Speeds and stance of titanosaur sauropods: analysis of *Titanopodus* tracks from the Late Cretaceous of Mendoza, Argentina

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ABSTRACT

Speed estimations from trackways of *Titanopodus mendozensis* González Riga and Calvo provide information abo[...] the locomotion of titanosaurian sauropods that lived in South America during the Late Cretaceous. *Titanopodus* ichnit[...] were found at Agua del Choique, a newly discovered track site in the Loncoche Formation, Late Campanian-Ear[...] Maastrichtian of Mendoza, Argentina. This speed study follows the hypothesis of dynamic similarity proposed [...] Alexander. As a refinement of this method, a complementary equation is presented here based on an articulat[...] titanosaurian specimen collected in strata that are regarded as correlative to those that have yielded *Titanopodus* trac[...] (Allen Formation, Neuquén Basin). This analysis indicates that hip height can be estimated as 4.586 times the leng[...] of the pes track in derived titanosaurs. With an estimation of the hip height and the stride measurements, the spe[...] is calculated. The study of two wide-gauge trackways indicates that *Titanopodus* ichnites were produced by mediu[...] sized titanosaurs (hip height of 211-229 cm) that walked at 4.7-4.9 km/h towards the south and southwest, followi[...] in part, a sinuous pathway. These speeds and some taphonomic features of tracks (prominent rims, distorted elonga[...] shapes) indicate the capacity of derived titanosaurs for walking effectively over a very wet and slippery substrate. In t[...] ichnological record, the walking speeds of *Titanopodus* trackmakers are somewhat faster than those previously inferr[...] for most sauropods.

Key words: speed, Sauropoda, *Titanopodus*, Cretaceous, Argentina.

INTRODUCTION

Important dinosaur tracksites have been described in South America, particularly in Chile (Casamiquela and Fasola 1968, Moreno and Pino 2002, Moreno et al. 2004, Moreno and Benton 2005), Bolivia, and Brazil (Leonardi 1989, Meyer et al. 2001, Lockley et al. 2002). In Argentina, dinosaur track sites are known from Salta, Neuquén, and Mendoza provinces.

In Salta (near eastern Puna), theropod and ornithopod tracks were discovered in the upper levels of the Yacoraite Formation (Maastrichtian) (Alonso 1980, Alonso and Marquillas 1986). In this province, sauro-

In Neuquén (northern Patagonia), dinosaur[...] have been found in the Picún Leufú and El C[...] areas (Fig. 1). These tracks were found in outc[...] the Candeleros Formation (Cenomanian), a unit[...] characterized by deposits corresponding to mea[...] rivers, poorly channeled ephemeral flows, and[...] lakes. Titanosaurian tracks from this formatio[...] named *Sauropodichnus giganteus* (Calvo 1991,[...]

Recently, a new tracksite, the first to be de[...] from Mendoza Province, was discovered in th[...] Campanian-Early Maastrichtian strata of the Lo[...] Formation (González Riga and Calvo 2007[...]

BERNARDO J. GONZÁLEZ RIGA

pod tracks were recently assigned to a new ichnotaxon named *Titanopodus mendozensis* (González Riga and Calvo 2009). These tracks are an excellent example of the wide-gauge style of sauropod locomotion without impressions of manual phalanges. These features, together with the fossil record of the Loncoche Formation and equivalent units in Patagonia (Allen and Los Alamitos Formations), suggest that the *Titanopodus* trackmakers were, probably, saltasaurine or aeolosaurine titanosaurs.

Titanosauria is a diverse sauropod clade that includes more than 50 species of worldwide distribution. However, studies of speed, gait and stance of these dinosaurs are scarce and most biomechanical aspects related to titanosaur locomotion are unknown. Only *Sauropodichnus* tracks, which have been attributed to basal titanosaurs, have been studied in this regard (Mazzetta and Blanco 2001, Calvo and Mazzeta 2004). In this context, the objective of this paper is to study, for the first time, the speeds and stance of the *Titanopodus* trackmakers. This study is important for understanding the locomotion and behavior of the latest titanosaurs that lived during the Late Cretaceous.

MATERIALS AND METHODS

This paper is based on a dinosaur track site located at Agua del Choique, 14 km west of the city of Malargüe in Mendoza Province, Argentina (Fig. 1A). At this paleoichnological outcrop, the author and his team discovered multiple track-bearing levels both in the Anacleto and Loncoche Formations.

