

# The Maastrichtian–Danian Maimará tracksite (Yacoraite Formation, Salta Group), Quebrada de Humahuaca, Argentina: environments and ichnofacies implications

Carlos Cónsole-Gonella<sup>a,\*</sup>, Silvina de Valais<sup>b</sup>, Rosa A. Marquillas<sup>c</sup>, María Cristina Sánchez<sup>d</sup>

<sup>a</sup> Instituto Superior de Correlación Geológica (INSUGEO), Universidad Nacional de Tucumán – CONICET, Miguel Lillo 205, 4000 Tucumán, Argentina

<sup>b</sup> Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro – CONICET, Av. Roca 1242, General Roca 8332, Río Negro, Argentina

<sup>c</sup> Universidad Nacional de Salta – CONICET, Complejo Universitario Castañares, 4400 Salta, Argentina

<sup>d</sup> Instituto del Cenozoico INCE, Universidad Nacional de Salta, Complejo Universitario Castañares, 4400 Salta, Argentina

## ARTICLE INFO

### Article history:

Received 28 March 2016

Received in revised form 29 October 2016

Accepted 5 November 2016

Available online 15 November 2016

### Keywords:

Yacoraite Formation

Maastrichtian–Danian

Dinosaur and avian tracks

Lagoon shoreline

Playa lake

*Scoyenia* and *Skolithos* Ichnofacies

shorebird ichnosubfacies.

## ABSTRACT

The shoreline carbonate lagoon deposits of the Yacoraite Formation in the Maimará locality, Quebrada de Humahuaca (Jujuy, northwestern Argentina) reveal invertebrate and vertebrate trace fossils that are distributed in two distinct subenvironments: (A) the subtidal-lower intertidal zone (S-LI), a moderate/high energy shoreline under wave and tide action, and (B) the playa-lake zone (PL), a protected supratidal/eulittoral zone that characterizes low energy ephemeral bodies of water. In the S-LI zone there are three suites: I, composed of *Skolithos linearis* and dinosaur tracks (*Hadrosauropodus* isp., titanosaurian, ornithischian and theropod tracks); II, composed of monoichnospecific tiers with cf. *Taenidium* isp.; and III, constituted by abundant didactyl tracks maybe belonging to swimming tracemakers. The trace fossils of the PL zone are included in two suites: I, composed of *Lockeia siliquaria* and ?*Ptychoplasma* isp., and II, composed of *Palaeophycus tubularis* and *Planolites* cf. *montanus* with avian tracks (cf. *Alaripeda* isp.; *Avipeda* isp., cf. *Gruipeda* isp., cf. *Yacoraitichnus avis*) and indeterminate biped dinosaur tracks. The invertebrate trace fossils in both zones (S-LI and PL) display low ichnodiversity and are restricted to the shallow tier with substrate penetration of a few centimeters, which is characteristic of an unfavorable environment for the establishment of a permanent benthic community. Dinosaur tracks were preserved in an “optimal preservation area”, located in between both zones. The trace fossils of the S-LI zone are ascribed in general sense to the *Scoyenia* and *Skolithos* Ichnofacies. Following the current knowledge, the trace fossils of the PL zone are assigned to the shorebird ichnosubfacies, within the *Scoyenia* Ichnofacies.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

During the Late Cretaceous–Early Cenozoic chronostratigraphic lapse in the Central Andes, a series of extensional systems developed, generating epicontinental seas and very extensive lakes, in mixed carbonate-type clastic sequences (Uliana et al., 1988; Salfity and Zambrano, 1990; Hallam, 1991; Filho et al., 2000; Gayet et al., 2001; Marquillas et al., 2005, 2007, among others). In this geological context, the Yacoraite Formation represents a shallow epeiric system composed mainly of carbonates with varied depositional textures, with calcareous sandstones and pelites as major components in some of the proximal sections (Marquillas et al., 2005). Its palaeontological record is abundant but lacking in diversity, according to the interpretation of the

unit as part of an epeiric restricted sea (Marquillas et al., 2005, and references therein). The Yacoraite Formation is well known for the presence of dinosaur and avian tracks. The first mention of dinosaur tracks from this unit is from the Quebrada de la Escalera locality, Valle del Tonco, Salta province (Raskovsky, 1968); these tracks were subsequently reviewed by Alonso (1978, 1980). These and other ichnological contributions regarding specimens from Valle del Tonco are pioneering (Alonso, 1989; Alonso and Marquillas, 1986), originally describing five different vertebrate ichnotaxa, assigned to theropod (*Salfitichnus mentoor* Alonso and Marquillas, 1986), hadrosaurid (*Taponichnus donottoi* Alonso and Marquillas, 1986 and *Hadrosaurichnus australis* Alonso, 1980), ornithopod dinosaurs (*Telosichnus saltensis* Alonso and Marquillas, 1986), and avian tracks (*Yacoraitichnus avis* Alonso and Marquillas, 1986). Marquillas et al. (2003) subsequently described a new record of hadrosaurian footprints from Río Juramento, while Sánchez Rioja (2004) named *Acherlichnus leonardii* from the Quebrada del Acher, Alemania, all of them from the Salta province. Marquillas et al. (2011) have claimed that the Yacoraite Formation is homologous

\* Corresponding author.

E-mail addresses: [carlosconsole@csnat.unt.edu.ar](mailto:carlosconsole@csnat.unt.edu.ar) (C. Cónsole-Gonella), [sdevalais@yahoo.com.ar](mailto:sdevalais@yahoo.com.ar) (S. de Valais), [rosamarquillas@gmail.com](mailto:rosamarquillas@gmail.com) (R.A. Marquillas), [msanchez@unsa.edu.ar](mailto:msanchez@unsa.edu.ar) (M.C. Sánchez).

both chronologically and regarding facies with other units from the Central Andes, such as: a- El Molino Formation, Puca Group, Bolivia (Leanza, 1969; Reyes, 1972; Sempere et al., 1997); b- Vilquechico Formation, southern Peru (Jaillard et al., 1993); c- Estratos de Quebrada Blanca de Poquis, northern Chile, near the frontier with Argentina (Salfity et al., 1985); and d- Pirity basin, Chaco Occidental, Paraguay (Argentine stratigraphical nomenclature is followed; Clebsch, 1991). On the basis of the vertebrate ichnological record, there is an important correlation with the Bolivian deposits in the areas of Parotani (Santa Lucía Formation, Upper Maastrichtian), where trackways of large bipeds have been presented (Leonardi, 1981); and with the localities of Toro Toro (Toro Toro Formation, Santonian?–Maastrichtian), Potosí; Cal Ork'O (El Molino Formation, Maastrichtian–Danian), and Humaca (Chaunaca Formation, Campanian?–Maastrichtian), both in Sucre, where diverse dinosaur tracks have also been described (Leonardi, 1984; Meyer et al., 2001; Lockley et al., 2002). Trotter (1964) and Jaillard et al. (1993) have recognized dinosaur tracks from the Vilquechico area, in Peru (Vilquechico Formation, Upper Cretaceous), but did not study them in great depth. Recently, Cónsole-Gonella and colleagues (Cónsole-Gonella and Aceñolaza, 2009, 2010; Cónsole-Gonella et al., 2012a, 2012b, 2013; Díaz-Martínez et al., 2016) presented vertebrate and invertebrate trace fossil associations from the Yacoraite Formation in Maimará locality, allowing expansion of the ichnological knowledge in this area.

The comprehensive analysis of mixed suites, formed by vertebrate and invertebrate trace fossils, is an interesting approach to addressing such carbonatic/clastic environments. This kind of work has recently advanced, having already been applied successfully in carbonatic/clastic marine shoreline environments, among others, by Kvale et al. (2001) and Pazos et al. (2012); in fluvial systems and/or lacustrine environments by Melchor et al. (2006), de Gibert and Sáez (2009), Krapovickas et al. (2009) and Voigt et al. (2013); and inclusive in fluvial-eolian environments by Krapovickas et al. (2010). On the basis of the

current state of the art, it is suggestive the treatment of such a kind of mixed suites, regarding the expansion of the continental ichnofacies model. The continental distribution of ichnofacies is mostly independent from the proximo-distal type bathymetric relations, although there are some exceptions, such as the ichnoassemblages in lacustrine systems, reflecting the response of organisms to different environmental factors (MacEachern et al., 2012). In addition, Maimará trace fossils are an interesting study case in regard to the relatively new vertebrate ichnofacies model (after Lockley et al., 1994) that received a dissimilar consideration from the scientific community (see reviews in Hunt and Lucas, 2007, 2016; Lockley, 2007; Santi and Nicosia, 2008; Buatois and Mángano, 2011; MacEachern et al., 2012, among others).

The aims of this contribution are: (1) to document the distribution of invertebrate and vertebrate trace fossils from the Yacoraite Formation in the Maimará locality, Jujuy province, Argentina, (2) to evaluate their interpretation in a palaeoenvironmental and palaeobiological context, and (3) to discuss the significance of this record in the context of the continental ichnofacies model.

## 2. Geological setting

The origin and evolution of the rift-type basin of the Salta Group (Early Cretaceous–Eocene) is linked to a tectonic regional context of extensional type in northwest Argentina (Marquillas et al., 2011). This regional context is common in the basins of similar age to the Central Andes and nearby regions, from the latitude of the Titicaca Lake in Bolivia (16° S) to the north of Sierras Pampeanas in Argentina (26° S) (Marquillas et al., 2011). The sediments of the Salta Group were accumulated in seven sub-basins or fossae surrounding the Salta-Jujuy high: Tres Cruces, Lomas de Olmedo, Metán, Alemania (Reyes, 1972; Salfity, 1982), El Rey (Salfity, 1980), Sey (Schwab, 1984) and Brealito (Sabino, 2002) (Fig. 1). The Balbuena Subgroup (Late Cretaceous–Early Paleocene) is the early post-rift deposit of the Salta Group, and

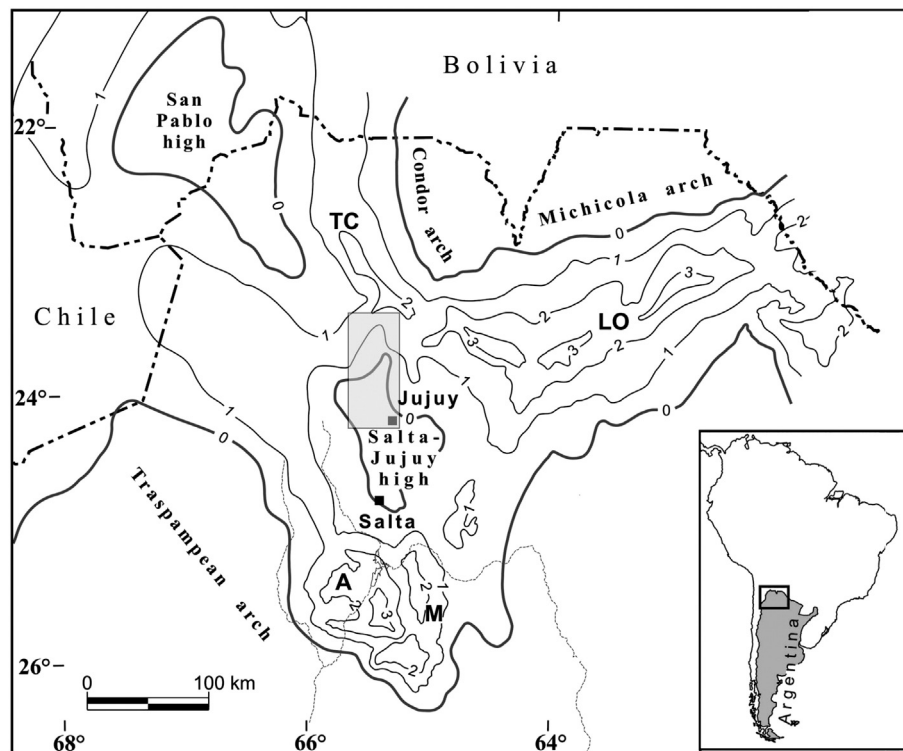


Fig. 1. Isopach map of the Yacoraite Formation. Main sub-basins: TC, Tres Cruces; LO, Lomas de Olmedo; A, Alemania; M, Metán. Thickness in hundreds of meters (after Marquillas et al., 2005). Inset: location of the study area at Tres Cruces sub-basin.

the Yacoraite Formation is the middle unit of this subgroup (see Marquillas et al., 2005, and references therein).

