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Tunasniyoj, a dinosaur tracksite from the Jurassic-Cretaceous boundary of Bolivia

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ABSTRACT

Here we report a superbly preserved and profusely represented five-ichnotaxa dinosaur track assemblage near Ic
village, 100 km southeast of Sucre, Bolivia. As preserved in reddish Jurassic-Cretaceous boundary aeolian sandston
this rich and uncommon assemblage is, additionally, the oldest dinosaur tracksite for Bolivia. Four trackmakers we
identified in the area: three quadrupedal and one bipedal, all of them with tracks of around 35 cm in lenght. O
of the quadrupedals is represented by no less than five adult individuals (ichnotaxon A), and four purported juveni
(ichnotaxon B) walking in association. The other two quadrupedals (ichnotaxa C and D) involve four trackways, a
the last, the bipedal trackmaker (ichnotaxon E), is represented by one trackway. The five ichnotaxa represented in t
"Palmar de Tunasniyoj" could be tentatively assigned to the following trackmakers: Ichnotaxa A and B are assign
to basal stegosaurians; ichnotaxon C to a basal tyreophoran, perhaps related to the ankylosaur lineage; ichnotaxon
to the Ankylosauria, and ichnotaxon E to Theropoda. The Tunasniyoj assemblage, the oldest dinosaur tracksite f
Bolivia, includes the oldest known evidence assigned to ankylosaurs and stegosaurs for South America.

Key words: Bolivia, Chuquisaca, dinosaur prints, ichnology.

INTRODUCTION

South American dinosaurs became relatively well known along the last decades. However, most of the available knowledge comes from the osteological data preserved in Argentina and Brazil (Bonaparte 1996, Leanza et al. 2004). The ichnological record is still patchy and chronologically redundant, even when it comes from several localities in several countries (e.g., McCrea et al. 2001, Thulborn 1990). Actually, some of the better samples come from latest Cretaceous rocks of Bolivia (Lockley et al. 2002, Leonardi 1994) and Early Cretaceous of Brazil (Leonardi 1994). On the other side, although tracks in the Chacarilla Formation and Baños del Flaco, Chile (e.g., Moreno and Pino 2002, Rubilar-Rogers et al. 2008), show a good abundance and preservatio
ity of Early Cretaceous dinosaur tracks, they are
represented by sauropods, theropods and some la
nithopods (Rubilar-Rogers et al. 2000, 2008). H
report, in the oldest dinosaur tracksite for Boliv
ancientmost southern evidence of tyreophoran
surprisingly, are represented by three different ta
cluding ankylosaurs and the only stegosaur tra
the Southern Hemisphere.

Locality

The dinosaur track locality of the Palmer of Tun
is placed in the Icla Area, 100 km southeast of

Fig. 1 – Map location of the dinosaur track locality Tunasniyoj, Chuquisaca Department, Bolivia.

Tracksite record in Bolivia

The tracksites in Bolivia are actually abundant, but very poorly known, even for the best represented sites, such as Cal Orck'o, Humaca and Toro Toro (Lockley et al. 2002, Apesteguía et al. 2007, Ríos Cordero 2005). Besides, dinosaur tracks were already found in four of the nine Departments of Bolivia, in the localities of Camargo; Toro Toro and Arampampa, in Potosí (Branisa 1968); Sucre, Ñujchu and Maragua in Chuquisaca; and Santivañez and Parotani in Cochabamba, the latter discovered by Leonardi (1981) and lost after a landslide. However, whereas some of these areas preserve rocks that represent coastal to lacustrine deposits related to the Atlantic transgression of the Pacha Sea (e.g., Sucre and El Molino formations), some others show expositions of slightly older rocks (e.g., Toro Toro and Chaunaca formations). This means that most of these tracksites basically preserves the same ichnofauna, probably indicating the existence of a same fauna that lived along the coasts of the seaway that flooded the southern half of the Potosí basin (Fiedler et al. 2003) by the end of the Cretaceous.