In the upper section of the Anacleto Formation (Early Campanian), three levels with sauropod tracks were located in floodplain fluvial facies (Fig. 1B).

In the middle section of the Loncoche Formation (Late Campanian-Early Maastrichtian), two different levels with dinosaur tracks were found (Fig. 1B). One of them occurs in a yellow grey calcareous sandstone and pertains to *Titanopodus mendozensis* (González Riga and Calvo 2009). The other track level is located 80 cm above the former and is exposed only in cross-section.

Province, this Formation is comprised by marginal marine facies (e.g., tidal flats, deltas, sabkhas deposits) that were produced by a shallow transgression of the Atlantic Ocean that covered central-northern Patagonia (González Riga and Parras 1998). In the Ranquil-Có and Calmu-Co sections, the Loncoche Formation has yielded a varied association of fossil fishes and reptiles (González Riga 1999, Previtera and González Riga 2008). These vertebrate assemblages are associated with ancient tidally dominated deltaic deposits and include a mixture of terrestrial vertebrates (dinosaurs and snakes), together with freshwater taxa (e.g. turtles, fishes), as well as marine or littoral forms (plesiosaurs and rays).

Parras et al. (1998) recognized two depositional environments in the Agua del Choique area. The first is attributed to a river-dominated delta and lake setting, and the second corresponds to a river-dominated delta that changed to a tide-dominated delta. A detailed environmental analysis of the *Titanopodus* track site, including sedimentological and paleopalynological data, is presently in progress and will be published elsewhere.

The *Titanopodus* level dips 12 degrees towards the northeast (80°). It extends across three areas. Area A (35°26′55.2 S; 69°44′2.0″ W) includes approximately 160 tracks in four principal trackways (AC-1 to AC-4 in this paper). Area B is located 234 m to the south of area A and comprises around 100 tracks partially covered by sediments. Area C is located 150 m south of area B and includes more than 50 tracks (González Riga and Calvo 2009). In this paper we analyze trackways from area A.

The trackways were photographed and mapped, and some tracks were cast with plaster under the abbreviation of IANIGLA-PV.

The first method for estimating the speed of dinosaurs was proposed by Alexander (1976), who supported his analysis using 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 the Froude number. This number is a non-dimensional parameter used where inertia and viscous forces interact. This parameter is de-
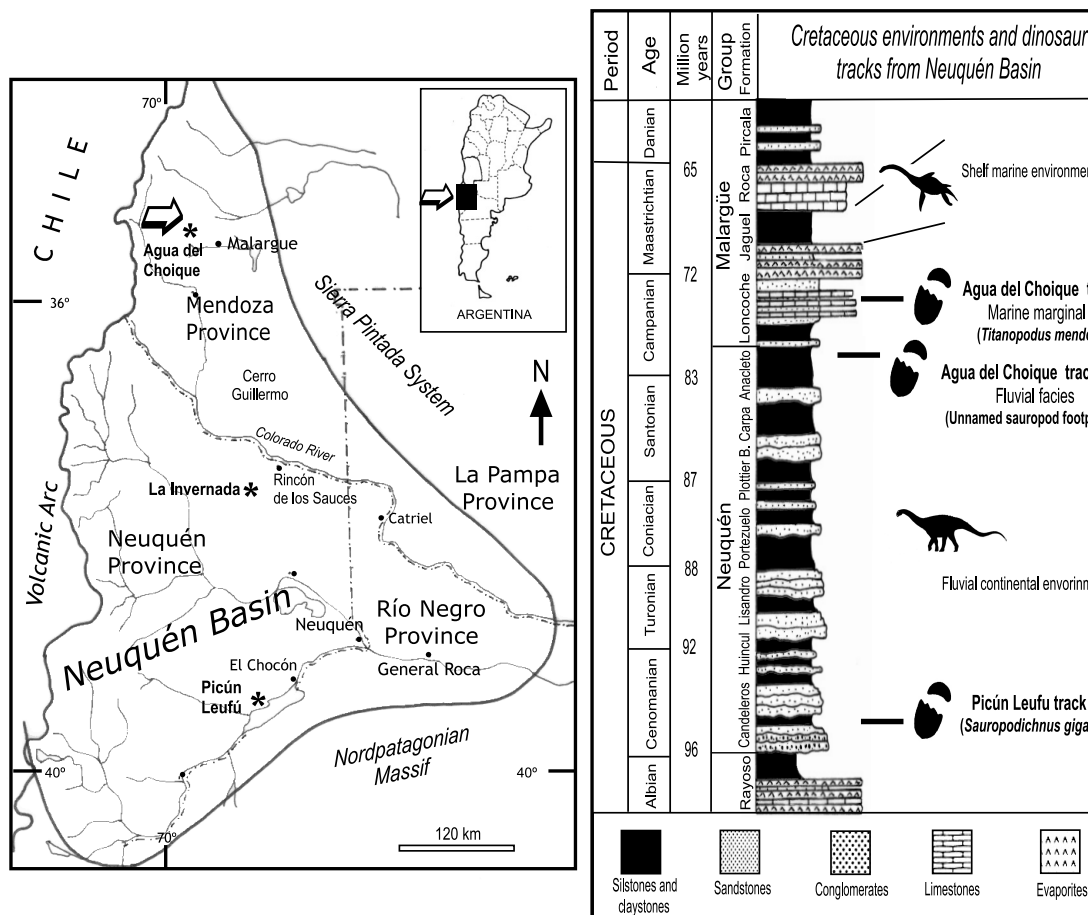
SPEED OF TITANOSAUR SAUROPODS