Given that the Yacoraite Formation is Maastrichtian–Danian in age (Marquillas, 1985), the Cretaceous–Paleogene boundary occurred during its accumulation. The formation contains Cretaceous dinosaur tracks (Alonso and Marquillas, 1986; Díaz-Martínez et al., 2016) and Maastrichtian and Danian palynomorphs (Moroni, 1984). Also, U–Pb dating in the Metán sub-basin (Salta province) is indicative of a Maastrichtian age (Marquillas et al., 2011). However, dated strata are located several meters below the top of the unit (Marquillas et al., 2011). The overlying Tunal Formation (Danian, Paleocene) contains the palynomorph *Mtchedlishvilia saltenia* Moroni, 1984, which defines a palynozone of Danian age (Quattrocchio et al., 2000).

Sial et al. (2001) have identified the K–Pg transition in the Maimará locality, although unfortunately the paper not provides the detailed position of the stratigraphic section. However, the most parsimonious approach is that dinosaur trampled surfaces of the Maimará section (Fig. 4) belong to Maastrichtian levels.

### 2.1. Stratigraphy: the Maimará section

The study area corresponds to the eastern side of the Quebrada de Humahuaca (23°37'30.92" S, 65°23'56.07" W), Jujuy province (Figs. 2 and 3), and paleogeographically, to the austral sector of the Tres Cruces sub-basin (Fig. 1). This position is near the Salta–Jujuy ridge, which confers basin edge features on the deposit, distinguishing it from the austral sectors of the Salta Group basin (Fig. 1). In Tumbaya Grande, approximately 10 km to the south of Maimará, Sánchez and Marquillas (2010) established the presence of the complete stratigraphic column of the Salta Group, though with smaller thicknesses than in austral sectors of the basin, such as the Metán and Alemania sub-basins. However, the Pirgua Subgroup is not represented in the Maimará section. In Maimará the deposits of the Balbuena Subgroup (Maastrichtian–Danian) lie unconformably above the quartz sandstones of the Mesón Group (Middle–Upper Cambrian) (Fig. 3). It is not possible to distinguish the Lecho Formation s.s. and only the lower section, with a dominant clastic component, can be attributed to it. This unit is composed of a fining-upward succession of matrix supported conglomerates and coarse to fine sandstones (Figs. 4 and 13). The clasts of conglomerates are angular and poorly sorted, product of debris flows in an environment with sparse water supply, probably alluvial fans (Díaz-Martínez et al., 2016). The Lecho Formation is overlain transitionally by the Yacoraite Formation (see Section 3).

### 3. Materials and methods

Most of the vertebrate and invertebrate trace fossils are recorded in three trace-bearing surfaces (Fig. 4). In some areas, track density is so high that individual footprints are difficult to distinguish, while in others there is no overprint and preservation quality is good to moderate.

Main levels and trampled surfaces were sampled for petrographic studies. For lithofacies analysis and definitions, we follow the criteria by Dunham (1962) and Flügel (2004) for carbonate rocks, Logan (1961) and Logan et al. (1964) for stromatolite-bearing beds, and Reineck et al. (1990) for petee structures.

Regarding the ichnological record, many of the vertebrate tracks from the Maimará locality have been mentioned and/or briefly described previously (Alonso, 2007; Cónsole-Gonella and Aceñolaza, 2009, 2010; Cónsole-Gonella et al., 2012a, 2012b, 2013), but only a few of them have been properly analyzed (Díaz-Martínez et al., 2016). Herein, both previously mentioned and unpublished ichnotaxa are dealt with.

There is one slab (PIL 16.100) housed in the INSUGEO collection (Instituto Superior de Correlación Geológica), San Miguel de Tucumán (Argentina). The holotype of *Yacoraitichmus avis* is a single slab housed

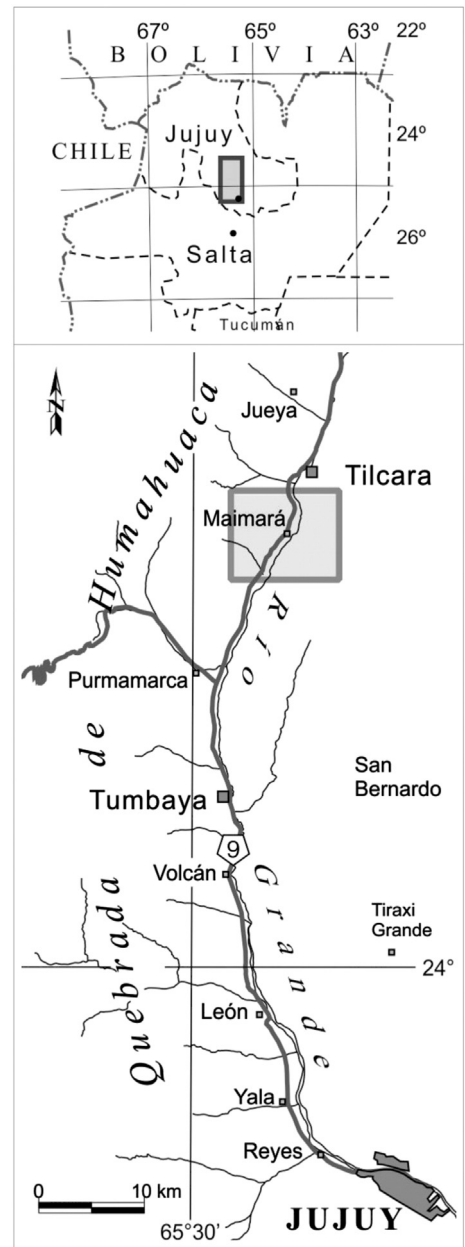


Fig. 2. Map of the Quebrada de Humahuaca, Jujuy province, Argentina, South America, showing the location of the Maimará section at the region of the Tres Cruces sub-basin (gray rectangle in the upper inset).

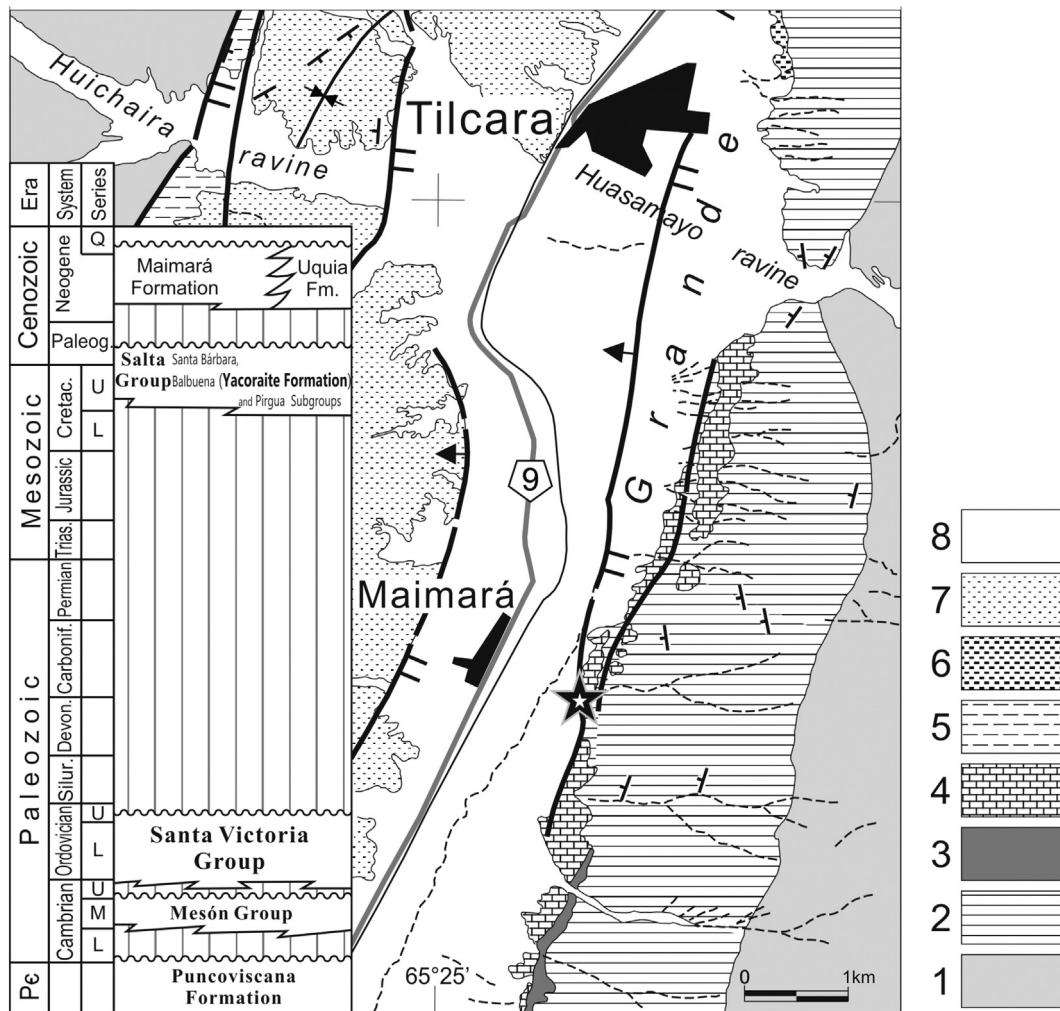
in the Departamento de Paleontología of the Universidad Nacional de Salta, Salta province, Argentina, with no formal number assigned.

Criteria for description and interpretation of trace fossils follow Bromley (1981), Bertling et al. (2006) and Rindsberg (2012). Ichnotaxonomic assignment of the invertebrate and vertebrate trace fossils is based on careful examination of the relevant literature. When available material is scarce or poorly preserved and lacking in morphological detail, it has been left in open nomenclature.

The ichnofacies analysis follow Buatois and Mángano (2011) and MacEachern et al. (2012). The archetypal ichnofacies are spelled capitalized and italicized following MacEachern et al. (2012).

### 4. Facies and facies assemblages

The integrated section is 45 m thick (Fig. 4). The deposits of the Yacoraite Formation correspond to a lagoon-type littoral system. It is



**Fig. 3.** Geological setting and stratigraphy of the study area. 1: Puncoviscana Formation (Upper Precambrian–Lower Cambrian). 2: Mesón Group (Middle–Upper Cambrian). 3: Ordovician? 4: Balbuena Subgroup (Lecho and Yacoraita formations; Maastrichtian–Danian). 5, 6: Maimará and Uquiá formations (Neogene). 7, 8: Quaternary. The star indicates the ichnofossiliferous locality.

composed of well-stratified fossiliferous limestones and calcareous sandstones with thin intercalations of laminate pelite and levels of stromatolitic limestones. The facies are indicative of high and low energy, and are described below. A summary of facies, facies assemblages and fossil content is provided in Table 1.

#### 4.1. Oolitic grainstone

##### 4.1.1. Description

Oolitic facies dominate in the middle and upper parts of the Yacoraita Formation. Yellowish-white oolitic limestones with some dark pelite intercalations attain a maximum thickness of 1.5 m. The layers are very regularly packed. It is host rock for isolated *Bonarelliella* and *Percosmannella* gastropods, which have affinity with the family Cerithiidae Fleming, 1822 (Cónsole-Gonella et al., 2012b). The teleconch ornamental features are well preserved, although with different degrees of fragmentation. Microscopically, the rocks are oolitic grainstones with microsparitic and micritic-microsparitic ooids (Fig. 5a–d). The ooids are spherical, concentric and radial-concentric with mainly detrital nuclei, with different sizes, but predominantly 1.5 mm in diameter. There may be ostracod fragments and micritic intraclasts among them. Some ooids are cerebroid; others are compound with two nuclei. Porosity is obliterated by sparite and some anhydrite and gypsum.

##### 4.1.2. Interpretation

The presence of well-sorted ooids in this facies suggests a high-energy subaqueous, wave-agitated coastal environment associated to shallow migratory ooids banks. The presence of gypsum, anhydrite and cerebroid ooids suggests periods of hypersalinity (Wigforss-Lange, 2007) during which the water body was hydrologically closed, or periods of climate change during which evaporation exceeded water entry due to autocyclic processes. This is also suggested by the alternation with micritic layers.

#### 4.2. Wackestone-packstone

##### 4.2.1. Description

The main trampled surfaces are represented in this facies (Figs. 7 and 8). The rocks are yellowish due to weathering, but fresh sections are whitish. There are entire and broken ostracods, and minuscule micritic (microsparitic) ooids (Fig. 5e–g). This facies contains vertebrate tracks (*Hadrosauropodus*, theropod, titanosaur and ornithischian tracks, and indeterminate didactyl tracks, see Fig. 11a,b,c,e,f,g,h), and invertebrate trace fossils (*Skolithos linearis*, cf. *Taenidium* isp., Fig. 9d,e,f,g). The thickness of the layers is in the order of decimeters. Strata show low angle laminar cross-stratification.