Conversely, the new locality of Tunasniyoj represents levels that are considered around 73 million years

Geological setting

The Tunasniyoj tracksite is located in the Chuquisaca side of the Incapampa-Icla syncline. This forms part of a syncline system that exposes a Tertiary core surrounded by Cretaceous to Jurassic verticalized beds that outcrop in several Departments of Bolivia in the eastern part of the Andes. The bearing beds, thus, form well-developed walls of reddish sandstones, locally covered by basalt flows originated during the Early Cretaceous (Almeida et al. 1996). The track-bearing beds are part of the fluvial to aeolian La Puerta Formation, deposited in Late Jurassic to Early Cretaceous time (Almeida et al. 1996). As different units considered to have been deposited during the latest Jurassic to earliest Cretaceous from Brasil, Bolivia, Paraguay, Uruguay and Argentina show an aeolian signature, it is possible that the La Puerta Formation could be a distal extension of the Brazilian unit, known as the Botucatú desert (Scherer 2000).

MATERIALS AND METHODS

Tracks were exposed by clearing away sand, small rocks and debris. Measurements were taken directly from trackway impressions, following standard ichnological conventions (see Table I).

From the impressions, we obtained the following measurements (Thulborn 1990): pes length (maximum antero-posterior measurement) and pes width (maximum medio-lateral measurement), pace length (distance between corresponding points in two successive footprints), internal trackway width (distance between the inner edge of left and right footprints; negative values indicating track overlapping), external trackway width (distance between the outer edge of left and right footprints), and pace angulation (angle formed between line segments connecting the anteriormost point of consecutive pes tracks) (see Fig. 2D). Additionally, we considered the rotation of the track in respect to the midline of the trackway. Individual tracks and trackways

TABLE I
Measurements of the Tunasniyoj tracks. (?) unknown. (–) not applicable.

		Length (cm)	Width (cm)	Pace length (cm)	Internal trackway width (cm)	External trackway width (cm)	Pace angulation (°)	Rotatio midlin
Ichnotaxon A	Adult manus	11	14	50	3	33	120	5-
	Adult pes	35	25	50	3	60	120	0
	Juvenile manus	3	5-6	40	5	18	145	2
	Juvenile pes	12	9	40	1	20	145	–1
Ichnotaxon B	Manus	21	30	?	?	?	?	13
	Pes	25	35	122	48	103	100	0
Ichnotaxon C	Manus	15	23.5	52.5	16.5	60	?	16
	Pes	18	35	52.5	–25	45	?	0
Ichnotaxon D	Manus	–	–	–	–	–	–	–
	Pes	35	35	?	?	?	?	?

RESULTS

Five ichnotaxa, named as A, B, C, D, and E, were described in the area. They were later assigned to four different trackmakers, three of them quadrupedal and one bipedal.

Ichnotaxon A (Fig. 2A-D). It is the most abundant ichnotaxon and is represented by several trackways. They are not undertracks. They correspond to quadrupedal animals, presumably adults. The four digit pes impressions show a paraxonic arrangement and a probable syndactily between the imprints of digit I and II. The heel mark is separated from the rest of the footprint showing a transversal positive epichnial ridge in some impressions (Fig. 2B). The pes impression length is about 35 cm, and its width is 25 cm. A great number of prints was preserved as long and continuous trackways that reach 30 m in length (Fig. 3A), with an average pace angulation of 120° for the footprints. Both pes and manus paces length is 50 cm. Further, the average outer trackway width is 60 cm, and the inner trackway width ranges from 0 cm to 5 cm, thus corresponding to a narrow trackway. Manus imprints are tetradactyl, short and broad, with about 11 cm in length and 14 cm in width. The manus impressions are located anterior and medially to the pes impressions, and show a slight rotation relative

Ichnotaxon B (Fig. 2E-G). These tracks were m
a quadrupedal animal and they are three times
than those of ichnotaxon A. The tetradactyl pes i
sion is symmetrical, with the imprints of the dig
and III directed forwards, and the IV laterally pro
The heel mark is well separated from the anteri
of the footprint by 3 cm. Pes impression length i
12 cm, and the average width is 9 cm. The longes
ways comprise 20 continuous steps (Fig. 3B), v
average pace angulation of 145° for the footprin
pes and manus imprints display an average pace
of 40 cm, while an external/internal width range
20 cm to 5 cm, respectively.