Fig. 1 – A, Location of the Neuquén Basin (Argentina) showing the Agua del Choique and Picún Leufú tracksites (after González Riga a[...] 2009); B, Stratigraphic column of the Neuquén Basin showing track levels (modified from González Riga 2002).

Dynamically similar movements (i.e., those with equal Froude numbers) require equal values of relative stride length (S/H where S is stride length). The relationship between the relative stride length and the Froude number allows one to estimate speed. On this basis, Alexander (1976) proposed the following equation:

$$V = 0.25G^{0.5}S^{1.67}H^{-1.17} \qquad (1)$$

In this formula, the S and H values are entered in meters and V is solved in meters per second. Although refinements to the method have been proposed in attempts to make it more accurate (see critical review

This method involves the measurement o[...] length (S) and the estimation of height at the h[...] The parameter S is the distance among corresp[...] points on successive prints of the same foot, and [...] ily measured in trackways. In contrast, the esti[...] of H is difficult because it is related with the le[...] the hind foot print (L) through some mathemat[...] tios. This parameter is tested for derived titanos[...] this paper.

Alexander (1976) has pointed out that ext[...] restrial mammals change from a walk to a run [...] when the ratio of stride length to hip height [...]

and Wade 1984), Alexander's (1976) observations on the gaits 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 ($S/H > 2.9$).

Finally, the equation (1) 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).

INSTITUTIONAL ABBREVIATIONS

IANIGLA-PV – Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Colección Paleovertebrados, Argentina.

MUCPv – Museo de Geología y Paleontología, Universidad Nacional del Comahue, Argentina.

RESULTS AND DISCUSSIONS

ANALYSIS OF ANATOMICAL EVIDENCES

An estimation of the height at the hip joint (H) is the first step for calculating the speed of a given dinosaur. Alexander (1976), following the skeletal proportions of the diplodocid sauropod *Apatosaurus*, considered that H is four times the length of the pes footprint (L). He estimated similar values (e.g., $L = 0.23 - 0.38H$) for many bipedal dinosaurs of a wide range of sizes, both theropods and ornithopods.

Thulborn (1990) claimed that the assumption of $H = 4L$ is likely to be incorrect for two reasons. First, the H/L ratio varies in systematic fashion among dinosaur taxa. Second, the H/L ratio certainly changes during ontogeny, on account of the allometric growth that prevails in terrestrial vertebrates. This author supposed that juveniles have relatively larger feet (and therefore smaller H/L ratio) than do adults of the same taxon.

In bipedal dinosaurs, Alexander (1991) and Thulborn and Wade (1984) proposed some refinements to this estimation using allometric equations in some cases. Alternatively, Henderson (2003) studied other methods using computer models. In contrast, recommendations for quadrupedal dinosaurs are less clear because, in many groups like sauropods, the pes has a large padded area

In this paper, as refinements of previous studies, I estimate the hip height of derived titanosaurs using anatomical and ichnological lines of evidence.