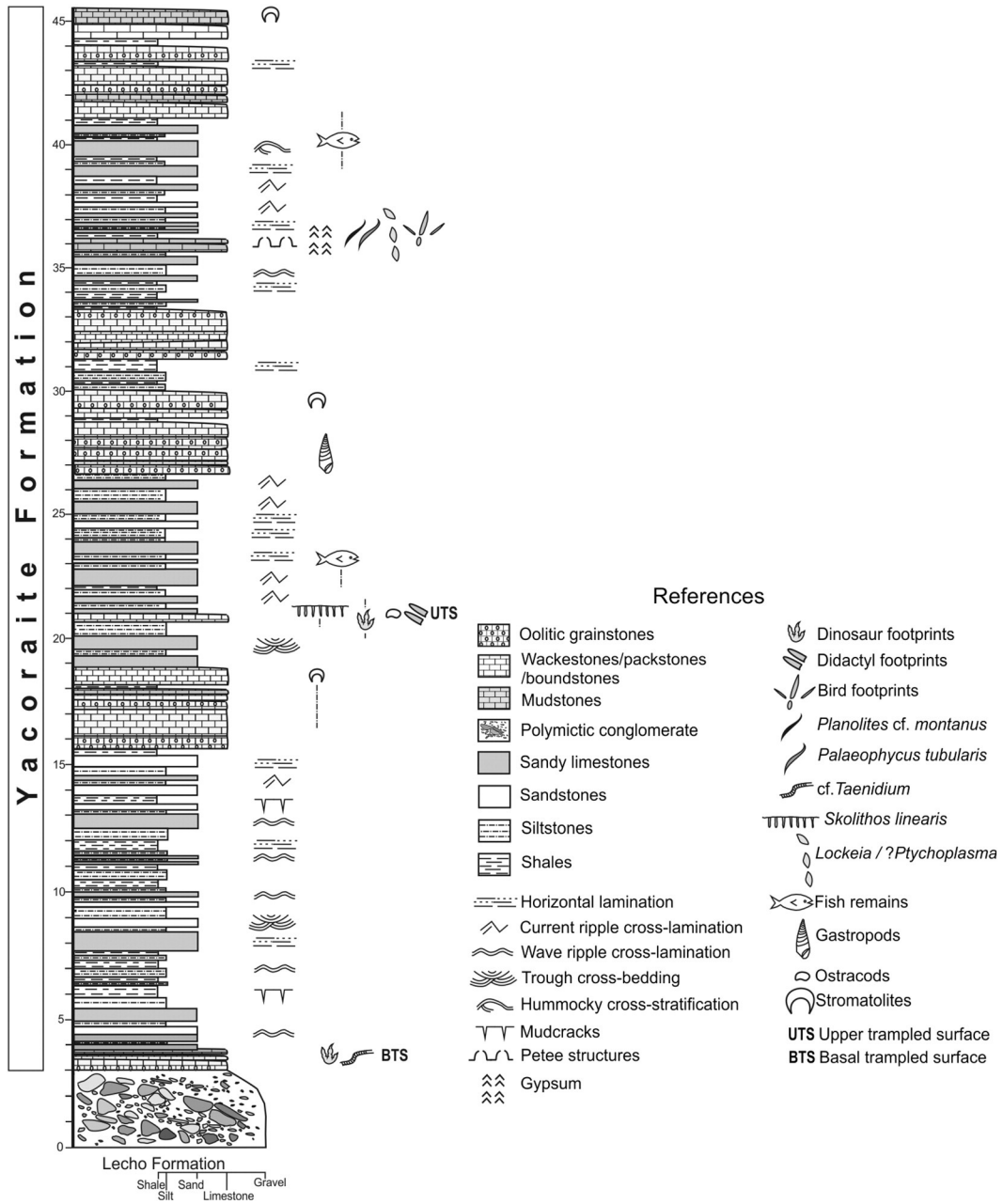
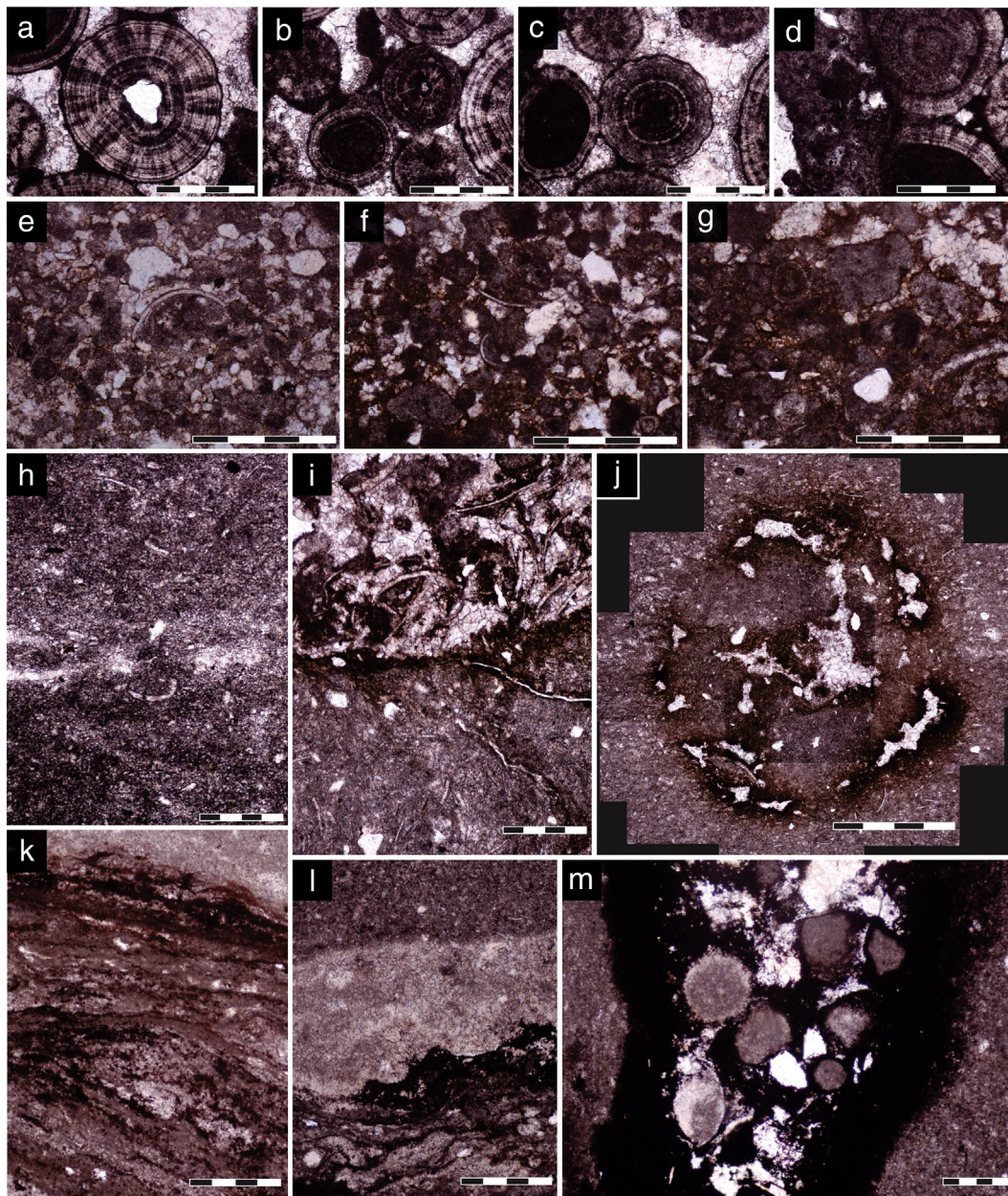


Fig. 4. Integrated logged section and track-bearing strata in the Maimará section, Tres Cruces sub-basin.

Table 1  
Facies, facies assemblages and fossil/ichnofossil record from the Maimará tracksite.

Facies associations	Sedimentary facies	Body fossils	Trace fossils	
			Invertebrate	Vertebrate
A – Subtidal-lower intertidal zone (S-LI)	1) Oolitic grainstone	<i>Bonarelliella</i> and <i>Percossmannella</i> gastropods	<i>Skolithos linearis</i> and cf. <i>Taenidium</i>	<i>Hadrosauropodus</i> isp.; theropod, titanosaur and ornithischian tracks; indeterminate didactyl tracks
	2) Wackestone-packstone			
	3) Stromatolitic boundstone	Ostracods indet. and bone fragments		
	4) Calcareous siltstones and sandstones	Fish remains: Pycnodontiformes, Siluriformes and ?Semionotiformes		
B – Playa-lake zone (PL)	1) Mudstones–Petee structures	Indet. ostracods	<i>Planolites cf. montanus</i> , <i>Palaeophycus tubularis</i> , <i>Lockeia siliquaria</i> and ? <i>Ptychoplasma</i> isp.	Indeterminate biped dinosaur and avian tracks (cf. <i>Alaripeda</i> isp., cf. <i>Gruipeda</i> isp., <i>Avipeda</i> isp. and cf. <i>Yacoraitichnus avis</i> )



**Fig. 5.** Photographs of petrographic slides. a–d: Oolitic grainstones with microsparitic and micritic-microsparitic ooids. Note ooids with cerebroid-type morphology. Porosity is obliterated by sparite and some anhydrite and gypsum. e–g: Bioclastic-peloidal wackestone-packstone. Note entire and broken ostracods. h–j: Mudstones interlaminated with bioclastic wackestones. Note in j a transverse section of *Palaeophycus* isp. with mucus lining. The fill is composed of a packstone with pellets, ostracods and sparite, with traces of hematite. k–m: Stromatolitic boundstone. Note wavy lumpy micritic lamination in two directions. Note in m an eroded surface filled with ooids and ostracods; and also micaceous micrite filling. Scale bar: 1 mm in a–d and m, 2 mm in e–g and j, h and i, 4 mm in k and l.

#### 4.2.2. Interpretation

This facies is interpreted to have been produced in a moderate- to high-energy shoreline environment subject to wave agitation. It suggests water in movement and a soft ground on which tracks have been preserved. Subaerial exposure may be related to variations in tides, and probably wind action (Kvale et al., 2001; Pazos et al., 2012), although the tracks may have been preserved in the presence of a film of water. Sparite patches indicate obliterated porosity.

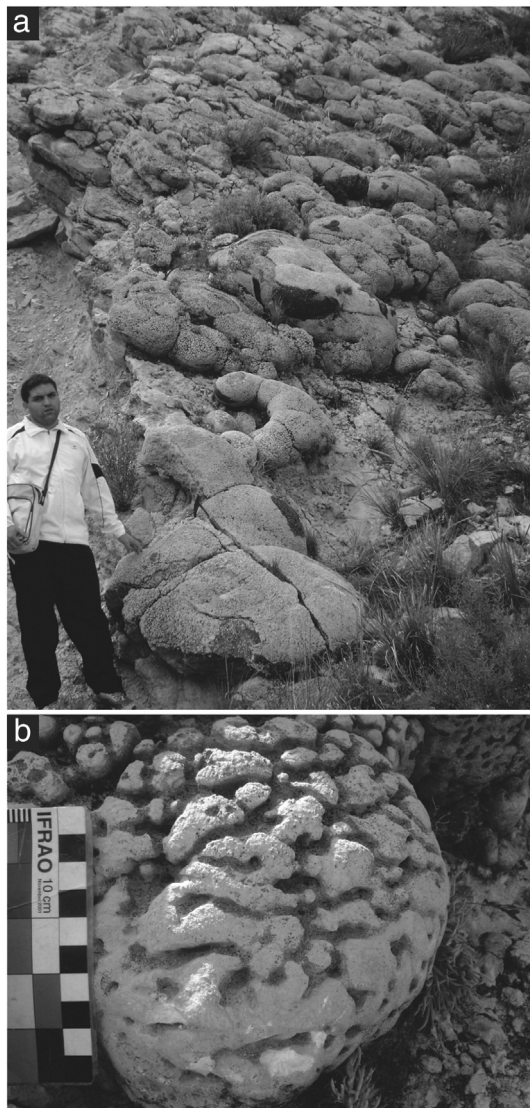
#### 4.3. Mudstones–Petee structures

##### 4.3.1. Description

The rocks integrating this facies are bioturbated mudstones, interlaminated with bioclastic wackestones (Fig. 5h–j). There are

levels with isolated light-colored detrital fragments, with some sparite. Gypsum (diagenetic or original) obliterates cavities. The rocks are laminar or massive rocks, with desiccation cracks and intercalated thin lenses of fine sandstone. In the outcrops, this facies is characterized by grays, light and dark greens, and dark yellow colours. There are abundant, although not diverse, invertebrate trace fossils (*Planolites* cf. *montanus*, *Palaeophycus tubularis*, *Lockeia siliquaria* and ?*Ptychoplasma* isp.; Fig. 9a,b,c), indeterminate biped dinosaur tracks (Fig. 11d), and avian tracks (cf. *Alaripeda* isp., cf. *Gruipeda* isp., *Avipeda* isp. and cf. *Yacoraitichnus avis*; Fig. 10). *Palaeophycus* has filling of packstone with pellets, ostracods and sparite, with hematite (Fig. 5j). Petee-type structures (sensu Gavish et al., 1985) are frequent (Fig. 12). These are cylindrical/sub-cylindrical sedimentary structures, preserved as convex





**Fig. 6.** a: Some stromatolite facies views at Maimará section. b: Surface view of a stromatolite dome.

epirelief that join together forming a 3-dimensional branching system covering the bedding plane (Fig. 12). The petee structure average diameter is 3 cm, with walls (sensu Assereto and Kendall, 1977) 0.5 to 1 cm thick. Wall lithology is a bioclastic mudstone-packstone. Petee structures have a filling made up of ooids, in a matrix of coarser texture than the host rock, an oolitic wackestone-packstone (Fig. 12). In bedding plane view, the meeting points of the polygonal structures are t-shaped and y-shaped.

