Asociación Paleontológica Argentina. Publicación Especial 7 ISSN 0328-347X
VII International Symposium on Mesozoic Terrestrial Ecosystems: 133-138. Buenos Aires, 30-6-2001

The Late Cretaceous vertebrate ichnofacies of Bolivia - facts and implications

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Abstract. Cretaceous dinosaur tracks are known in Central Bolivia since 1968. Recent work shows that tracksites are widespread and occur in multiple layers from the Campanian to the Late Maastrichtian. The ichnofauna is associated with alluvial to deltaic as well as lacustrine settings. Several new sites with tracks of titanosaurids and theropods in the upper part of the Chaunaca Formation (Campanian) correspond to similar stratigraphic levels in the Toro-Toro Formation further north. The Late Maastrichtian deposits yield a megatracksite that spreads from southern Peru (Vilquechico Formation) to the Central Bolivian Andes (El Molino Formation) down to the Salta province in northern Argentina (Yacoraite Formation). The ichnofauna of the El Molino Formation has been studied at the Cal Orcko locality, close to Sucre (Bolivia). The main trackbearing surface is a lacustrine limestone (25,000 m^2) which is steeply inclined (70°); it has been mapped with heavy climbing equipment in 1998. The trackbearing levels show episodic pedogenesis, stromatolites and tempestites and were deposited in ephemeral and perennial lakes. 313 trackways on nine levels have been registered. Five different types of dinosaurs are present. Among those are medium-sized titanosaurs, small to intermediate sized theropods and few ornithopods. For the first time, tracks of ankylosaurs on the South American continent can be demonstrated. The high diversity of the track assemblage clearly demonstrates that there was no gradual decline in dinosaur diversity towards the end of the Cretaceous and favours a drastic event at the K/T boundary.

Key words. Dinosaur tracks. Sedimentology. El Molino Formation. Maastrichtian. Paleoenvironment. Bolivia.

Introduction

Up to now only four dinosaur tracksites are known in Bolivia. The most important site is Toro-Toro (Departamiento Cochabamba; Leonardi, 1984); photographs have been published by Bonaparte *et al.* (1984: figs. 11-114). This site is about 2000 m^2 and displays sixty trackways of small theropods (FL: 25-30 cm), probable ceratopsians or ankylosaurs and eight sauropod trackways including two subadult individuals (*cf.* figure 4; wide gauge morhotype *sensu* Lockley *et al.*, 1994). Leonardi (1984) has shown that the Toro-Toro site yields a highly diverse track assemblage, not recorded anywhere in the world. Other sites like Parotani (Cochabamba), Arampampa (Potosi) and Camargo (Chuquisaca) have never been studied in detail. Apart form Leonardi's work (see 1984) only two detailed studies on vertebrate track localities are available at present. One is dealing with a recently discovered site near Sucre (Maragua syncline) reporting for the first time gregarious behaviour in Late Cretaceous sauropods (Lockley *et al.*, in press); the other report deals specifically with the occurrence and the comparison of ankylosaurs tracks in the Cretaceous (McCrea *et al.*, in press). We report here on the discovery of one of the largest dinosaur track locality from the Late Cretaceous of Bolivia. Initially, the site has been discovered by J.H. Heymann, a Bolivian geologist and Klaus Schuett (Sucre) in October 1994. In spring 1998 the senior author visited the locality to prepare the logistics for further study. The new site in the FANCESA quarry is close to Sucre (Departamiento Chuquisaca) and is the largest tracksite reported so far.

Geographical and geological setting

The Cal-Orcko syncline is situated approximatively 6 km w of Sucre (Departamiento Chuquisaca). FANCESA (Fabrica Nacional de Cementos) is operating a cement plant in an open pit mine operation extracting limestones (Loc.; S 19° 00′ 06.9″/W 65° 14′ 09.5″; 3080 a.m.s.l.). This activity created a 1.2 km long and up to 80 m high limestone surface, dipping with an average of 72° to the east (figure 1).