First, it is important to analyze the anatomical proportions of the probable trackmakers. The ichnological features of *Titanopodus* indicated that its trackmakers were sauropods of wide-gauge stance where both manus and pes prints were well separated from the midline, as is described in titanosauriforms (Wilson and Carrano 1999). In trackway AC-1 (Fig. 2, holotype of *Titanopodus*), the total width of the trackway is about 125-132 cm, and the inner trackways width is about 40 cm. This feature can be carefully analyzed following the manus and pes trackway ratios (MTR and PTR) proposed by Romano et al. (2007). These indices are defined as the ratio of the track width measured transversely to the midline (side width, SW) relative to the total width of the trackway (overall width, OW) as follows: $TR = SW/OW \times 100$. In the present case, trackway AC-1 shows MTR and PTR values of 22.09 and 31.32 per cent, respectively. These values indicate that *Titanopodus* has a very wide-gauge trackway in comparison with other known trackways. Moreover, the absence of impressions of manual phalanges and the Late Cretaceous age of these ichnites indicate that the trackmakers were, probably, derived titanosaurs.

In Argentina, almost all Late Campanian-Maastrichtian sauropods correspond to Aeolosaurini and Saltasaurinae titanosaurs. The aeolosaurines include *Aeolosaurus rionegrinus* from the Angostura Colorada Formation (Powell 1987). The named species of saltasaurines comprise two forms from the Allen Formation: *Bonatitan reigi* (Martinelli and Forasiepi 2004) and *Rocasaurus muniozi* (Salgado and Azpilicueta 2000), and one species from the Lecho Formation: *Saltasaurus loricatus* (Bonaparte and Powell 1980).

It is important to consider that, in the same strata that have yielded *Titanopodus* tracks (precisely the Allen Formation, a lateral equivalent of the Loncoche Formation and also deposited in the Neuquén Basin), two saltasaurine titanosaurs have been found: *Bonatitan*
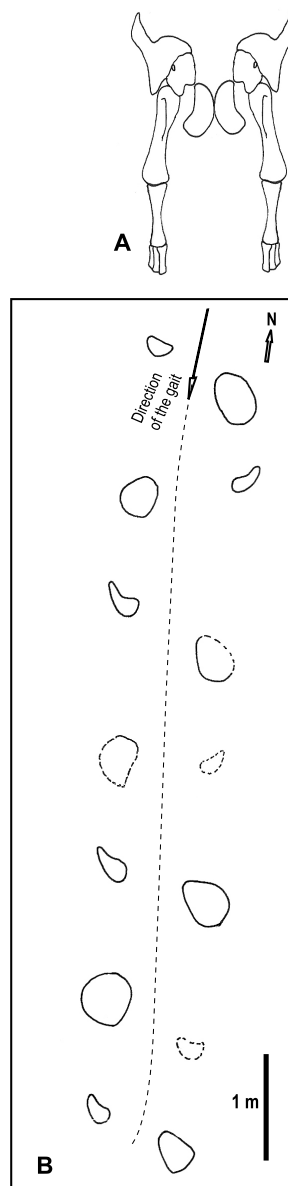
SPEED OF TITANOSAUR SAUROPODS

Fig. 2 – A, Schematic pectoral girdle and forelimbs of a derived titanosaur (modified from Borsuk-Bialynicka 1977). B, *Titanopodus mendozensis*, map of trackway AC-1 (after González Riga and Calvo 2009).

Among these titanosaurs, an interesting sp[...] for studying the appendicular skeleton is that [...] La Invernada taxon (MUCPv-1533). It was disc[...] 230 km south of the *Titanopodus* tracksite and pr[...] the caudal series and fore- and hind limbs, the la[...] cluding a complete and articulated left pes (Go[...] Riga et al. 2007, 2008).

The forelimb of MUCPv-1533 includes f[...] ticulated metacarpals, which form a semi-tubu[...] U-shaped vertical structure, as in other sauropo[...] church 1994, Wilson and Sereno 1998, Wilson [...] This particular morphology limited tensional st[...] the forearm, and was related to the gigantism o[...] quadrupedal dinosaurs (Bonnan 2003). This sp[...] preserves no evidence of manual phalanges, as [...] most all derived titanosaurs (Salgado et al. 1997[...] et al. 2007). A partially similar condition is ob[...] in *Epachthosaurus* from the Late Cenomanian[...] Turonian of Chubut Province, Argentine Pa[...] (Martínez et al. 2004), and *Opisthocoelicaudia* fr[...] Maastrichtian of Mongolia (Borsuk-Bialynicka [...] In these two species, no manual phalanges are p[...] with the exception of a vestigial element fused [...] distal surface of metacarpal IV.