#### 4.3.2. Interpretation

This facies suggests an intertidal environment with areas proximal to and more distant from the coastline, where sedimentation was controlled by alternating transportation by traction and suspension. The areas distant from the coastline lack bioturbation structures, whereas the closer mudflat areas have intense bioturbation, although discrete trace fossils are rare. The abundance of petee structures suggests the establishment of coherent microbial mats in the mudflat area, substrate stabilization and subsequent decay (Gehling, 1999; Catuneanu, 2006). Petee structures are common in intertidal and lower supratidal environments (Reineck et al., 1990). The process by which these petee structures are formed has been described in detail by Reineck et al. (1990). Growth expansion and the gas pressure from buried

decaying mats produces buckling of the mats, with sinuous and polygonal surface patterns (Gehling, 1999). These structures, given their complex morphology, as mentioned above, were previously assigned to the ichnogenus *Thalassinoides* by Cónsole-Gonella and Aceñolaza (2010).

An increase in energy conditions is suggested by the oolitic filling of the petee structures. The presence of gypsum may be related to retreat of the water body and subsequent evaporation (Reineck et al., 1990).

#### 4.4. Stromatolitic boundstone

##### 4.4.1. Description

Five stages of stromatolitic facies can be distinguished (Fig. 6). For descriptive purposes we have generally followed the stromatolites classifications by Logan (1961) and Logan et al. (1964). In the first stage, stromatolites are in relation to siltstones, and are mainly matlike in structure extending over large areas, and less frequently hemispheroidal domes with an average height of 17 cm, variably spaced (types LLH-S and LLH-C sensu Logan et al., 1964). In the second stage, stromatolites are type LLH-S domes (sensu Logan et al., 1964). They are better developed than in the first cycle; they cover smaller surface areas, with an average height of 40 cm. The third cycle begins with an erosive surface that truncates the second cycle and has produced oolite-filled surface cavities. Ooids show little size selection, with an average diameter of 1.2 mm. A matlike stromatolitic develops over these, which is more homogeneous, and in which domes are not defined, whose thickness is variable, ranging from 5 to 35 cm. The fourth cycle begins after a second erosive surface, immediately over a pelite layer. It is also matlike, of regular thickness, averaging 30 cm. Isolated and penecontemporaneous to the fourth cycle, there are oblate to semicircular stromatolites, type SS-I (spheroid structures, sensu Logan et al., 1964), with a maximum thickness of 43 cm. In a transverse section view, some stromatolites show lamination in two directions around a nucleus of sold micrite (Fig. 5k-m). The fifth cycle is the most highly developed, composed of laterally joined hemispheroids (LLH-C), whose shape on the surface varies from semicircular to semi-oval. The set forms a “stromatolite reef” very similar to the one observed by Logan (1961). In some sectors the surface is distinctively colored by iron oxide, and some surface areas have cracks that are circular or elongated in bedding plane view. Some stromatolites have cerebriform-type surfaces (Fig. 6). The domed stromatolites of the fifth cycle develop on wackestones, constituted from the base, by alternating wavy lumpy micritic and containing organic matter laminae (Fig. 5k-m). There is an eroded surface filled with oolites of various sizes at the base, with an average diameter of 1.5 mm, and also laminate micaceous micrite filling (Fig. 5m). There are few detrital fragments in the laminae, gypsum, sparite, and lumps of micrite and presence of fragments and also entire indeterminate ostracods. There are also some indeterminate bone fragments in the filling.

##### 4.4.2. Interpretation

The first stromatolitic cycle, which has matlike morphology, is interpreted as a sector with higher energy and lower accommodation space (Jahnert and Collins, 2012), closer to the shoreline, with a shallower water body, although in areas protected from direct wave action. Similar morphologies have been observed in current protected marine environments at the limit between the supratidal and intertidal zone of Hamelin Pool, Shark Bay, Australia (e.g., Logan, 1961; Jahnert and Collins, 2011, 2012), in Castle Roads, Bermuda (e.g., Gebelein, 1969), and even in lakes subject to tides, as in Socompa Lake, Northwestern Argentina (Farías et al., 2011). The development of extensive matlike surfaces may be due to limited accommodation space. Greater wave energy, and consequently greater transportation of particles in the stromatolite-water interface, may be a limiting factor in the vertical development of stromatolites (Andres and Reid, 2006).

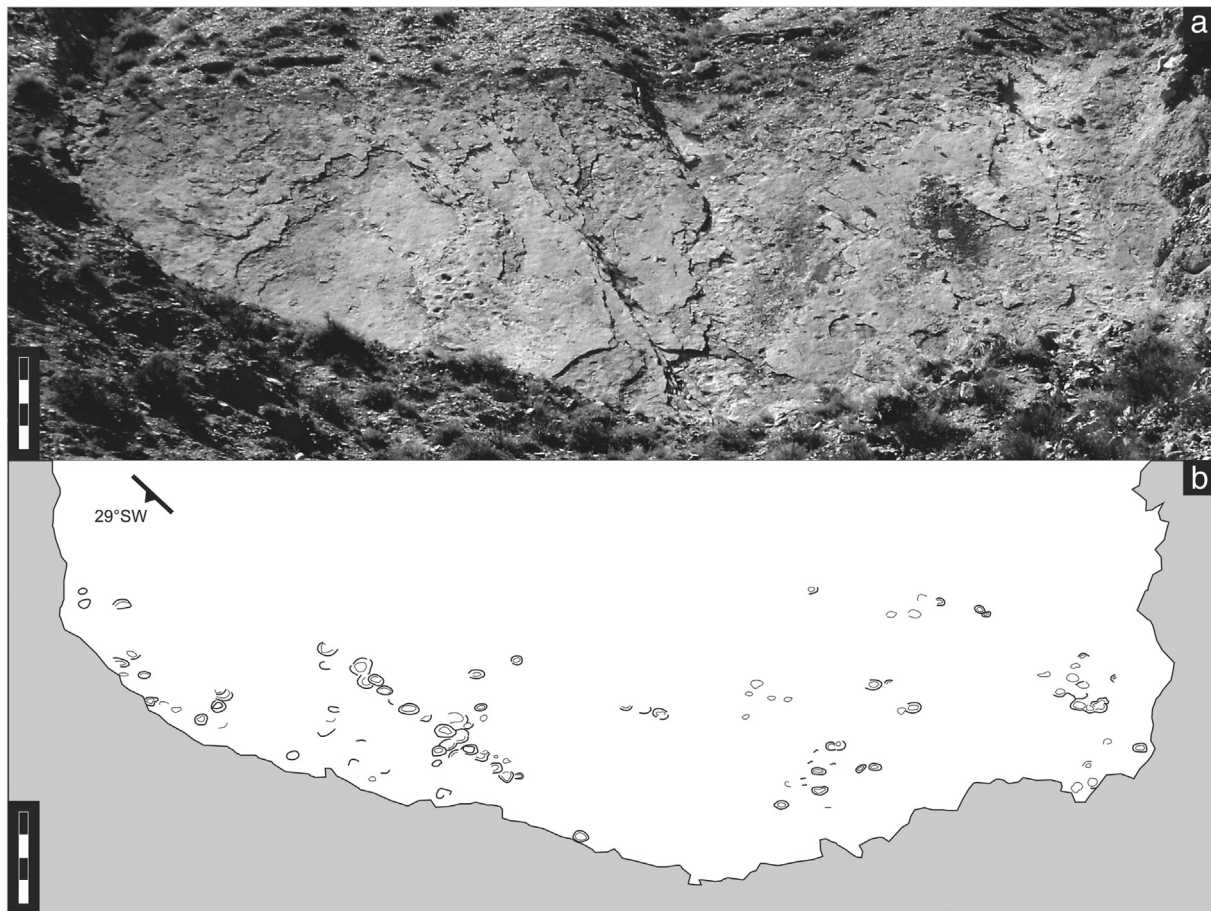


Fig. 7. a: Basal trampled surface at Maimará section. b: Distribution map of footprints. Scale bar: 2 m.

The second cycle suggests an increase in depth, which provided accommodation space for greater development of lamination, enabling the establishment of more height LLH-C domes, as observed in other cases (e.g., Andres and Reid, 2006; Kah et al., 2006). This also explains the increase in upward convexity of stromatolites, which is at least partly due to reduced abrasion at topographic maxima (sensu Bosac et al., 2013). The presence of an erosion surface that truncates the second cycle is interpreted as a withdrawal of the water body, which exposed stromatolitic domes to erosion by wave action, explaining the presence of oolitic material filling cavities.

The third and fourth cycle, with matlike morphology, probably also developed in shallower protected zones, at places where detrital/oolitic contribution was lower but there was not enough accommodation space for the development of domes, as has been observed in analogous modern cases (see review in Kah et al., 2006).

The fifth cycle develops after an erosive surface, which might record another withdrawal of the water body, consistent with the presence of gypsum.

The SS-I type structures, which are biconvex, occur due to dome tops breaking and falling into the growing base. If adequate conditions become reestablished, the stromatolite begins to grow again, this time with inverted convexity (sensu Logan et al., 1964).

#### 4.5. Calcareous siltstones and sandstones

##### 4.5.1. Description

In outcrop, the rocks of this facies are yellowish to gray, and reddish through weathering. It is composed of fine to silty sandstones and siltstones, with intercalations of gypsum. The siltstones

are mainly homogeneous and massive. Among the most frequent sedimentary structures, sandstones have parallel lamination, cross-lamination, and less frequently, symmetrical wavy lamination. There are frequent levels with *Skolithos linearis* (Fig. 9d,e). Towards the upper levels of the section, there are hummocky-type cross-stratification and abundant disarticulated fish remains: Pycnodontiformes, Siluriformes and ?Semionotiformes (Cónsole-Gonella et al., 2012b).

##### 4.5.2. Interpretation

This facies suggests the lower zone of the tidal flat, dominated by transportation of the sand and silt bed from the continent, with currents where the wave oscillations are dominant. These features suggest that the early part of the section may have been dominated by intertidal activity in fair weather conditions. The presence of evaporites may indicate migration to supratidal conditions (e.g., Shinn, 1983).

The hummocky cross-stratification structures (HCS) of the upper part of the section are interpreted here as a change in the conditions as result of storms in a shallow water deposit, and do not imply deepening, as have been recorded in several lacustrine and lagoonal deposits (e.g., Van Dijk et al., 1978; Hobday, 1978; Duke, 1984, 1985; Eyles and Clark, 1986; Fairchild and Herrington, 1989; Donato et al., 2009). The HCS structures are common in the Yacoraite Formation, mostly in the lower and middle parts of the unit (see Marquillas et al., 2005). Similar storm deposits have been recognized in the homologous Bolivian El Molino Formation (Maastrichtian–Paleocene) by Fink (2002). The exhumation of fish remains has been produced probably as result of storm events.