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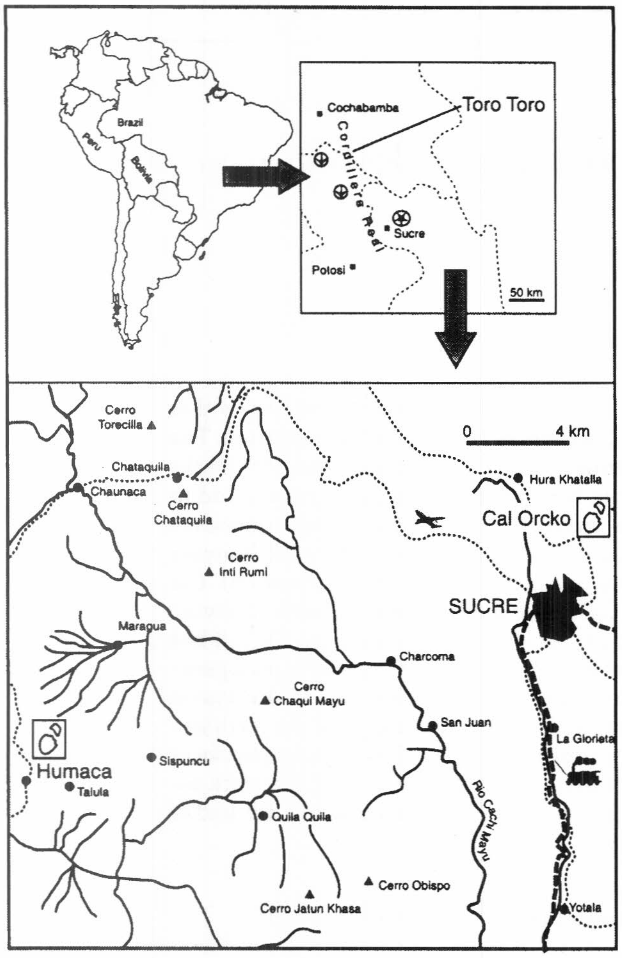

Figure 1. Geographic location of studied localities.

Furthermore the main tracklevel (figure 3, level 5) could not be used for concrete production because of its high content of quartz (35%).

Methods and material

The steeply inclined surface was first mapped with GPS receivers, then equipped with vertical measuring lines before detailed mapping with a Laser-Distometer started. The second step consisted in equipping the wall with a fine grid of static ropes with a mesh distance of 20 m by setting 350 spit pitons and using 1500 m of rope. Subsequently, all tracks and trackways were marked by chalk and individual measurements were taken directly in the wall conveyed to the base camp by walkie-talkies. In this manner, we produced in 6 weeks an accurate map of the trackways (1:100). The most important tracks and several trackways were casted with silicone. At the same time the section was logged and sampled for a detailed sedimentologic and stratigraphic study (Hippler, 2000).

Results

Sedimentology

At the Cal Orcko locality the El Molino Formation can be divided into two depositional cycles: the inner marginal lacustrine facies unit (IMLF) shows channel sandstones. Upsection alternating white/yellowish