In the ichnological record, the semi-tubula[...] ture of the sauropod metacarpus is preserved, i[...] cases, as a characteristic crescent shape of manu[...] (e.g., Farlow et al. 1989, Lockley 1991, Santo[...] 1994, Calvo 1999, Lockley et al. 2004, Wright [...] In particular, the manus tracks of *Titanopodus* [...] a strongly asymmetrical crescentic contour and e[...] no evidence of manual phalanges (Fig. 3B-C[...] asymmetry is in agreement with the manus [...] specimen MUCPv-1533, where the metacarpals[...] II are very robust elements in comparison wit[...] laterally-positioned metacarpals (Fig. 3D). This [...] metry is absent in the Patagonian titanosaur *Epa*[...] *saurus* (Fig. 3E), since the metacarpals III and [...] almost as robust as the medial-positioned meta[...] (Martínez et al. 2004). In contrast, in *Rapeto*[...] *krausei* from the Maastrichtian of Madagascar, [...]

Obviously, we cannot definitively identify the trackmaker of *Titanopodus* to the genus level; however,
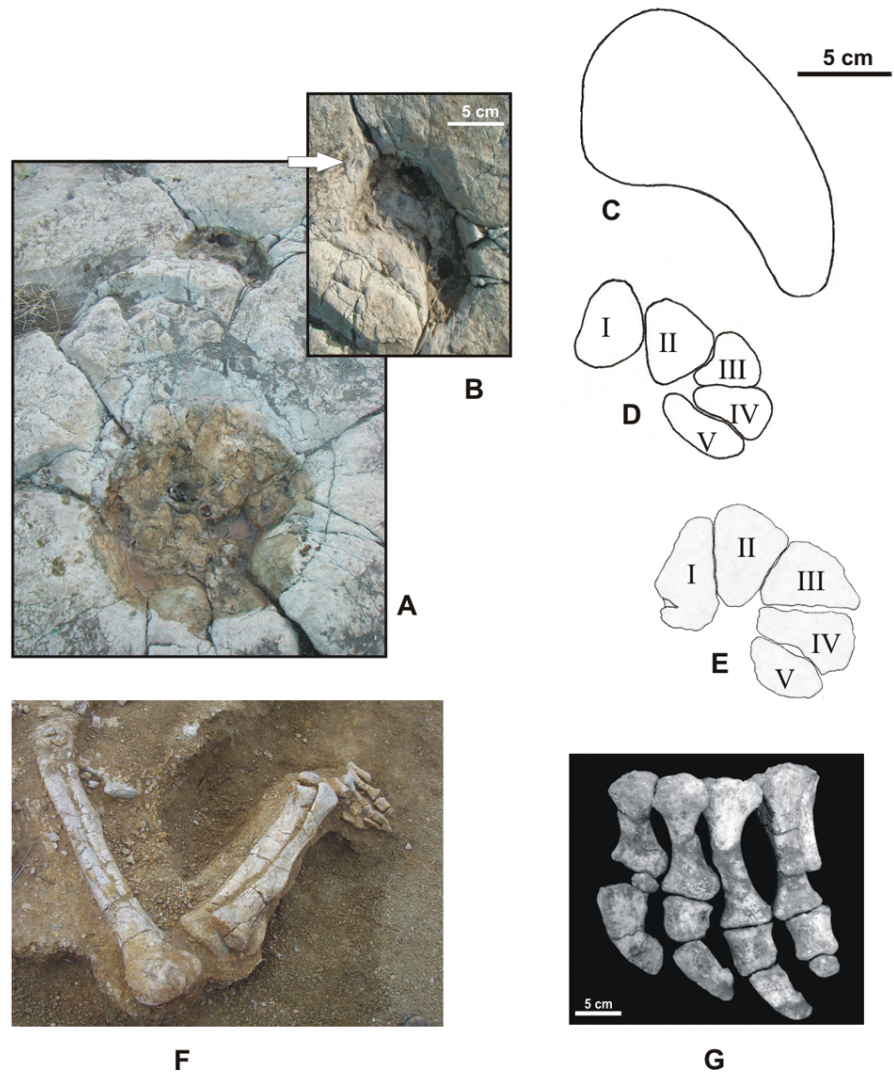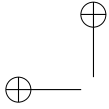
Fig. 3 – A-C, *Titanopodus mendozensis* tracks from Mendoza Province, Argentina: A, field photographs of a manus-pes track set and a left manus (B); C, left manus track of *T. mendozensis* in comparison with the articulated left metacarpus in dorsal views of the titanosaur MUCPv-1533 (D) and *Epachthosaurus* (E). F-G, Titanosaur MUCPv-1533 from La Invernada, Neuquén Province, Argentina: F, articulated left hind limb, G, complete left pes in dorsal view (E, after Martinez et al. 2004, and F-G after González Riga et al. 2008).