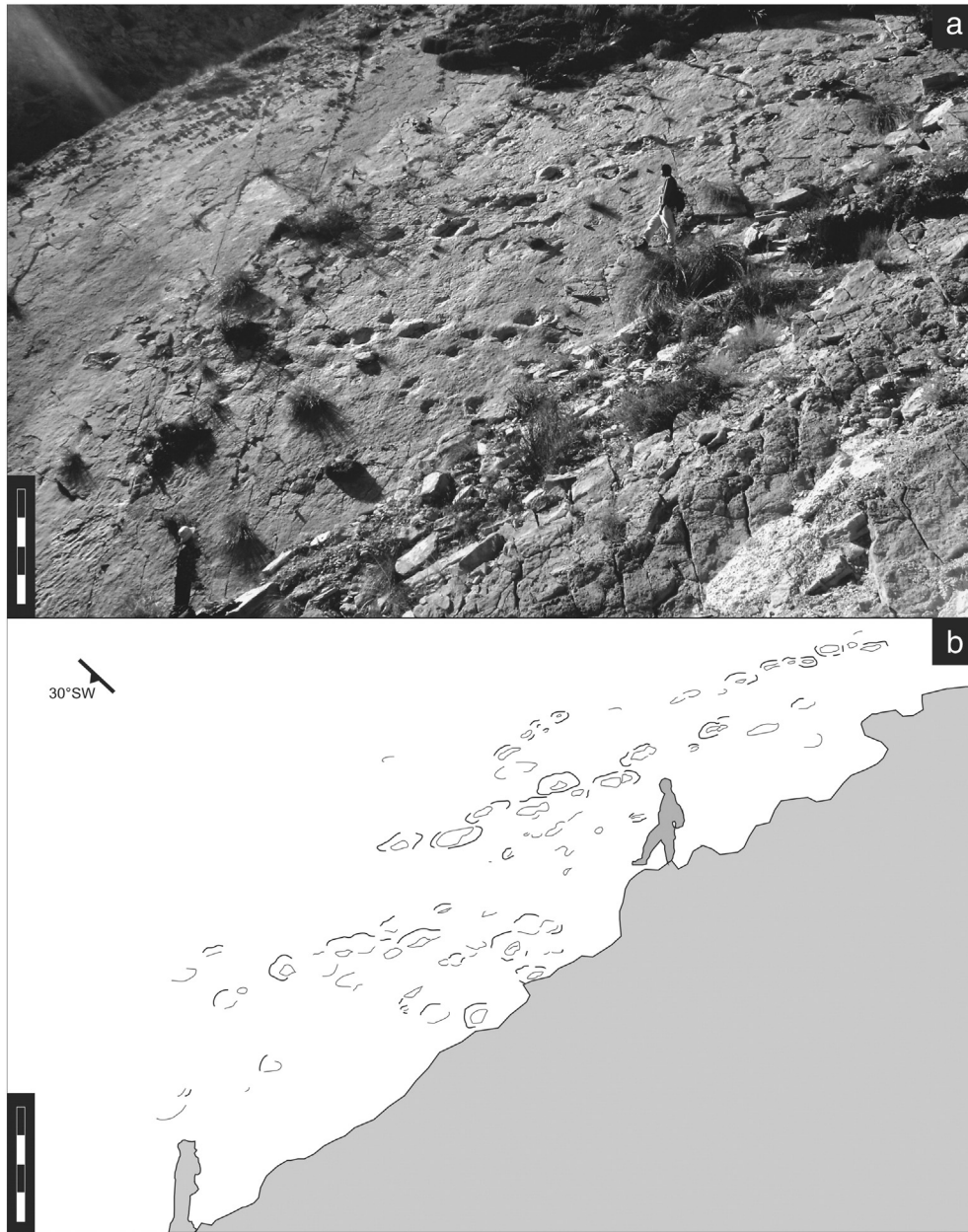


Fig. 8. a: Upper trampled surface at Maimará section. b: Distribution map of footprints. Scale bar: 2 m.

These facies are colonized by burrowers (suspension feeders mostly), which take advantage of short-term colonization windows.

## 5. Invertebrate trace fossils

### 5.1. Ichnogenus *Lockeia* James, 1879

#### 5.1.1. Remarks

The first interpretation of *Lockeia* was made by James (1879) who considered it as the activity of an alga. *Lockeia* is an ichnogenus of small, almond-shaped, oblong bodies preserved as convex hyporelief, tapering to sharp and obtuse points at both ends (Häntzschel, 1975). General consensus is that it is a resting trace of burrowing pelecypods (e.g., Seilacher, 1953; Osgood, 1970; Häntzschel, 1975; Vossler and Pemberton, 1988; Kim, 1994; Mángano et al., 1998). It is generally

associated to the bivalve locomotion trace *Protovirgularia* (e.g., Seilacher and Seilacher, 1994; Mángano et al., 1998; Ekdale and Bromley, 2001).

### 5.1.2. Ichnospecies *Lockeia siliquaria* James, 1879

**5.1.2.1. Description.** Abundant specimens with almond or amygdaloid shaped structures, mostly asymmetric, preserved as convex hyporelief, with smooth surfaces (Fig. 9a). Terminal angles of each structure range from acute to slightly obtuse. Sizes range from 0.3 to 0.6 cm wide and 0.4 to 0.8 cm long. Vertical spreite is not observed.

**5.1.2.2. Remarks.** The amendment on the definition of this ichnospecies by Schlirf et al. (2001) is followed. Schlirf et al. (2001) consider that *L. amygdaloides* (Seilacher, 1953), *L. avalonensis* Fillion and Pickerill, 1990, and *L. triangulichnus* Kim, 1994 are junior synonyms of *L.*

*siliquaria*; and *L. elongate* (Yang, 1984) and *L. serialis* Seilacher and Seilacher, 1994 are considered as *nomen nudum*.

## 5.2. Ichnogenus *Palaeophycus* Hall, 1847

### 5.2.1. Remarks

*Palaeophycus* is composed of cylindrical burrows, but distinguished from *Planolites* because *Palaeophycus* has a wall lining, which is lacking in the latter (Keighley and Pickerill, 1995).

### 5.2.2. Ichnospecies *Palaeophycus tubularis* Hall, 1847

**5.2.2.1. Description.** Several specimens composed of small burrows, preserved mainly as positive epireliefs (Figs. 5j, 9b). The arrangement of traces is mainly parallel to the stratification surface. Bedding plane view ranges from almost straight to curved or slightly meandering. Margins are sharp with circular to ovoidal sections. Maximum length of 8 cm, with 0.4 cm of maximum diameter; in thin section the structure is almost circular (Fig. 5j). In some portions of the course, collapse structures are observed. Lining is of mucus, partly replaced with sparite. Filling of structures consist of a packstone, with micrite and sparite, pellets and a few ostracod fragments.

**5.2.2.2. Remarks.** *P. tubularis* is the type ichnospecies. Here, we follow the proposals of Pemberton and Frey (1982) and Keighley and Pickerill (1995) on ichnotaxonomy.

## 5.3. Ichnogenus *Planolites* Nicholson, 1873

### 5.3.1. Remarks

We follow the proposal of Keighley and Pickerill (1995). *Palaeophycus* is distinguished from *Planolites* by the presence of a burrow lining.

### 5.3.2. Ichnospecies *Planolites* cf. *montanus* Richter, 1937

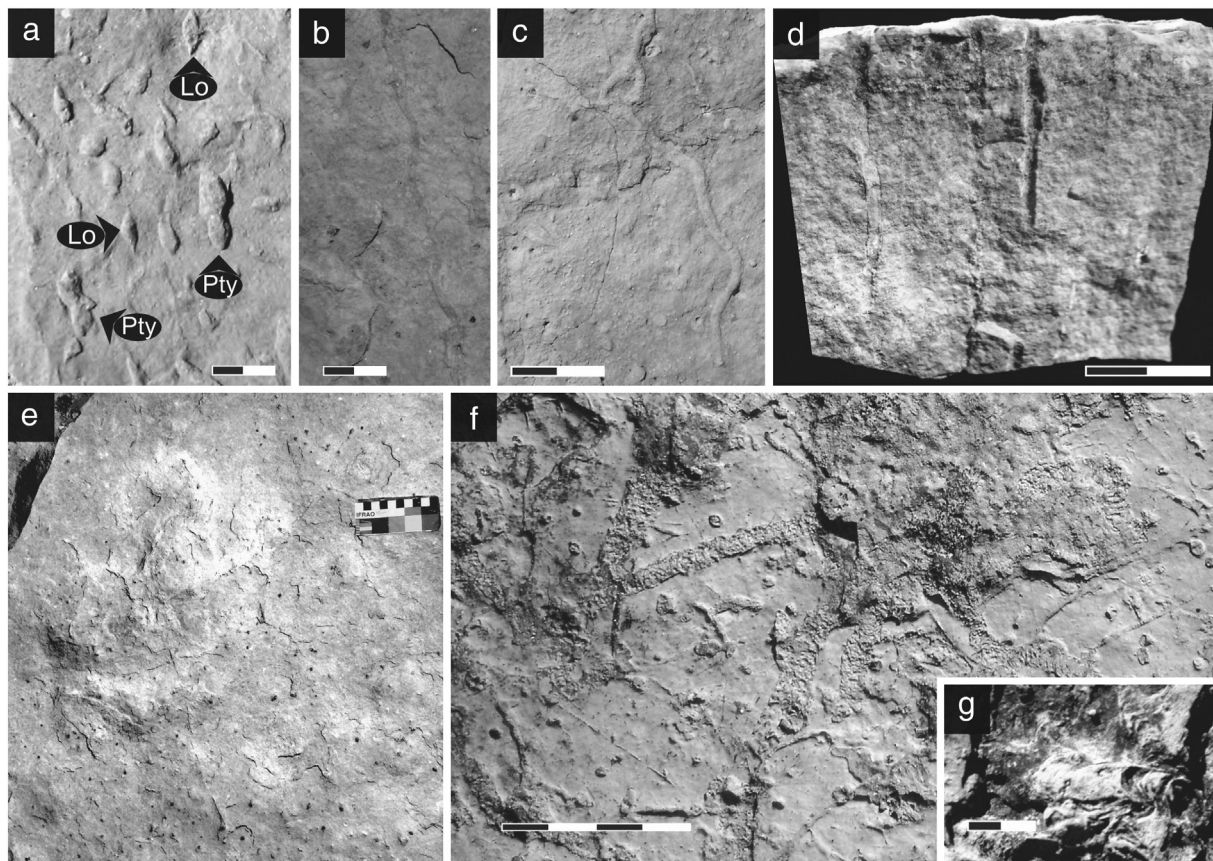
**5.3.2.1. Description.** Several specimens represented by small burrows as continuous structures, without wall or lining, primarily parallel to bedding or slightly inclined to vertical (Fig. 9c). Structures are preserved mainly as positive epireliefs, with circular cross-sections. Orientation in bedding plane view is straight to curved. Margins are sharp or slightly disturbed. Secondary successive branching is present (sensu D'Alessandro and Bromley, 1987). Length is more or less constant along the course, with a maximum of 8 cm, and a maximum diameter of 0.4 cm. Texture of fill is structureless and finer than host rock.

**5.3.2.2. Remarks.** We follow on ichnotaxonomy the proposal of Pemberton and Frey (1982), and subsequent amendments by Keighley and Pickerill (1995). *P. montanus* is shorter, more curved and tortuous than *P. beverleyensis* (sensu Pemberton and Frey, 1982).

## 5.4. Ichnogenus *Ptychoplasma* Fenton and Fenton, 1937

### 5.4.1. Remarks

Uchman et al. (2011) reviewed this ichnogenus in detail, reporting that *Ptychoplasma* differs from *Oravaichnium* Plička and Uhrová, 1990 because the shape of the latter is wall-like dominated, with only



**Fig. 9.** Invertebrate trace fossils. a: *Lockeia siliquaria* and ?*Ptychoplasma* isp. preserved as positive hyporelief. b: *Palaeophycus tubularis* preserved as positive epirelief. c: *Planolites* cf. *montanus* preserved as positive epirelief. d: *Skolithos linearis* in cross section. e: *Skolithos* isp. in plain view with an indeterminate tridactyl undertrack. f, g: cf. *Taenidium* isp. Scale bar: 2 cm in a–d and g, 10 cm in e, and 4 cm in f.



sporadic amygdaloid segments. *Ptychoplasma* is interpreted as the movement trace of non-cleft wedge-foot bivalves, and can thus be considered the “repichnion form” of the related ichnogenus *Lockeia* (after Uchman et al., 2011).

#### 5.4.2. ?*Ptychoplasma* isp.

**5.4.2.1. Description.** Specimens continuous as amygdaloid or almond-shape ridges, preserved as convex hyporeliefs (Fig. 9a). Each structure overlapped by the next. Ridge surfaces are smooth.

**5.4.2.2. Remarks.** These specimens are comparable to *Ptychoplasma*, in particular to *P. excelsum*, which includes amygdaloid bodies that overlap or are welded together in a mostly continuous series (Uchman et al., 2011). However, due to the discontinuity of the specimens, this assignment is dubious.