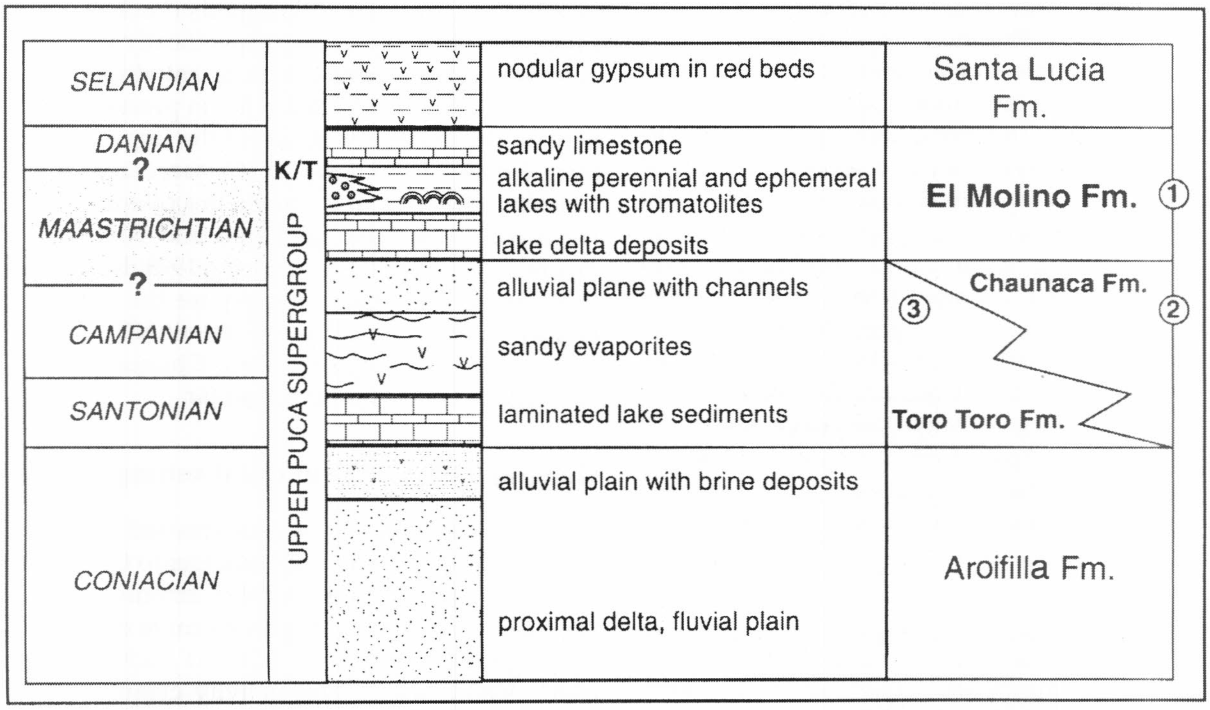

Figure 2. Litho- and chronostratigraphic context of study area: 1, Cal Orcko; 2, Humaca; 3, Toro Toro.