The manus print has four digit impression
short and broad, with a manus length of about 3
range width from 5 cm to 6 cm. Digit imprints ar
metrically arranged in a wide arch of 140° to 16
in ichnotaxon A, manus prints are located in f
footprints displaying an outward rotation from m

Ichnotaxon C (Fig. 4). This ichnotaxon C is
represented by large and continuous trackways w
and manus impressions. However, most trackw
represented only by pes impressions that we c
overlapping manus prints. The tetradactyl pes i
sion is symmetrical, with rounded end digit i

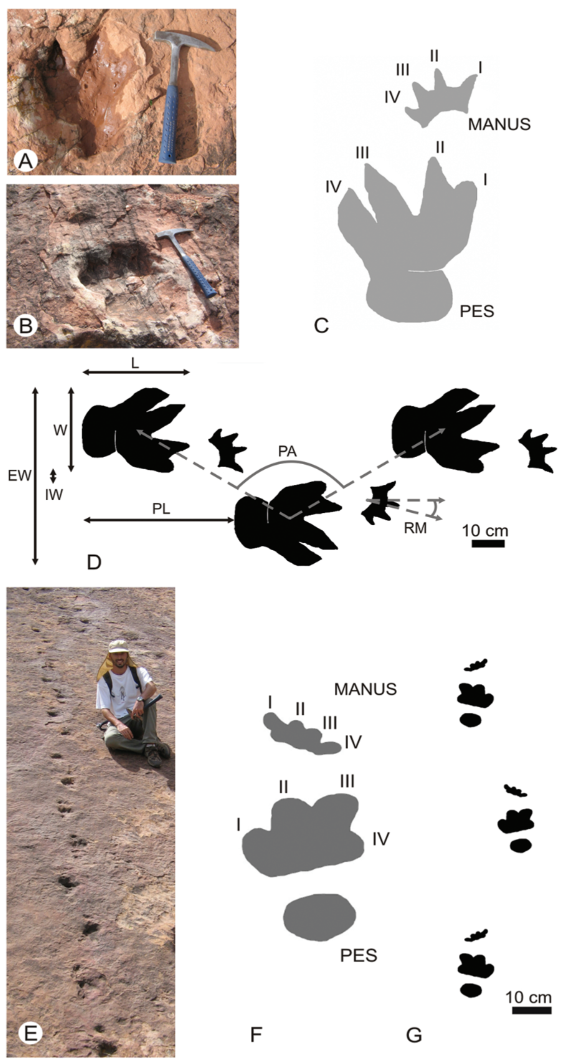

Fig. 2 – Ichnotaxa A and B. Pes and manus of the Icnotaxon A (A, B, C), trackway scheme with distances preserved and principal measurements taken (D). Ichnotaxon B trackways (E), track and trackway scheme (F, G). Abbreviations: EW, external trackway width; IW, internal trackway width; L, length; PA, pace angulation; PL, pace length; RM, rotation from midline; W, width.

sented by four trackways about 15 m in length and with an average pace angulation of 100°. Pes impressions have a pace length of about 122 cm. There is an evident

the normal pace width, is 103 cm, and the internal width is 48 cm. On the other hand, by the zone of change direction, the maximum width decreased to 71 cm, and the internal width became 20 cm (negative value), overlapping the midline of the trackway.

Manus prints are only present in few specimens, but all of them are well preserved. Manus print is pentadactyl, short and kidney-shaped, with a deep posterior excavation. It is transversally long and the finger impressions depict a splayed arch. All digits imprints but V have evident claw marks. Digits imprints are symmetrically displayed, but some specimens show digit I opposed to the rest. The impressions of the digits IV and V are in syndactily.

Ichnotaxon D (Fig. 5A-B). This ichnotaxon, less frequent than ichnotaxa A, B, and C, is represented by some few trackways, with manus and pes impressions from a large quadrupedal animal.

The four-digited pes imprint is asymmetric with digit IV directed laterally, which is separated from the others. Digit I imprint, even smaller, is opposed (anteromedially directed) to digit IV imprint. Digits II and III imprints are projected forwards and partially fused at the base.