#### 5.5. Ichnogenus *Skolithos* (Haldeman, 1840)

##### 5.5.1. Remarks

*Skolithos* is characterized as straight vertical to slightly inclined cylindrical parallel tube burrows, with smooth and structureless fill walls (Alpert, 1974; Fillion and Pickerill, 1990). Specimens are very common in many types of environments, both marine (e.g., Cornish, 1986; Mac Eachern et al., 2007) and continental (e.g., Buatois and Mángano, 1998, 2004; Netto, 2007).

##### 5.5.2. Ichnospecies *Skolithos linearis* (Haldeman, 1840)

**5.5.2.1. Description.** Several (burrow density about 7–8 per dm<sup>2</sup>) vertical to subvertical burrows in field and a hand specimen (PIL 16.100; Fig. 9d,e). The burrows are circular in cross section with a diameter of 2 to 4 mm; the length ranges between 30 and 80 mm. In cross-section, some structures are slightly sinusoidal, although most are mainly straight, and the diameter is regular along the structure, with minor reductions. The fill is fine-grained and lighter-colored than host rock (Fig. 9d).

**5.5.2.2. Remarks.** Some apparently paired structures observed in bedding plane, have been previously assigned to *Arenicolites* and *Diplocraterion* (Cónsole-Gonella and Aceñolaza, 2009, 2010). However due to lacking of appropriate preservation in cross-section these assignments are dubious. Minimum vertical changes in diameter might indicate adjustment to different sedimentation rates (Melchor et al., 2006).

#### 5.6. Ichnogenus *Taenidium* Heer, 1887

##### 5.6.1. Remarks

The recommendations of Frey et al. (1984), D'Alessandro and Bromley (1987) and Keighley and Pickerill (1994) are followed. *Taenidium* is simple, unbranched and unwallled, or “thinly lined” (after D'Alessandro and Bromley, 1987). *Taenidium* differs from *Ancorichnus* because the latter has a wall. *Beaconites* can be referred as a junior synonym of *Taenidium*, although *Beaconites* ichnospecies can be distinguished by variations within the meniscate backfill, thus the ichnogenus *Beaconites* is maintained (sensu D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994).

##### 5.6.2. cf. *Taenidium* isp.

**5.6.2.1. Description.** Several specimens preserved as positive epireliefs, with circular to ovoid cross sections (Fig. 9f,g). They are small unlined and unwallled burrows with poorly preserved meniscate backfilling, primarily parallel to bedding or slightly inclined to almost vertical, with a maximum diameter up to 7 mm. In bedding plane view, structures are not bifurcated; straight to slightly curved, although false branching is frequent. Width is more or less constant along the course, with a maximum length of 74 mm. The margins are disturbed. The grain size of menisci are variable between specimens.

**5.6.2.2. Remarks.** These specimens are comparable to *Taenidium*, but this assignment is dubious because of the faintly meniscate fill.

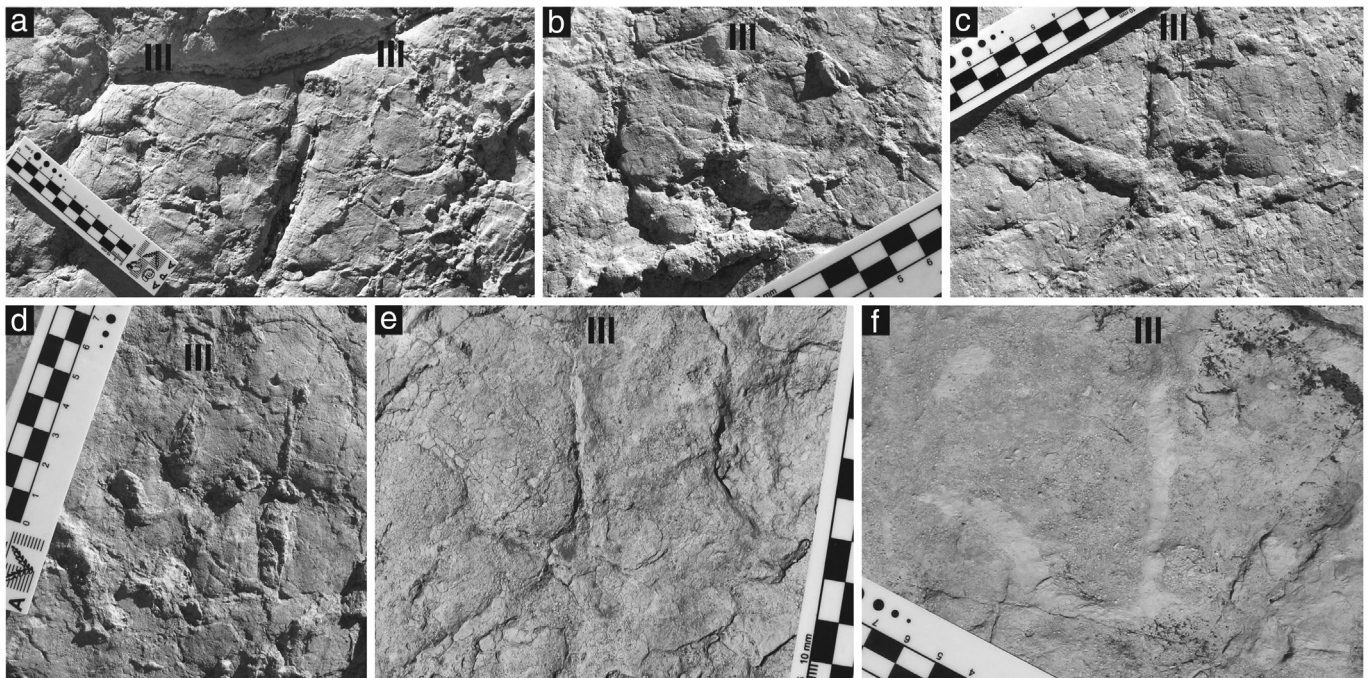


Fig. 10. Photographs of avian footprints. a, b: cf. *Alaripeda* isp. c, e: cf. *Gruipeda* isp. d: *Avipeda* isp. f: cf. *Yacoraitichnus avis*. Scale bar divisions is in cm.

## 6. Vertebrate trace fossils

### 6.1. *Ichnogenus Alaripeda* Sarjeant and Reynolds, 2001

#### 6.1.1. Remarks

Originally, this monotypic ichnogenus was erected to include at least seven tetradactyl footprints with slender curved digit impressions and wide divarication, preserved on a single slab (Sarjeant and Reynolds, 2001). It was subsequently revised, and several tracks assigned to or compared with *Alaripeda* have been included (Johnson, 1986; Scrivner and Bottjer, 1986; Sarjeant and Reynolds, 2001; de Valais and Melchor, 2008; García Raguél et al., 2009; Mansilla et al., 2012).

However, some authors consider that *Alaripeda* represents a preservational bias and not the trackmaker foot morphology, therefore it could be considered a *nomen dubium* (Lockley and Harris, 2010), opinion not supported herein.

#### 6.1.2. cf. *Alaripeda* isp.

**6.1.2.1. Description.** The specimens are four tetradactyl footprints, poorly preserved as negative epichnial, mostly with slight evidence of artificial digital elongation by desiccation (Fig. 10a,b). Two of them are apparently arranged side by side by the right foot stopping beside the left, resembling a stopping or hopping posture, while the others are isolated specimens. The length of the tracks averages 52.5 mm – one case includes a posteriorly directed hallux imprint: 113.4 mm total length – while the footprint width averages 76.3 mm. The footprints have slender digit imprints, up to 4 mm wide; the outer digit imprints (II and IV) are curved inward, whereas the hallux impression is slightly curved and one specimen displays a straight III imprint. The impression of digit III is the longest, while digits II and IV are subequal in length. The average digit II–IV divarication angle measured along the axis taken from the proximal digit tip is 137°. Digit imprints converge in a nearly rhomboid sole. No webbing trace was observed.

### 6.2. *Ichnogenus Avipeda* Vialov, 1965

#### 6.2.1. Remarks

Vialov (1965) named the ichnotaxon *Avipeda* as a term to include the whole record of tracks with avian features. Subsequently, Sarjeant and Langston (1994) amended and redefined the ichnogenus to embrace tridactyl tracks with short, thick digit impressions, with distinct claw traces and without webbing marks. Their suggestion is followed here.

#### 6.2.2. *Avipeda* isp.

**6.2.2.1. Description.** The specimen is a partial track, poorly preserved as positive epichnial, lacking the sector of the sole, with a 41.1 mm partial length and 48.5 mm width (Fig. 10d). It is not possible to know whether it is a left or right track. The proximal ends of the impression of the digits are not in contact. Digit impressions are thick, with a maximum width of 7.8 mm, lacking distinguishable digital pad traces, and only digit III imprint displays an acuminated claw trace. The angles formed by the digit imprints are 30° and 38° between both lateral digits and digit III, while the divarication angle II–IV is 65°.

### 6.3. *Ichnogenus Gruipeda* Panin and Avram, 1962

#### 6.3.1. Remarks

The ichnogenus *Gruipeda*, originally created by Panin and Avram (1962) considering the producer of the tracks, was subsequently revised by Sarjeant and Langston (1994) and de Valais and Melchor (2008), whose ichnotaxonomical criteria and conclusion about this ichnotaxa were followed herein.

#### 6.3.2. cf. *Gruipeda* isp.

**6.3.2.1. Description.** The specimens are at least seven tridactyl and tetradactyl footprints, poorly preserved as negative and positive epichnial (Fig. 10c,e). There are two pairs of tracks (i.e., four tracks altogether) apparently arranged side by side by the right foot stopping beside the left; one of the pairs displays elongated hallux imprints. The length of the tracks averages 101.8 mm with a hallux imprint and 56.5 mm without, while the footprint width is approximately 72.1 mm. The footprints have straight, slender digit imprints, less than 4 mm wide. The impression of digit III is the longest, with an average length of 45.2 mm; digit II and IV imprints are subequal in length. The average divarication angle between II and IV digit imprints is 138°, and between I and III is 161°. The digit imprints converge in a small, sometime nearly rhomboid sole. No webbing or claw traces were observed.

### 6.4. *Ichnogenus Yacoraitichnus* Alonso and Marquillas, 1986

#### 6.4.1. Remarks

The holotype is a complete tridactyl footprint and several isolated digit imprints preserved in a single siltstone slab covered by a submillimeter thick clay drape. The lack of proper description and illustration make comparisons with other specimens difficult. Provisionally, we keep the authors' original assignment.

#### 6.4.2. cf. *Yacoraitichnus* avis

**6.4.2.1. Description.** The specimen is a partial footprint of 79.2 mm long, with the central and lateral (probably IV) digit impressions, both displaying accurate claw traces (Fig. 10f). The lateral imprint displays a slight S-shaped and is about 69.3 mm long, while the central digit has parallel straight edges and is 73.2 mm long. The angle between digit impressions is 43°.