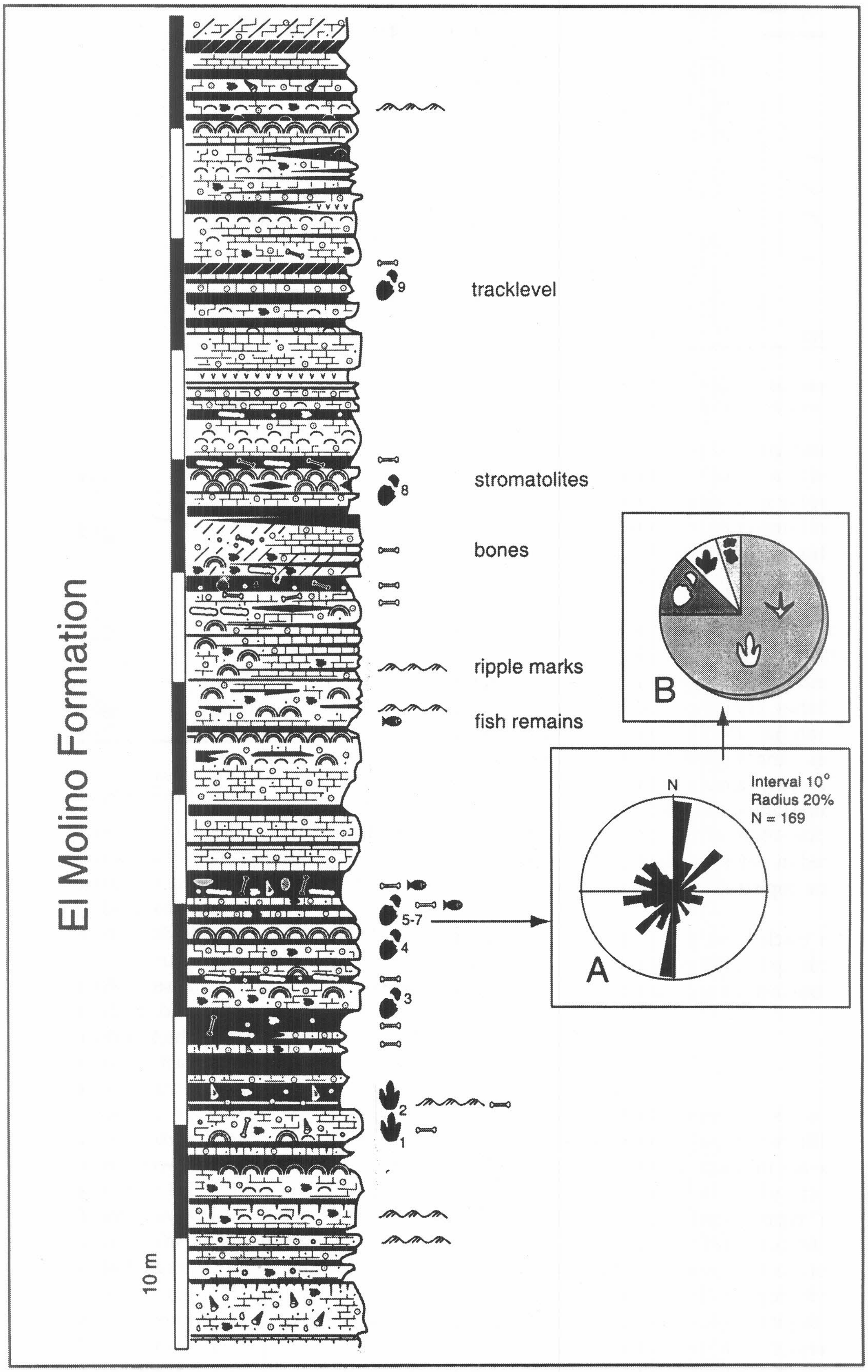

Figure 3. Part of the section at the Cal Orcko quarry showing dinosaur track levels and occurence of other vertebrate remains. **A,** rose diagramm of dinosaur trackways of level 5. **B,** ichnotaxonomic composition of tracklevel 5.

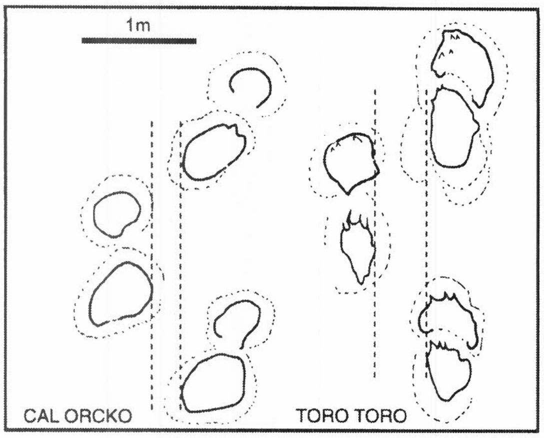

Figure 4. Comparison of sauropod trackways from Cal Orcko (Maastrichtian) and Toro Toro (Campanian).

sandstones and green claystones and oolithic sandy limestones with a steady increase in carbonate content; they display mud cracks, stromatolites, pedogenesis, contain intraclasts, various amounts of quartz, and ooids. This unit represents a deltaic environment at its base, followed by a shallow, ephemeral lacustrine facies.

The outer marginal lacustrine facies unit (OMLF) shows an alternation of thickly-bedded oolitic sandy limestones and green to grey calcareous claystones. Remains of fishes, characeans, ostracods, gastropods and plant material are common. Sometimes ostracods/bivalves -and coprolite- tempestites are present. Ripple marks, cross bedding and mud cracks, as well as stromatolites can be observed, the latter growing to diameters of up to 2 m. The OMLF has been deposited in perennial lakes, dry periods are indicated by the repeated passage of large number of dinosaurs.