Footprint is wide and short, and no heel mark is present (Fig. 5A, B). The length of the pes is 18 cm and 35 cm in maximum width between digits I and IV. This taxon is represented only by a single partial trackway that includes two pes and manus couples. The pace of the pes tracks is about 52.5 cm in length. Manus print is pentadactyl, very short, and with very small digits impressions depicting a serrated anterior border. It shows an inwards rotation of 37° from the midline. There is no evidence of claw marks. The first three digit impressions are medially oriented, with digit IV projected forwards and digit V directed anterolaterally.

Ichnotaxon E (Fig. 5C-E). This ichnotaxon includes isolated footprints that probably correspond to a bipedal animal. The pes track is tridactyl and symmetric. The impressions of the digits are divergent and display a clover-leaf shape, with narrow claw marks at least in

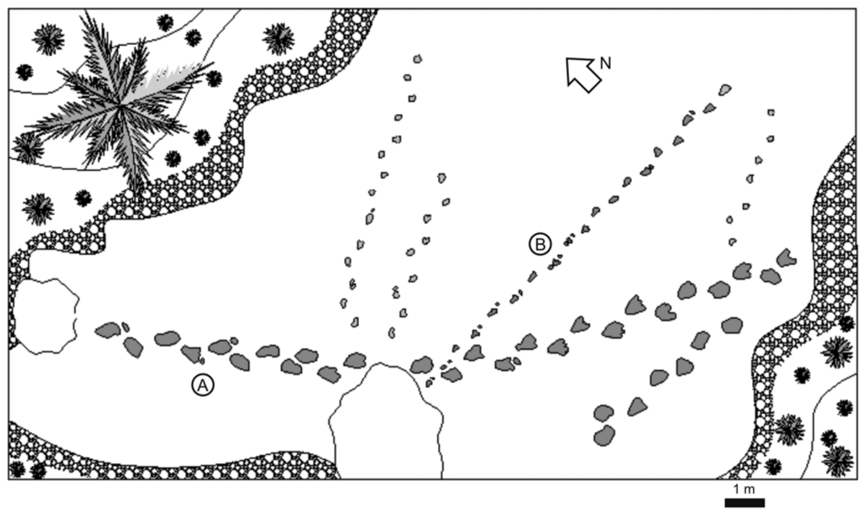

Fig. 3 – Trackway map of ichnotaxa A and B showing spatial relation between both ichnotaxa trackways.

DISCUSSION

Identification of the Tunasniyoj Trackmakers

The establishment of unequivocal relationships between a fossil track and its possible producer is highly speculative, and assignations are, as much, tentative. However, the knowledge gathered after the study of the skeletal anatomy of several dinosaur groups allows a correlation between skeletal structure and track shape.

In this case of study, most of the tracks were produced by taxa that are poorly known or very debated in bibliography. Among them, stegosaurians are one of the most problematic. Most of the discussion on stegosaurian footprint assignment is based on time correlation and its osteological presence in the bearing locality. However, in South America, the only stegosaur remains are restricted to basal forms found in Barremian rocks of Patagonia (Bonaparte 1996). This opens the panorama to find stegosaurian tracks in any South American Early Cretaceous tracksite and perhaps in all Gondwanan, after the re-assignment of the material from the Early Jurassic of Australia originally described by Hill et al. (1966). The finding of the Late Jurassic stegosaur *Kentrosaurus* Hennig (1915) in Tendaguru, Tanzania, is in agreement with this hypothesis. After

Five ichnotaxa are represented in the "Pal
Tunasniyoj". Four of them were likely produ
non-ornithischian ornithopods, and one by a pr
saurischian.

Ichnotaxa A and B. The material from Boli
cludes a separation of the pes impressions in tw
metrical units: the digit imprints and the anteri
of the sole and the heel mark (Fig. 2B, E). F
the impressions of the digits splayed in two diva
axes, partially resembling the situation present i
dactyls like cows and camels.