The pes of MUCPv-1533 is also typically asymmetrical, relatively short and wide (Fig. 3F). Metatarsals III and IV are the longest elements; the phalangeal formula is: 2-2-2-2-0, and the first three digits carry sickle-shaped unguals (González Riga et al. 2008). The asymmetry of the South American titanosaur pedes

Recently, several aspects of sauropod pedes have been explained as a hypermorphism process, following a morphodynamic approach (Lockey 2007, Lockley and Jackson 2008).

In a preliminary reconstruction of the hind limb, I assume a semi-plantigrade posture, with an angle of
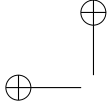
(2005) proposed a similar disposition (45°) for sauropods in general, following the hypothesis that these dinosaurs had an elastic plantar pad. There are no detailed studies of these postural aspects in titanosaurs, but it is possible that, within a single pes, different metatarsals had differing inclinations, as in modern elephants. In these mammals, the digitigrade pedes are functionally plantigrade (Miller et al. 2007) due to the presence of a fatty foot pad that acts in a fashion analogous to high-heeled shoes in humans.

In the graphic reconstruction of the specimen MUCPv-1533 (Fig. 4), the acetabulum (e.g., the hip joint) is located 197 cm above the ground.

ESTIMATION OF HIP JOINT HEIGHT

Based on the reconstruction of the titanosaur hind limb (Fig. 4), the hip joint height can be expressed as an equation:

$$H = F - Af + Ke + T + A + Mt.\cos\alpha + Php \quad (2)$$

In this equation, F is the femur length, Af is the distance between the proximal end of the femur and the horizontal axis of movement of the femoral head ($\sim$7% of the femur length), Ke (Knee) is the space for the femoral-tibial articulation (preliminarily, I assumed a value of $\sim$3% of the femur length), T is the tibia length, A is the height of the astragalus, Mt is the length of the metatarsal III, a is the inclination of the metatarsals (usually interpreted as 40-50°), and Php is the height of a hypothetical pad located ventral to the phalanges, following Gallup's (1989) reconstruction of the pes of the titanosauriform *Pleurocoelus*. In this formula, I assume that Php is 50% of the dorsoventral diameter of the first phalanx of digit III (see Php in Fig. 4).

Also included in this reconstruction is an elastic plantar pad (as a heel) that distributes the weight transmitted through the pes. Obviously, the development of this plantar pad can modify the reconstruction of the length of the pes track. I assume that the track length (L) can vary by about 5% depending on different interpretations of this plantar pad (PL). Other feature is the lateral orientation of the ungual phalanges (U), which
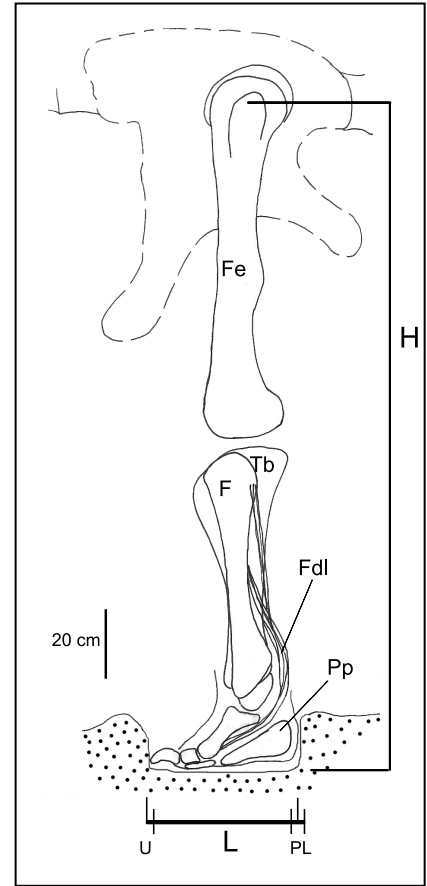