The main track level (n° 5, figure 3) is a sandy limestone with up to 35% quartz, ooids (15%), sparitic cement, intraclasts, fragments of bones and biodetritus.

Ichnology

313 trackways on nine levels have been registered. Five different types of dinosaurs are present. Among those are medium-sized sauropod footprints forming spectacular trackways. They are of the "wide-gauge" type (*sensu* Lockley *et al.*, 1994) and are attributed to titanosaurid sauropods.

In addition to that we have mapped numerous trackways of theropods. There appear to be two morphologically distinct types: a small form (FL max. 25 cm) with slender well separated digits indicating speeds between 5 km/h up to 32 km/h and a larger form (FL max 45 cm) with blunt toes that gives maximal speeds of 11 km/h. In one instance a theropod trackway can be followed for more than 350 m representing the longest record so far known.

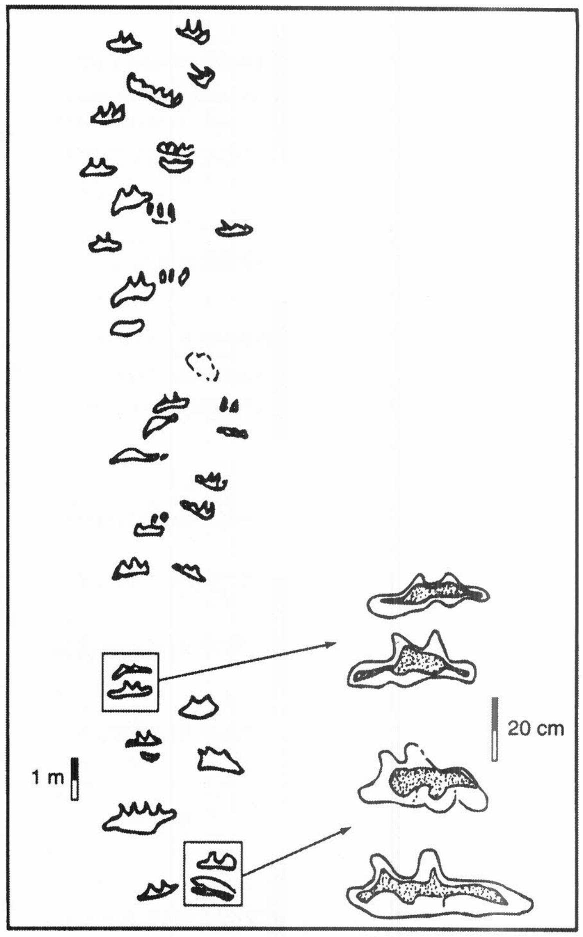

Figure 5. Trackway of an ankylosaur (n° T 4/5/1) from Cal Orcko (level 4) with inset of detailed morphology.

We have also revealed the presence of at least a half dozen tracks of ankylosaurid origin. It is outside the scope of this paper to describe these tracks in detail, as they are currently under investigation as part of a detailed study of this site (McCrea *et al.* in press). One reveals a long step and stride (1.5-1.65 m and 3.0 to 3.3 m respectively) which indicates an individual running or moving at a fast trot of between 11 and 12 km per hour, others give values of around 4 km/h.

46% of the trackways on level 5 were made by large theropods, small theropods make up 5.4%. A total of 34.5% trackways were made by sauropods whereas large ornithopods comprise 9.2% of the sample. 2.8% of the trackways come from ankylosaurs and 0.5% were made by small ornithopods.