Besides the discussion of bipedal or quadr
gait in stegosaurs, which is irrelevant in anima
were anatomically capable to use both stances,
the main concerns to consider the identity of ich
A and B is that their pedal tracks are not tridac
diagnosed for *Stegopodus* and presumed for mo
ported stegosaur tracks (e.g., Gierlinski and
2008). Ichnotaxa A and B also differ from *Steg*
in the blunt and short toed pedal prints of the latt

Considering *Deltapodus* tracks, which are al
sidered as tridactyles, some specimens show a
bulging (Whyte and Romano 2001, Fig. 4) of t
ond toe that could actually correspond to the r
digit I of ichnotaxon A. This is especially vis

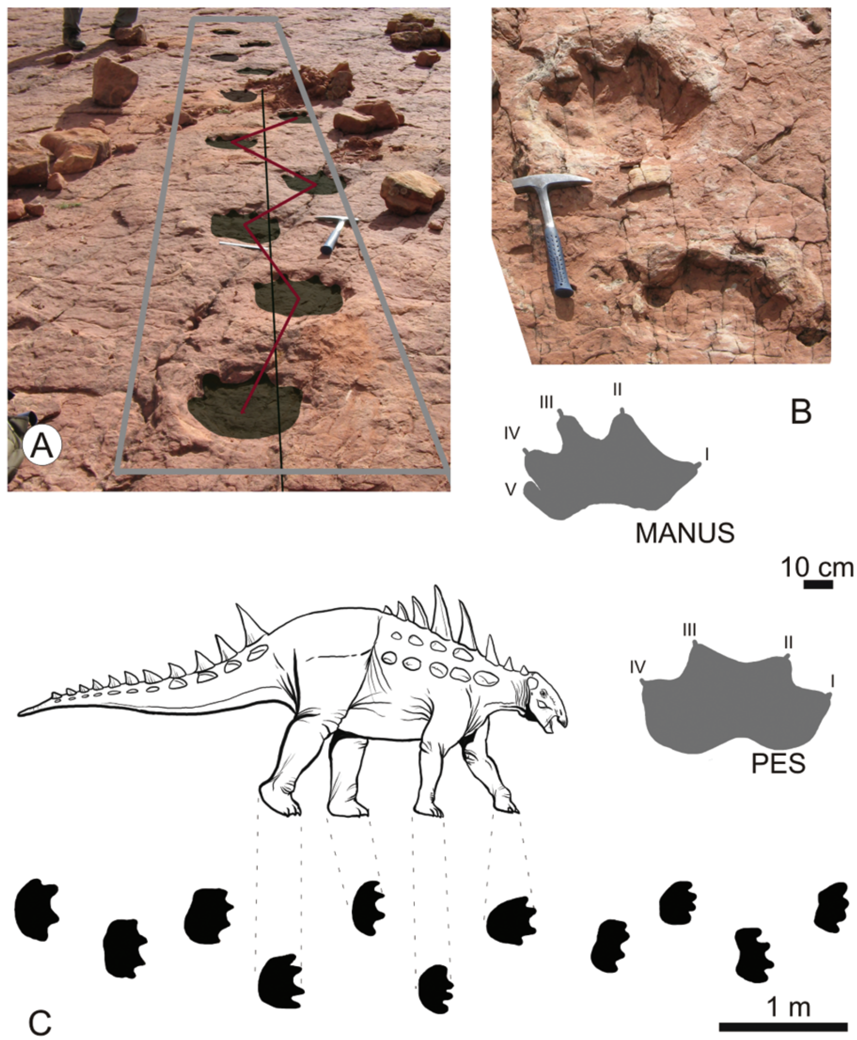

Fig. 4 – Ichnotaxon C. Trackway (A), isolated pes and manus of adult specimens in photograph (B up) and scheme (B down), detailed trackway scheme with distances preserved (C).

brucker et al. 2008), with an extremely wide inner digit, and the clearly tetradactyle footprints from the Early Jurassic of Morocco (Jenny and Jossen 1982, Type C) were already suggested to be related to stegosaur activity. Furthermore, the Australian tracks reported by Long (1998) show this more clearly, not having only an additional toe but also showing it in a position that seems to support sindactily between toes I and II (Scanlon 2006, Fig. 5D). Additionally, they share with the

In this sense, an interesting fact is that pes in purported stegosaurs, differing from iguanodonts, is asymmetrical, with the proximal pad located posterolaterally. In both ichnotaxa A and B, the symmetry axis of the footprints is between digits II and III. If A and B were made by a basal stegosaur, it is logical that secondarily tridactyl forms that reduced the digit I could have shown an asymmetrical tridactily, different from that of iguanodonts. Although derived stegosaurians present only three digits