### 6.5. *Ichnogenus Hadrosauropodus* Lockley et al., 2003

#### 6.5.1. Remarks

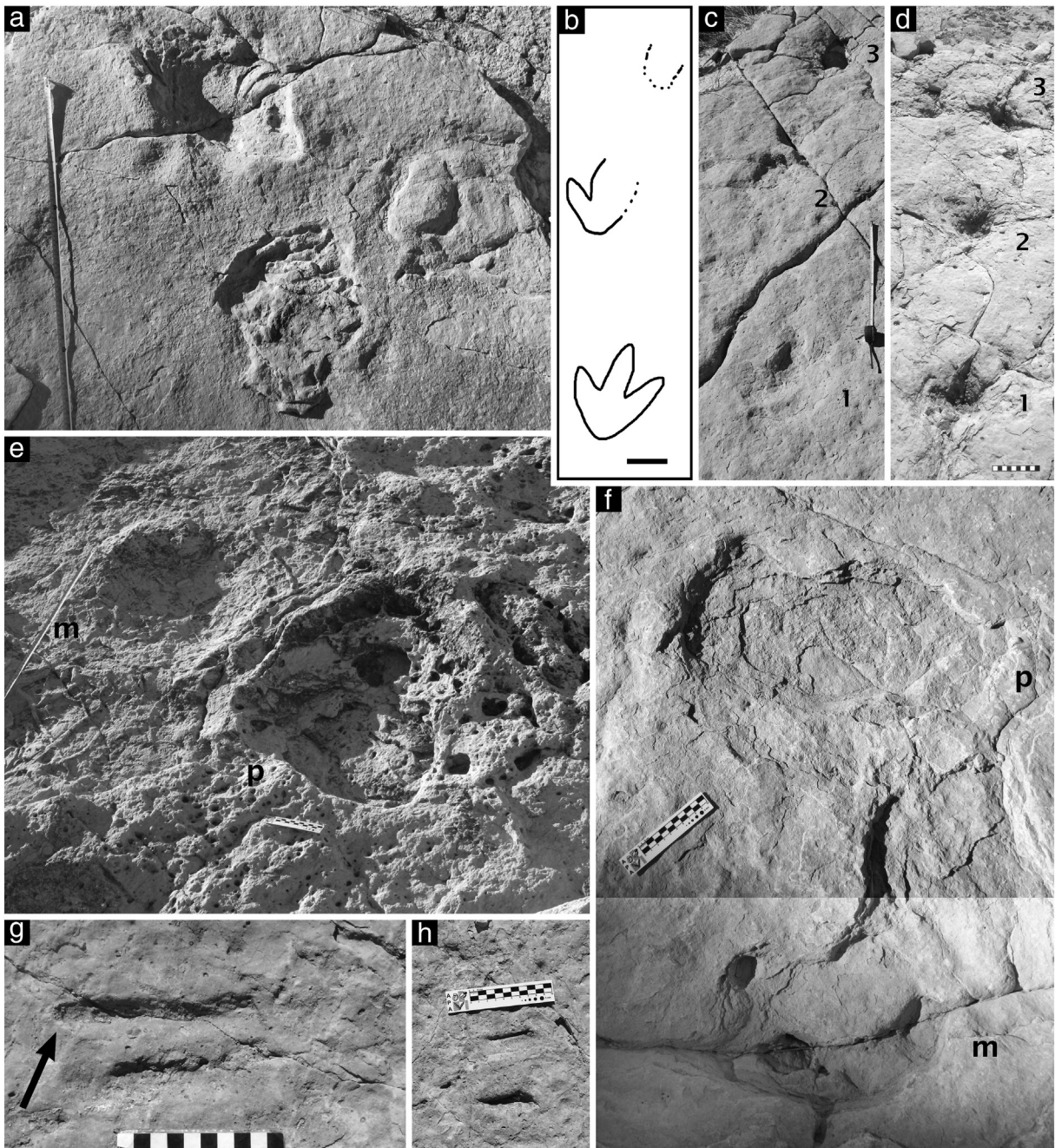
Recently, the ichnogenus *Hadrosauropodus* was ichnotaxonomically revised and its diagnosis amended (Díaz-Martínez et al., 2015).

Lockley et al. (2003) defined *Hadrosauropodus* on the basis of the large ornithopod tracks with bilobed heel impression and short, wide digit impressions from the Maastrichtian of Canada. Díaz-Martínez et al. (2015) amended the original diagnosis to homogenize the comparison with the other Iguanodontopodidae ichnogenes, claiming that *Hadrosauropodus* presents wide, bilobed heel impression and short, wide digit impressions, while *Iguanodontipus* has a small, rounded heel and elongate, narrow digit impressions, and *Caririchnium* has a large, rounded heel and short, wide digit impressions. This suggestion is followed here.

#### 6.5.2. *Hadrosauropodus* isp.

**6.5.2.1. Description.** The material comprises one uncollected specimen preserved as positive epichnia (Fig. 11a) (Díaz-Martínez et al., 2016). The footprint is tridactyl and mesaxononic with one pad impression in each digit and one in the heel; digit pads longer than wide and well-developed notches in the proximal part of the digit II and IV impressions. It is longer than wide, and has blunt or rounded digits and a broad heel impression. The impression of digit III is longer than those of digits II and IV, which are sub-equal in length, and it protrudes farther anteriorly than these. Digit III impression presents a sub-triangular shape, with a hoof-like claw mark at the distal end. Digits II and III have an elliptical to tear-drop shape and show a less robust hoof-like claw mark. The impression of the heel pad is wide and preserves a bilobed outline.





**Fig. 11.** Photographs of dinosaur tracks. a: *Hadrosauropodus* isp. b: Drawing of the theropod trackway in c. c: Theropod tracks. d: Biped dinosaur trackway. e: Set manus-pes of sauropod tracks. f: Set manus-pes of ornithischian tracks. g, h: Didactyl tracks, the arrow indicates the distal end of the trace. Scale bars: 20 cm in a–c, 10 cm in d–h. In c and d, numbers 1 to 3 indicate the tracks. In e and f, m and p indicate the manus and foot impressions respectively. (Picture from Díaz-Martínez et al. (2016)).

### 6.5.3. cf. *Hadrosauropodus* isp.

**6.5.3.1. Remarks.** With the previous footprint, another three footprints, and probably two associated hand prints, very poorly preserved, are arranged in a single partial trackway (Fig. 11a) (Díaz-Martínez et al., 2016).

### 6.6. Theropod tracks

#### 6.6.1. Description

The specimen is a trackway accounting for three tridactyl, mesaxonic footprints, with an average length and width of 40 cm and 37 cm, respectively (Fig. 11b,c). The first two tracks are moderately

preserved while the third is almost destroyed due to erosion, so it will not be taken into account for track measurements. The impressions of the digits III display claw marks, but lack clear digital pad traces. The average angle formed by the impressions of digits II–IV. The trackway is relatively narrow, with high pace angulation and stride length of 220 cm.

#### 6.6.2. Remarks

The lack of morphological details precludes a confident and complete description of the tracks. The scanty record of tridactyl theropod tracks in the outcrops of Maimará is particularly strange, given the huge number of herbivorous dinosaur footprints that have been preserved.



## 6.7. Titanosaur tracks

### 6.7.1. Description

The material comprises several poorly preserved tracks on a fairly deteriorated surface, and at least one better preserved manus-pes set (Fig. 11e). The tracks are represented by pes imprints with subtriangular posterior edge, located posteriorly to the manus imprints. Both manus and pes impressions lack clear digital or claw impressions, probably due to poor preservation. The footprints are longer than wide, with an average width of 42 cm, and an average length of 71 cm. The manus imprints have no clear morphological details and display about a half of the size of the footprints, are semicircular with a major axis of 33 cm rotated outwards relative to the trackways midline.

Despite the high degree of trampling and consequent impossibility of measuring trackway parameters, it appears that the trackways are moderately wide gauge.

### 6.7.2. Remarks

The Maimará locality has yielded abundant tracks assigned to titanosaur dinosaurs, although track density and poor preservation preclude most of the imprints and different trackways from being distinguished correctly.

There is variation in the size of manus-pes tracks, probably due to slight or incipient sediment collapse and not to morphological differences among trackmakers.

## 6.8. Ornithischian tracks

### 6.8.1. Description

The specimens are represented by a manus-pes set, both laterally symmetrical, kidney-shaped, and apparently pentadactyl, with rounded end digit imprints and forwardly directed, with poor preservational condition (Fig. 11f). The manus track is about a third of the size of the footprint, 20 cm long and 31 cm wide. The footprint is posteriorly located to the manus imprints, and it is about 25 cm long and 50 cm wide.

### 6.8.2. Remarks

The manus print is partially comparable to the manus of *Deltapodus brodricki* Whyte and Romano, 1994, because of the semicircular distribution of the digit imprints. This ichnotaxon was originally assigned to sauropod activity (Whyte and Romano, 1994) and subsequently associated to stegosaurian dinosaurs (Whyte and Romano, 2001). Considering that the stegosaurian group was extinct in the Maastrichtian (e.g., Pereda-Suberbiola et al., 2012, and references therein), we consider that these tracks were produced by a member of the Ankylosauria. However, the scarce available material and its poor preservation preclude both ichnotaxonomic assignment and a more precise, confident suggestion of the trackmaker.

## 6.9. Didactyl tracks

### 6.9.1. Description

The specimens are represented by abundant tracks preserved on a single surface, often arranged in apparently bipedal trackways (Fig. 11g–h). Each didactyl track consists of a pair of elongated, straight and parallel edge traces, arranged parallel or slightly divergent, occasionally united proximally. The lateral distance between the traces of each pair ranges from almost in slight contact to up to 5.2 cm. The length of each individual traces is highly variable, from 5.9 cm to 18.9 cm, not the width, about 3 cm. They lack both digital pad and claw traces. The averages of the stride length and the pace angulation are 84 cm and 156° respectively.

### 6.9.2. Remarks

Although the origin of the tracks is unknown and further studies are needed, their particular morphology allows them to be compared to those associated with swim tracks (e.g., Kvale et al., 2001; Ezquerro et al., 2007; Vila et al., 2014).

## 6.10. Biped dinosaur tracks

### 6.10.1. Description

The specimen is a bipedal trackway accounting for three tridactyl tracks (Fig. 11d). The footprints are badly preserved, almost with no distinguishable morphological features. The average length and width is 164 mm and 150 mm respectively. The average angle formed by the impressions of digits II and IV is 115°. The trackway is relatively narrow, with high pace angulation, and stride length 76 cm.

### 6.10.2. Remarks

Given that it is a biped trackway composed of tridactyl footprints, it is quite probable that the trackmaker is a theropod or an ornithopod. But the lack of morphological details precludes a confident description of the tracks, and consequently, it is almost impossible to suggest an

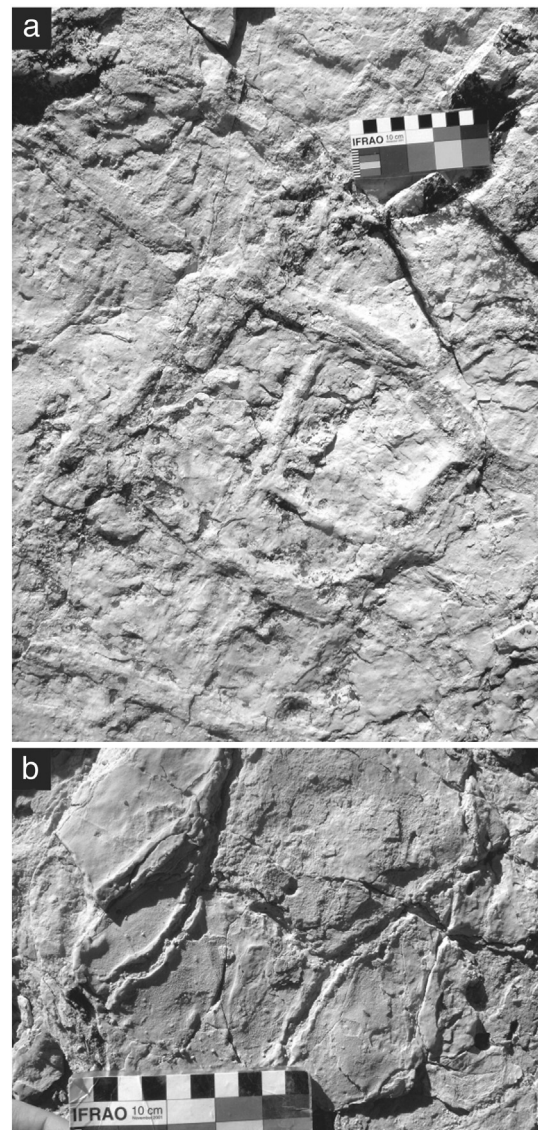


Fig. 12. Polygonal overthrust structures. a: Gamma-petee structures (sensu Reineck et al., 1990). b: Beta-petee structures (sensu Reineck et al., 1990). Scale bar: 10 cm.

ichnotaxonomic assignment and an interpretation more precise of the identity of the trackmaker.

## 7. Discussion

### 7.1. Palaeoenvironmental framework

The overall depositional regime was characterized by a succession of flooding stages and prograding processes with desiccation cycles that produced records of shallowing-upward sequences of a decimeter-to-meter range, formed mainly by shales and followed by oolitic grainstones and stromatolitic boundstones (Fig. 4). This pattern is comparable with the upper third section of the Yacoraita Formation in the Metan and Alemania sub-basins (Fig. 1) (see Marquillas et al., 2005). Entry of sediments and water was approximately equal to accommodation potential (e.g., balanced-fill lake) in a setting dominated by waves and subordinate tides, with a fluctuating-profundal to evaporative type arrangement of facies (Bohacs et al., 2000; Carroll and Bohacs, 2001).

Two types of facies associations have been determined (Table 1), which record distinct hydrological stages: (A) a subtidal-lower intertidal zone (S-LI), which records moderate to high-energy depositional events in a shoreline zone submerged most of the time, with variable depth; and (B) a supratidal playa-lake zone (PL), a low energy zone of ephemeral ponds adjacent to the main water body which was sporadically flooded and suffered evaporation and desiccation. Fig. 13 is a block diagram of the integrated palaeoenvironmental framework.