The Humaca site is situated about 25 km WSW of Sucre (figure 1) and is only accessible by foot. Access to the site is not advisable without official authorization and a guide. The site was discovered by D. Keremba (Sucre) in 1995 and visited by our study group on two separate occasions in 1998. A preliminary study of the Humaca dinosaur tracksite (figures

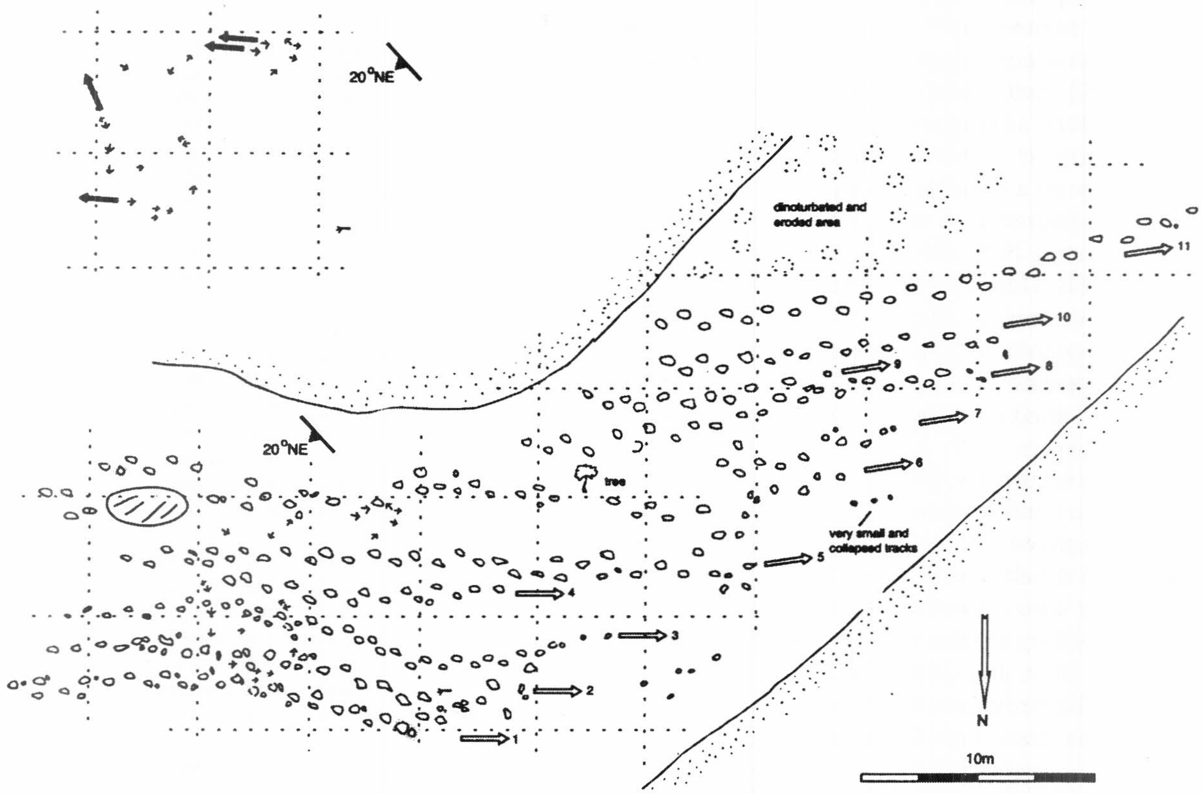

Figure 6. Map of the Humaca locality (see also figure 1) showing eleven parallel trackways of small sauropods and theropods (inset top).

1, 2, 6) reveals eleven parallel trackways of subadult sauropods traveling to the WNW as a group, whereas evidence from the nearby Cal Orcko site reveals more variable trackway orientation (figure 3) produced by larger individuals (Lockley *et al.*, in press). The tracks are found in silty sandstone with an average depth of 25 cm (figure 6) On the same surface trackways and isolated prints of small-sized theropods can be observed. However they are preserved as a thin crusty iron-oxid film with no trace of sediment deformation. This points to time averaging, e.g. the theropods walked on a higher surface that was subsequently removed by erosion (figure 6). This time averaging must be taken into account when interpreting the distribution and ecology of this site.