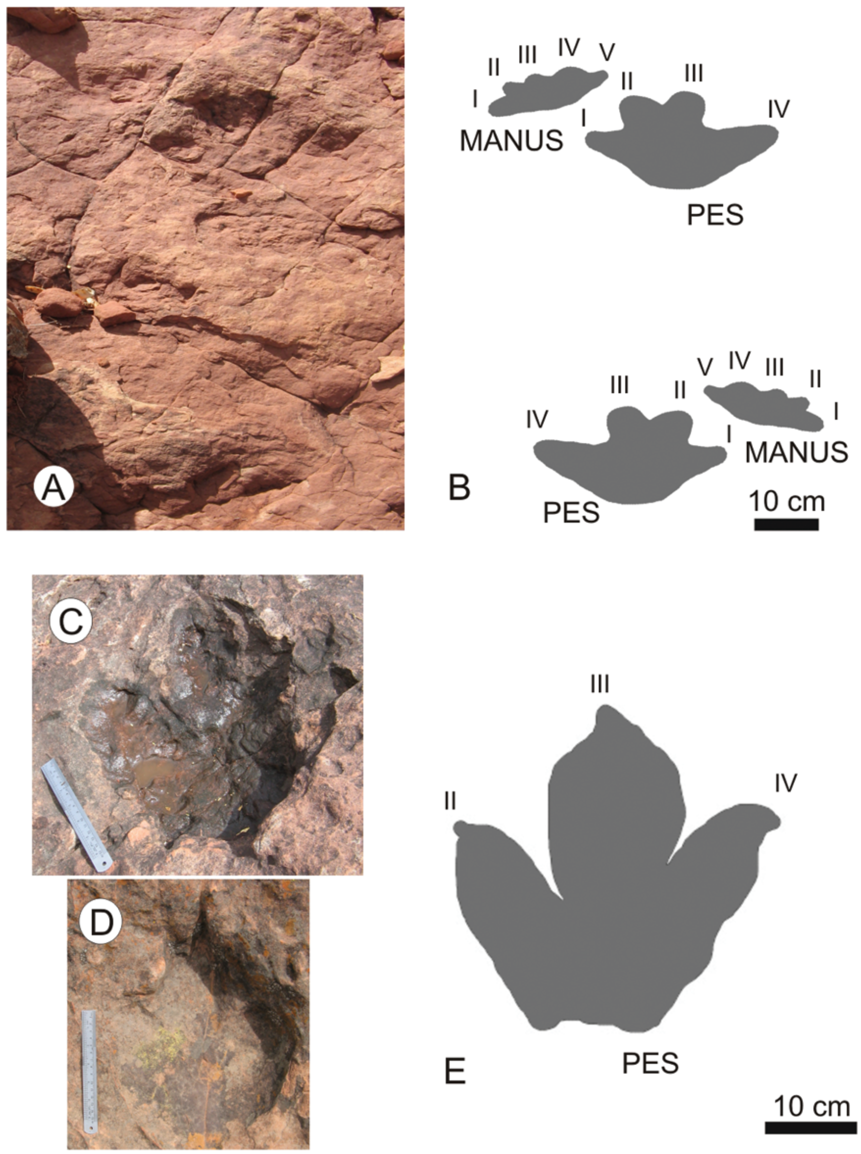

Fig. 5 – Ichnotaxon D. Trackway (A) and scheme with distances preserved (B). Ichnotaxon E. Track (C, D) and detailed scheme (E).

trackways (Lockley and Hunt 1998), the available material shows that, by the Early Cretaceous, only basal forms were present in South America (Bonaparte 1996). Basal stegosaurians are considered to have four pedal digits with a reduced digit I, as also regarded for the long-toed form *Tetrapodosaurus* (Sternberg 1932) considered as

Conversely, Laurasian forms as those from T Cliffs, Spain (Lires et al. 2002, García-Ramos 2004), with less asymmetrical pes, more crown- and with digits more similar in length than thos Utah (Gierlinski and Sabath 2008) and Poland, an derived, despite the older age. The material from creasing the pedal diversity of the group.