Fig. 4 – Reconstruction of the hind limb of the titanosaur 1533 (Neuquén, Argentina) and interpretation of a hypoth track. Abbreviations: F, fibula; Fe, femur; Fdl, flexor digitoru muscle; H, height of hip joint; L, length of the pes track; PL, of the track length after different development of the plantar plantar pad; Tb, tibia.

ESTIMATION OF SPEED AND SIZE

Both graphic and numerical estimations (Fig. equation 2) of hind limb reconstruction for M 1533 indicate a hip height (H) of 197.2 cm and track of 43 cm length (with a variation of $\pm$ 2 cm

This implied that $H/L = 4.586$, where:

$$H \text{ is about } 4.586\ L$$

The relation (3) can be used to estimate

BERNARDO J. GONZÁLEZ RIGA

TABLE I

Estimated speeds of *Titanopodus* trackmakers (Agua del Choique track site, Mendoza, Argentina). Abbreviations: MPD, manus-pes distance (measured between the anterior margin of both manus and pes tracks); MLP, manus-pes length; H, height of the hip joint; S/H, stride length-hip height ratio.

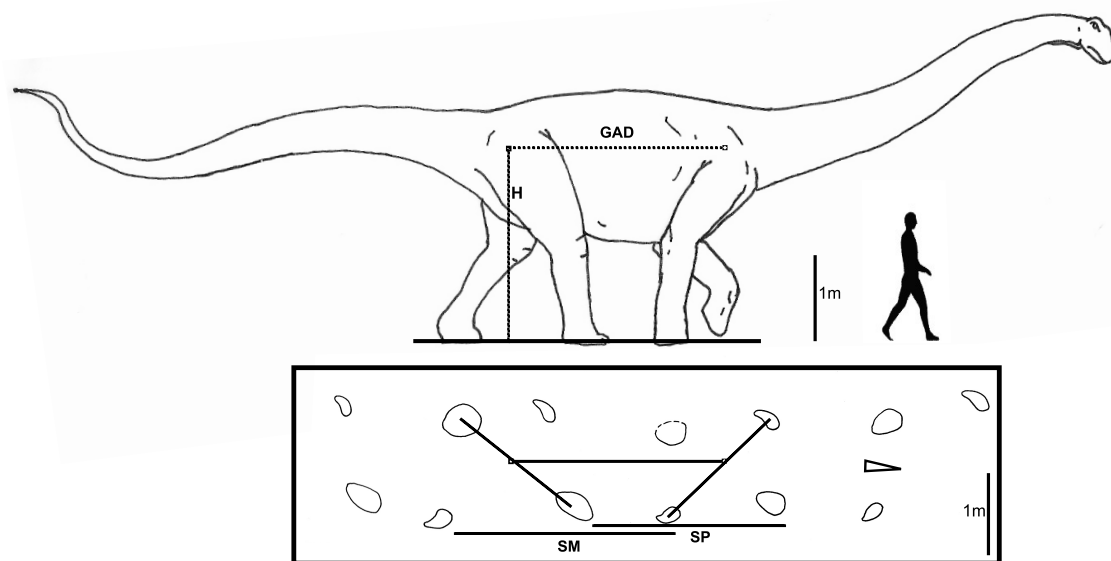| Trackways	Pes track length (cm)	MPD (cm)	MPL (cm)	H (cm)	S Pes stride (cm)	Estimated speed	S/H
AC-1	46	80.4	123.6	210.9	235	1.361 m/s 4.901 km/h	1.11
AC-4	50	102.9	148	229.3	245	1.323 m/s 4.765 km/h	1.06

Fig. 5 – Size of *Titanopodus* trackmaker. Sketch of a derived titanosaur in scale with the *Titanopodus* footprints of the trackway AC-4. Abbreviations: GAD, gleno-acetabular distance; H, height of hip joint; SM and SP, manus and pes stride, respectively.