Conclusions

A first sedimentological analysis of the Maastrichtian El Molino Formation (Sucre, Bolivia) indicates a cyclic deposition throughout the lithostratigraphic unit. The sedimentation starts with an interbedding of fine-grained quartz- rich sandstones with ripple marks and thin mudstone layers that were deposited in an alluvial plain. Upsection a gradual change from these deposits into oolithic sandy lacustrine carbonates is recognized within the El Molino Formation. These latter sediments show episodic features of pedogenesis, shallow water sedimentation, stromatolitic layers and tempestites. When compared with published sections in the area (Potosi, Agua Clara; Sempere *et al.*, 1997, and Camoin *et al.*, 1997) the Cal Orcko outcrops seem to cover the lower and middle part of the El Molino Formation. The El Molino Formation itself has an extendcd fossil record, including charophytes, molluscs, selachians, actinopterygians, other fishes and lower vertebrates. Several of these fossils (charophytes, some selachians and actinopterygians, dinosaurs) indicate a Lata Campanian to Maastrichtian age. Palynology indicates a Maastrichtian age for the second sequencc of the El MolinoFormation (Sempere *et al.*, 1997).

The cyclic deposition of green marls with abundant gastropods that represent still water deposition and wave accumulated oolithic sandstones indicates fluctuations in the width of lacustrinc facies belts. However, whether these hydrologic changes reflect climatic oscillations or tectonic events remains to be solved. Sempere *et al.* (1997) indicate shortening along the margin and resumption of foreland subsidencc in the Potosi basin that could well account for the observed sedimentary cycles observed in the Sucre area.

Earlier ideas about the identity of wide-gauge trackmakers expressed by Lockley *et al.* (1994) is being those of titanosaurids, seems now to be confirmed by biomechanical evidence. Wilson and Carrano (1999) stated that saltasaurid titanosaurids show locomotory adaptations (e.g. eccentric femora) such as an angled femoral axis and beveled knee joints that require a broader footstance.

The rose diagrams of all trackways on level 5 show a preferred N-S orientation with a submaximum at NW-SE. This is in agreement with the orientation of interference ripples (NW-SE) and gastropods and points to a principal travel direction along the shoreline of the lake (figure 3). Further studies should shed more light on the true identity of other trackmakers such as the ornithopods and theropods. Nevertheless, the Cal Orcko site shows a recurrence of a similar ichnofacies at nine individual levels. The Humaca trackways are interpreted as evidence of social behavior among titanosaurids, also evident at the Toro Toro site and together represent the first compelling evidence of sauropod herding so far reported from the Late Cretaceous. All three Bolivia sites also provide useful evidence on the morphology of the titanosaurid manus, pes, and trackway gauge.

If the tracklevels from the Upper Vilquechico Group of southern Peru are indeed in the same stratigraphic position and sedimentary sequence then they are by definition part of the same megatracksite covering more than 100,000 km^2. If the tracksite in the Yacoraite Formation of northern Argentina (Quebrada de Escalera) forms part of the same recurrent track assemblage then the megatracksite comprises about 260,000 km^2.

Furthermore, the high diversity track-assemblage as demonstrated by the Cal Orcko and Toro Toro site indicates that there was no gradual decline in dinosaur diversity towards the end of the Cretacoous and favours a drastic event at the K/T bonndary.

Acknowledgements

Study of the Cal Orcko site, Bolivia, was made possible by the support of the Swiss National Science Foundation (Grant 21-52649.97) and the cooperation of the Fancesa cement quarry operators. The substantial support of the Cal Orcko research team (G. Leonardi, S. Bucher, J. Meyer, V. Spencer, A. Schulp, K. Graf, L. Cavin, F. Anaya and J. Salomon) helped considerably with the documentation of dinosaur tracks at this site. Thanks also to the help of the Sociedad Científica Universitaria de Paleontología for casting assistance. The sponsoring of the Senckenberg Museum (Frankfurt) and Arova-Mammut (Seon) is kindly acknowledged. Without the effort of Klaus Schuett (Sucre) and Jaime Ampuero (Zurich) this study would have been even more difficult.

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Accepted: January 17th, 2001.