The strong heel of ichnotaxa A and B, a feature frequently cited as present in stegosaurian tracks, turns the track much longer than wide. This strong heel is also present in the short-toed ichnogenus *Navahopus* (Baird 1980) or *Apulosauripus* (Nicosia et al. 1999), considered as produced by possible ankylosaurians, and *Deltapodus* (Whyte and Romano 1994) from the Saltwick Formation, considered as stegosaurian in origin (Whyte and Romano 2001, Fig. 3), and supported by additional stegosaurian skeletal remains from the Late Jurassic of Asturias (Spain) (Lires et al 2002, García-Ramos et al. 2004). Gierlinsky and Sabath (2008) have considered that *Deltapodus* bears a sauropod-like aspect. However, we agree more with the stegosaurian interpretation of Whyte and Romano (2001).

The manus imprints of *Deltapodus* are also similar to those coming from the Tunasniyoj locality, with a manus short, wide and describing an arch. However, several differences preclude assigning the Bolivian material to that genus (e.g., well-defined digits, outward rotation, and digit one in the same line of others in the Tunasniyoj material).

The manus of ichnotaxa A and B differs from the Australian material described by Long (1998) mainly in the higher heteropody and in the presence of four instead of five digits in the former.

In sum, we suggest that ichnotaxa A and B were produced by a basal stegosaur trackmaker, based both in an anatomical correlation plus the temporal framework. These tyreophoran dinosaurs, highly specialized heteropodal quadrupeds, show a short trunk relative to the length of their hindlimbs. Additionally, their short forelimbs produce a peculiar movement when walking; this is translated in the tracks as an orientation of the manus outwards. The manus imprint in ichnotaxon A is entaxonic and tetradactyl.

Ichnotaxon C. The comparison of this ichnotaxon also suggests a tyreophoran trackmaker. Four digited feet are well developed in basal tyreophoran forms comparable to *Scelidosaurus* (Norman 2001) and *Polacanthus* (Blows 1987) (Fig. 4C). Ichnotaxon C is very similar mented, this is not the case of ichnotaxon C, in which footprints overlap manus prints in most trackways. In this way, a similar condition seems to be present in trackways attributed to ankylosaurs from the Late Cretaceous of Brazil (Huene 1931, Thulborn 1990). *Tetrapodosaurus* trackmakers were assigned as ankylosaurs or related (Thulborn 1990, Whyte and Romano 2001), or ceratopsians (Gierlinski and Sabath 2008). In the case of ichnotaxon C, the anatomical correlation and temporal framework are consistent with a trackmaker assignment as a basal tyreophoran, perhaps related to the ankylosaur lineage. As this group spread very early along the Mesozoic world, it is expected that unspecialized basal tyreophorans lived in South America.

Ichnotaxon D. Besides represented by only few tracks, its distinct morphology allows its assignment to the Ankylosauria, which is already known from the younger strata of Cal Orck'o, Sucre (McCrea et al. 2001), in the El Molino Formation and in Toro Toro, Potosí, in the Toro Toro Formation or in the lower member of the El Molino (Gayet et al. 1991). The latter includes the holotype of *Ligabueichnium bolivianum* Leonardi 1984, considered both as a Ceratopsia or an Ankylosauria. Unfortunately, they are badly preserved for comparisons. Considering the age of the bearing rocks, these tracks actually represent the older evidence of these dinosaurs for the Southern Hemisphere, even older than the Early Cretaceous *Minmi* from Australia (Molnar 1980).

Ichnotaxon E. The only tracks assigned here to theropod dinosaurs, so abundant in other assemblages (e.g., Lockley et al. 2002, Leonardi 1994, Rubilar-Rogers et al. 2008), are those represented by ichnotaxon E. However, they are quite unusual for the group. The tracks are extremely wide, and digits are petal-shaped, resembling ornithopod tracks. Therefore, the main reason for its assignment to Theropoda is mainly based on the terminal sharp claw marks.