According to this analysis, the *Titanopodus* tracks were produced by medium-sized titanosaurs. Sizes and anatomical proportions are estimated in based on the equation 3 and ichnological data. Trackways AC-1 and AC-4 were produced by sauropod specimens that had a hip height (*H*) of 211 cm and 229 cm, respectively (Fig. 5). The ratio of glenoacetabular distance to hip joint height (*GAD/H*) is useful for estimating the body length and relative anatomical proportions. According

In trackway AC-1 (18.5 m long; 27 ichnites), one titanosaurian individual walked at 4.90 km/h towards the southwest (193-224 degrees). In trackway AC-4 (46.2 m long; 71 ichnites), a slightly larger titanosaur walked at 4.76 km/h following a sinuous pathway towards the south (176 degrees), southwest (224 degrees), south (172 degrees) and, finally, again the southwest (253 degrees). The stride values (245 cm for the pes) and the pes length are larger than those from trackway AC-1 (235 cm), but

SPEED OF TITANOSAUR SAUROPODS

length) in comparison with the best preserved prints that reach 46 and 50 cm in trackways AC-1 and AC-4, respectively. In elongated and distorted tracks, the presence of prominent rims indicates high water content in the substrate and some degree of sliding of the pedes during locomotion. Thus, the *Titanopodus* trackmakers moved at moderate speed, indicating their capacity to effectively walk over very saturated substrates. The ratio of stride length to hip height (S/H) reaches values of 1.11, indicating that the gait is a walk (not a trot or run), after the definitions of Alexander (1976) and Thulborn and Wade (1984).

The estimated speeds of sauropods generally never surpass 7.2 km/h (Thulborn 1990). For example, the sauropod trackmakers of *Rotundichnus muenchehagensis* from the Lower Cretaceous of Germany show ranges from 3.1 to 4.5 km/h (Lockley et al. 2004) (although these authors used the ratio $H = 5L$ to calculate the speed in these wide-gauge trackways). Another study of speed in a wide-gauge sauropod trackmaker was made using ichnites from the Candeleros Formation of northern Patagonia. In this unit, the *Sauropodichnus* trackmakers reached speeds of only 1.7-2.3 km/h (Mazzetta and Blanco 2001), indicating a very slow pace in a medium-sized basal titanosaur. In contrast, according to this analysis, the walking speeds of *Titanopodus* trackmakers (4.9 km/h) are somewhat faster than those previously inferred for most sauropods.

RESUMO

Estimativas de velocidade a partir de trilhas de *Titan...
mendozensis* González Riga e Calvo fornecem infor...
a respeito da locomoção de saurópodes titanossauria...
viveram na América do Sul durante o Cretáceo S...
Icnitos de *Titanopodus* foram encontrados em Agua d...
que, sendo este um sítio de pegadas recentemente des...
na Formação Loncoche, Campaniano Superior-Maastr...
Inferior de Mendonza, Argentina. Este estudo de vel...
segue a hipótese de similaridade dinâmica proposta p...
xander. Como um refinamento deste método, uma ...
complementar é aqui apresentada tomando como base...
pécime titanossauriano articulado coletado em estratos...
tidos como correlativos àqueles que forneceram as peg...
Titanopodus (Formação Allen, Bacia Neuquén). Esta...
indica que a altura da bacia pode ser estimada com...
4,586 vezes o comprimento da pegada do pé em titano...
derivados. A velocidade é calculada com uma estim...
altura da bacia e as medidas da passada. O estudo de ...
lhas de medidas amplas indica que os icnitos de *Tita...
foram produzidos por titanossauros de tamanho medi...
tura da bacia de 211-229 cm) que caminhavam a 4,7-4...
em direção ao sul e sudeste, seguindo, em parte, um ...
sinuoso. Estas velocidades e algumas características ...
micas das pegadas (margens proeminentes, formatos ...
dos distorcidos) apontam para a capacidade de titano...
derivados de caminhar efetivamente sobre um substrat...
úmido e escorregadio. No registro icnológico, as velo...
de caminhada dos geradores de *Titanopodus* são um pou...
rápidas do que aquelas previamente inferidas para a ...
dos saurópodes.

Palavras-chave: velocidade, Sauropoda, *Titanopodus*...
ceo, Argentina.

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SPEED OF TITANOSAUR SAUROPODS

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