, in wide-gauge trackways, manus prints are positioned closer to the midline than are pes prints, as noted by Wilson & Carrano (1999). Hence, this arrangement should preclude a total overprinting in the *Sauropodichnus* (wide-gauge) trackways.

Finally, if we assume again the unlikely although not completely discarded hypothesis that considered the differential deepening of forefoot and hindfoot prints to explain the selective preservation of the latter and, at the same time, we tentatively consider the farthest likely position for the forefoot prints in front of the hindfoot prints (i.e., with the centroid of each forefoot print located midway of the distance between the centroids of two successive hindfoot prints, as observed in some sauropod trackways), it is possible to estimate greater values for the ratio  $GAD/h$  in each of the *Sauropodichnus* trackways. However, the values estimated for this ratio (0.55 and 0.56, assuming a lateral sequence single-foot walk, or 0.86 and 0.84 assuming a walking pace, for trackways MUCPv-145 and MUCPv-146, respectively) are also lower than those observed in Table 2. As before, the highest ratio  $GAD/h$  estimated for the makers of the *Sauropodichnus* trackways (i.e., 0.86) represents a population whose mean is significantly lower ( $P < 0.05$ ) than that from which the sample included in Table 2 has been drawn. Hence, these hypotheses must be also discarded.

On the other hand, there are some cases in the literature where bowl-shaped bipedal ornithopod tracks appear to have been confused with sauropod tracks (see for example, the *Neosauropus lagosteirensis* trackway, originally attributed to a sauropod by



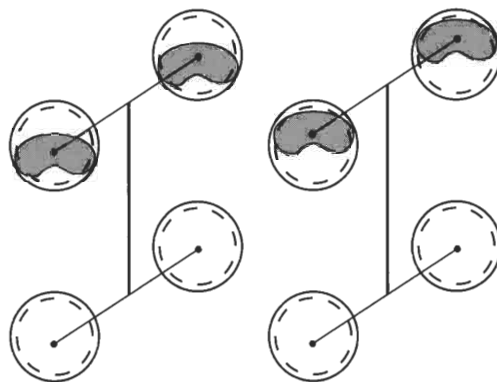


Fig. 3. Sauropod pes prints with hypothetical extreme positions of missing manus prints (shaded area). The track-maker is represented using a pacing gait while their manus prints are entirely obliterated by the pes prints. The vertical straight line indicates the gleno-acetabular distance inferred for the track-maker.

Antunes 1976, and later assigned to a bipedal ornithopod by Santos *et al.* 1992: p. 23). Evidently, these cannot be the cases considered in this study because, unlike typical bipedal ornithopod trackways (with pace angulation commonly in the range 130–160° for large ornithopods, according to Thulborn 1990), the trackways of the ichnospecies *Sauropodichnus giganteus* show much lower pace angulation values (between 60 and 80°). Moreover, the *Sauropodichnus* trackways are of the 'wide-gauge' morphotype (where the trackway pattern shows a clear space between the inside margins of pes tracks on either side) as already noted by Farlow (1992: p. 109) while the corresponding to bipedal ornithopods show tracks planted much closer (or even intersecting) the trackway midline.

In summary, by the use of independent arguments all hypotheses proposed so far were rejected. Consequently, in order to explain the absence of manus prints in the *Sauropodichnus* trackways, two alternative hypotheses should be considered. In the first one, we assumed that the sauropod track-makers were using some sort of unconventional progression, like that adopted by horses proceeding quadrupedally on a slippery surface (Janis personal communication). Under such very unusual conditions, the hindfeet may go through several cycles of strides before the obliteration of the first pair of forefoot prints. In this situation, and taking into account that we were not able to determine the very start of the sequence of footprints considered in each particular sauropod trackway, it would not be possible to know which measurement is appropriate to use to estimate the *GAD*. Hence, in this atypical case eventually the ratio  $GAD/h$  may yield a value that fit with the known normal body proportions in sauropods.

Finally, another alternative hypothesis to be considered is the one assuming that the sauropod track-makers adopted a bipedal stance while moving in a very slow walking gait. It seems plausible that such an extremely slow progression estimated in these sauropods would be associated with the maintenance of the body balance in a bipedal stance (such as in circus elephants and horses when they are obliged to rear up on their hindlegs).

To explain this situation, at least tentatively, it is possible to imagine a scenario where these two sauropods (perhaps an adult and a juvenile as suggested by their track dimensions) were walking bipedally in a defensive attitude when they were harried by predaceous dinosaurs (such as the ones identified from their footprints in the proximities of the *Sauropodichnus* trackways as shown in Calvo 1991: fig. 20). The pro-

posed sauropod ability to rear up and walk on their hindlimbs could have contributed to the moving away from the ground of those parts of the body probably most vulnerable to the attack of predators such as the head and the neck, and maybe at the same time could have enabled them to advance against the predators in an attempt at intimidation. Thus, this behaviour could be presumably considered as part of the defensive repertoire developed by sauropods. This interpretation seems to be consistent with the palaeoichnological evidence and, in turn, it could be used to support a similar bipedal action portrayed at a recently mounted exhibit in the American Museum of Natural History (New York). In this controversial dynamic exhibit we can observe a female *Barosaurus* rearing up on her hindlimbs to protect her offspring from a marauding *Allosaurus*.

It may be difficult to imagine enormous animals such as the sauropods rearing into a bipedal stance, though some studies suggest or even reveal that they may well have done so (Bakker 1978; Alexander 1985), particularly the titanosaurs as inferred from osteological features by Borsuk-Białynicka (1977), Powell (1986), and Wilson & Carrano (1999). Other authors also agree that sauropods may have reared up on their hindlegs on special occasions, for example during confrontational activities, for copulation, or in order to feed at high levels (Jensen 1988; Dodson 1990). Consequently, it does not seem inconceivable to assume that these habitually quadrupedal dinosaurs sometimes managed to progress bipedally at least a few short steps as circumstances demanded.

According to the argument above, the discovery of these thought-provoking *Sauropodichnus* trackways could be either providing evidence for short episodes of sauropod bipedalism (thus revealing a more varied repertoire of locomotor habits in this clade of dinosaurs than those previously documented world-wide) or alternatively could be indicating a quadrupedal progression on a slippery surface. In any case, it could be concluded that the trackways left by these sauropods certainly do not indicate any conventional quadrupedal gait.

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