The presence of large theropod dinosaurs in Late Jurassic to Early Cretaceous beds suggests the presence of large basal tetanurans like carcharodontosaurids and spinosaurids, as well as basal ceratosaurians, already re-

Limayichnus Calvo 1991, although assigned to huge ornithopods. Considering the evidence studied here, *Limayichnus* could also be related to large tetanurans like carcharodontosaurids, which are already known for the site (i.e., *Giganotosaurus carolinii* Coria and Salgado 1995). The presence of these theropods in Tunasniyoj is in agreement with the Early Cretaceous age of the site (Apesteguía 2002, Leanza et al. 2004), and different from the latest Cretaceous tracks of the El Molino Formation.

CONCLUSIONS

The discovery of a new well-preserved tracksite in horizons 73 million years older than all those previously known in Bolivia opens the possibility to acknowledge the different forms that lived towards the Jurassic-Cretaceous boundary and to explore how ichnofaunas evolved. As many researches demonstrated during the last years, several tetrapod lineages actually originated much earlier than expected, and long ghost lineages were proposed to explain their presences in Late Cretaceous outcrops, an aspect that highlights the importance of Late Jurassic-Early Cretaceous presences.

The presence of confirmed thyreophorans in Southern continents was proposed after the description of the Australian Early Cretaceous Broome Sandstone tracks (Hill et al. 1966) and later by osteological findings in South America (e.g., Bonaparte 1996, Coria and Salgado 2001), Africa (e.g., Hennig 1915) Antarctica (e.g., Gasparini et al. 1996), and New Zealand (e.g., Wiffen 1996).

The group is distinguishable in the tracksite record by their four to five short, hoof-like toes, different from the laterally reduced pattern seen in saurischians and ornithopods. Australian tracks show broad five-toed hands and narrower hind feet with three functional toes but up to four digits.

Other candidates for a similar kind of tracks, the neoceratopsians, are not considered as possible Gondwanan pre-Campanian inhabitors. Thus, the possible producers are reduced to scelidosaurs, early stegosaurs, or basal ankylosaurians. Despite stegosaurs were com-

tracks have only been described from Australia 1998). Their crescentic shape, five-fingered tracks and broad and notably heeled pes tracks ar acteristic of this group.

Considering that the Australian tracks and of Tunasniyoj share manus tracks with several (five) short and well-defined digits, no inward d pollex claw, and pes tracks broad and square in with a deep divarication in the case of the Bolivi terial, they were probably produced by stegosa longing to the same lineage, differing from the tri forms from the Jurassic of North America, as t *Deltapodus*.

Most of the track localities of South Amer represented in rocks from the uppermost Cret and older track assemblages display a poor to ate preservation, providing this discovery with bo poral and regional significance. The Tunasniyoj blage is the oldest dinosaur tracksite for Boliv includes the oldest known evidence assigned to losaurs and stegosaurs for South America.

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RESUMO

Neste estudo é relatado um conjunto magnificamente preservado de pistas de dinossauros representados por cinco táxons distintos, situado próximo à Vila de Icla, 100 quilômetros a sudeste do Sucre, Bolívia. Preservados em arenitos eólicos avermelhados do limite Jurássico-Cretáceo. Quatro formas geradoras foram identificadas na área, sendo três quadrúpedes e um bípede, todos com as pegadas com cerca de 35 cm de comprimento. Um dos quadrúpedes (trilhas tipos A e B) é representado por pelo menos seis indivíduos em dois grupos de três, com adultos e juvenis juntos. Os outros dois quadrúpedes (trilhas tipos C e D) são geradores de quatro trilhas, e um gerador bípede (trilha E), é representado por uma trilha. Os quatro icnotáxons representados em "Palmar de Tunasniyoj", podem provisoriamente ser atribuídos aos seguintes geradores: Icnotáxon A e B são atribuídos a estegossauros basais. Icnotáxon C a um tireóforo basal, talvez relacionado à linhagem dos anquilossauros. Icnotáxon D aos Ankylosauria; e icnotáxon E a Theropoda. Este raro e belo conjunto de trilhas de dinossauros de Tunasniyoj, representa ainda a icnocenose mais antiga de dinossauros da Bolívia. Além disso, inclui a mais antiga evidência conhecida atribuída a anquilossauros e estegossauros para América do sul.

Palavras-chave: Bolívia, Chuquisaca, pegadas de dinossauros, icnologia.

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