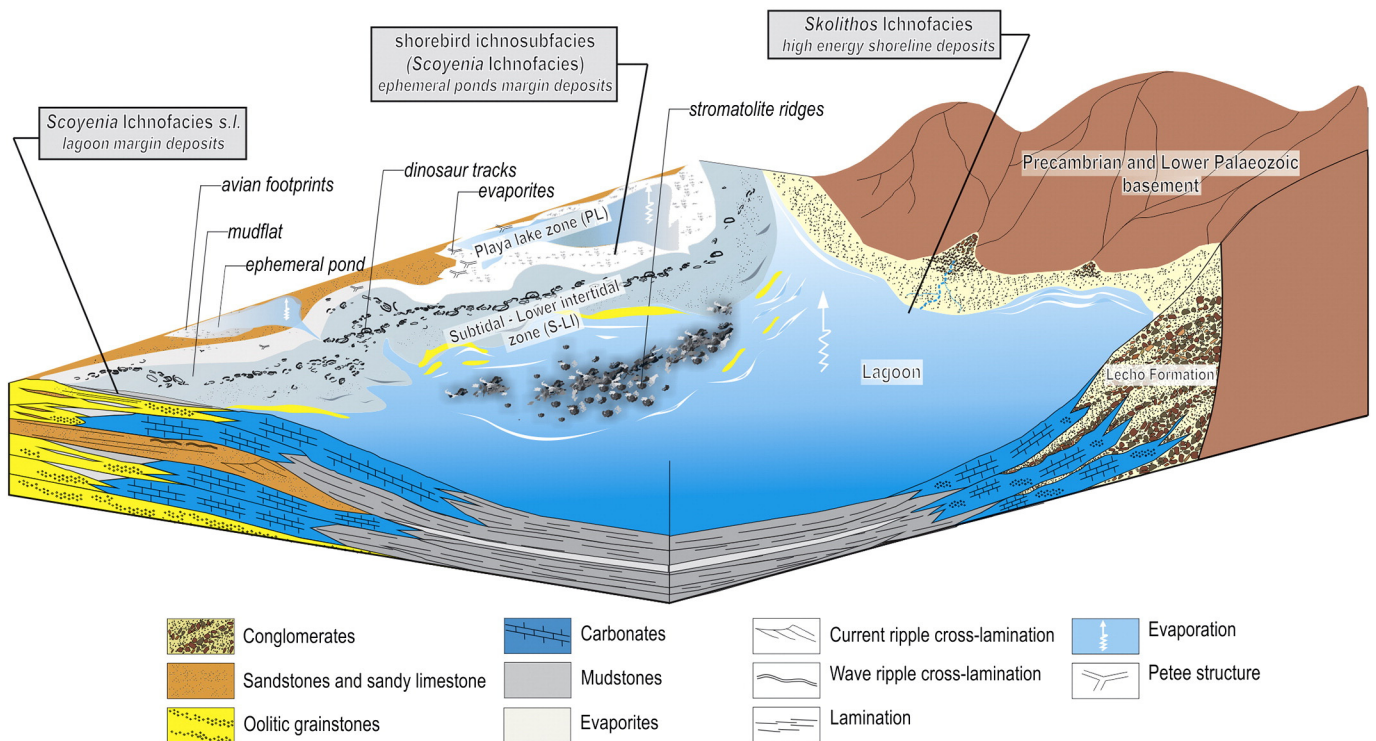
#### 7.1.1. Subtidal-lower intertidal zone (S-LI)

**7.1.1.1. Description and characteristics.** The S-LI zone (Table 1; Fig. 13) comprises facies of: 1) oolitic grainstone; 2) wackestone-packstone; 3) stromatolitic boundstone; and 4) calcareous siltstones and sandstones. The S-LI zone was generated in a subtidal/intertidal moderate to high-energy environment, shallow, though of variable depth (Fig.

13). So, it comprises a mosaic of subtidal sediments which are seldom if ever exposed (perennial lagoon facies) and intertidal sediments that are exposed depending on tide regime and wind conditions.

Fining-upward cycles are observed (Fig. 4). Each cycle begins with carbonate deposits (dominant subtidal conditions), overlain by calcareous sandstones and heterolithic successions (intertidal conditions). There has been subaerial exposure during low tide or during stages of withdrawal of the water body. The presence of oolitic bars is interpreted as having been formed in agitated waters, reworked by wave action (Tucker and Wright, 1990; Braithwaite, 2005). The presence of gastropods with different degrees of fragmentation in the oolitic bars, carbonatic fill and low size-selection, also indicate wave action and suggest a long time in the taphonomically active zone (TAZ), although low attrition and fragmentation rates suggest that lateral transportation was not important (Cónsole-Gonella and Aceñolaza, 2010). Disarticulated fish remains consisting of teeth, fragments of jaws and crania, and vertebrae, mainly of Pycnodontiformes, are frequent in the wackestone-packstone facies of the S-LI zone. Many pycnodontiforms inhabited marine environments, although they may also have inhabited freshwater environments (Cione and Pereira, 1985; see also Poyato-Ariza and Wenz, 2002, based on isotope analyses in Las Hoyas, Spain), therefore their presence is not determinant of whether the environment was marine or freshwater (Cónsole-Gonella et al., 2012b). Be that as it may, the presence of this paleoichthyofauna would indicate at least a perennial lacustrine system. The stromatolites of different morphologies also correspond to variable depth/energy stages in the sedimentary environment. Formation and development of dome-shaped stromatolites suggests the maximum intertidal range; this has been observed in protected environments, both marine (Logan, 1961; Logan et al., 1964; Gebelein, 1969; Andres and Reid, 2006; Jahner and Collins, 2011, 2012, among others) and continental (Farias et al., 2011).

As we mentioned before, the stages of withdrawal of the water body may also be related to wind action on a shallow water column (e.g., Shinn, 1983; Kvale et al., 2001; Genise et al., 2009). During these stages of minimal water column depth (e.g., in zones subject to wave action),



**Fig. 13.** Block diagram illustrating sedimentary facies, environments and subenvironments, trace fossil assemblages and ichnofacies/ichnosubfacies distribution in the Maimará locality. (Modified from Bohacs et al. (2000). Not in scale.)



and/or subaerial exposure, there are records of tracks indicating movement of dinosaurs. The degree of preservation of tracks was controlled by the variable environmental conditions in each microenvironment. Preservation of tracks in moderate/high energy shoreline areas has been observed in analogous neoichnological cases (e.g., “subaqueous zone” sensu Cohen et al., 1991, 1993) and in the geological record (Mackenzie, 1975; Lockley et al., 1994; Kim et al., 2012; Pazos et al., 2012). Indeed, as demonstrated by Laporte and Behrensmeyer (1980) in neoichnological studies on the shore of Lake Turkana (Kenya), the “optimal” zone for preservation of tracks is a narrow strip surrounding the lake. This zone lies between the edge of the water body, where waves obliterate tracks, and more distant zones where the substrate is too dry for tracks to form (Laporte and Behrensmeyer, 1980). And in that distant zone, even if tracks had been preserved, erosional processes (rain, wind, new trampling) would have obliterated them (Laporte and Behrensmeyer, 1980; Cohen et al., 1991). This necessarily indicates an “optimal window” for track preservation, where the conditions of substrate moisture, erosional agents and proximity to the water body work together. In Maimará, the degree of overprinting suggests a hiatus in high water-table conditions in deposition (omission surface), which has enabled tracks to be preserved (e.g., Marsicano et al., 2010), although erosional factors, such as wave energy, subsequently degraded them. This would explain why some tracks are well preserved yet frequently appear in isolation, and why there are not many trackways. In lakes, taphonomic pathways are known to often reflect shoreline fluctuations and associated changes in substrate consolidation (Buatois and Mángano, 2011).

The general absence of clear digit or claw imprints in most vertebrate tracks may be due to prolonged exposure obliterating them, which removed the anatomical features, or to a lack of adequate substrate properties (Laporte and Behrensmeyer, 1980). Preservation of tracks suggests a moist or slightly damp substrate (Melchor, 2015), probably produced in underwater soft sediments.

**7.1.1.2. Ichnological composition.** The ichnodiversity (based on composition of invertebrate trace fossils) is a tool that in general terms – though it needs to be used with precaution – is on the whole useful for estimating environmental conditions of sedimentary environments (Buatois and Mángano, 2011, 2013). The S-LI zone has low ichnodiversity, which is consistent with the interpretation of a sedimentary system where environmental conditions were dominated by stress factors, in this case periods of contraction of the water body, variations in salinity, and wave energy. In particular, conditions of hypersalinity play a major role regarding low ichnodiversity in subtidal environments (de Gibert and Ekdale, 1999), and especially in hydrologically closed systems (see review in Scott et al., 2012).

In the S-LI zone, trace fossils are restricted to the shallow tier, with substrate penetration of a few centimeters. There are three softground suites: suite I) constituted of *Skolithos linearis* and dinosaur tracks (*Hadrosauropodus* isp., titanosaurs, ornithischians, theropods); suite II) constituted of monoichnospecific tiers with cf. *Taenidium* isp.; and suite III) constituted of abundant didactyl tracks.

In suite I, the presence of *Skolithos*-dominated levels reflects non-specialized behavior (simple domichnia) probably of polychaete worms. Be that as it may, in non-marine or restricted marine environments, a series of potential producers should be considered, such as insects, spiders, or even crustaceans (see review in Melchor et al., 2006). In palaeo and neoichnological studies in Lake Bogoria (Kenya), Scott et al. (2009) observed incipient *Skolithos* isp. structures produced by tiger beetles (Coleoptera: Cicindelidae) and other unknown beetles, possibly Staphilinid adults, or spiders. *Skolithos* indicates deposition in a high-energy shoreface setting, in both marine and continental environments (Buatois and Mángano, 2004; Melchor et al., 2006). *Skolithos* is frequent in high-energy zones of tidal flats (e.g., Cornish, 1986) and also in association with dinosaur footprints on tidal flats (MacKenzie, 1975; Kvale et al., 2001), as in the case presented herein. Suspension-

feeder burrows of *Skolithos* tend to dominate under conditions of relatively high content of organic matter in suspension in the water and good oxygenation (e.g., Mángano et al., 1996; Mángano and Buatois, 2004). This association between tiers with *Skolithos* and dinosaur footprints has also been recorded in continental lacustrine high energy shorelines (Paik et al., 2006). In the case presented herein, the conformation of tiers with *Skolithos* and dinosaur tracks may indicate a soft-ground substrate (moist or slightly damp), and a shoreline subject to wave action and tide variation (e.g., MacKenzie, 1975; Kvale et al., 2001). Although in some cases, given the preservation of the footprints as undertracks, their relationship with *Skolithos* isp. is penecontemporaneous (Fig. 9e); in palaeoenvironmental terms it can be considered simultaneous.

The large quantity of sauropod tracks and their overprint may be due to repeated passage of these large dinosaurs, probably moving through zones used by their predecessors and which would thus have been safer (e.g., Thulborn, 2012).

In suite II, the presence of levels dominated by backfilled structures without ornamentation (cf. *Taenidium* isp.) in levels almost penecontemporaneous (a few centimeters below) with dinosaur tracks suggests a suite developed on a soft substrate, and perhaps progressive desiccation (Buatois and Mángano, 2004). It also suggests a freshwater influx, and a landward position (e.g., Netto and Rossetti, 2003), probably due to autocyclic processes. *Taenidium* is a trace associated to the action of invertebrates moving and perhaps feeding through the sediment, and has been assigned to various tracemakers, such as insect larvae and adults, as well as earthworms (see review in Melchor et al., 2006).

In suite III, the surface of the didactyl tracks may represent a well-established water column, e.g., at times of high tide or deeper zones. Given the morphological variety of the didactyl tracks, it is very difficult to associate them with a possible producer. So, although it is not possible to identify the trackmaker, we can infer that, due to the size of the tracks, the purported producer would have been an animal of medium to large body size. Therefore, if it is accepted that the tracks are related with swimming activities, we estimate that there was water enough to cover the body. There are many mentions in the bibliography of swim tracks and their trackmakers, such as theropods, phytosaurs and crocodiles (e.g., Coombs, 1980; Lockley and Milner, 2006; Vila et al., 2014). We consider that great caution should be exercised in this type of comments, because the universe of possibilities for type of producer, swimming (or diving) skills, population or age structure (presence of juvenile/adult individuals), make it very complicated to draw inferences regarding the depth of the water column based on this type of ichnological record. Most specimens are represented by a pair of elongated, parallel or slightly divergent traces, reminiscent of tracks assigned to Dromaeosaurids, which walk only on digits III and IV and only basally on digit II (Ostrom, 1969; Apesteguía et al., 2011). Moreover, theropod dinosaurs are known to have had swimming skills (Coombs, 1980; Milner et al., 2006; Ezquerro et al., 2007). However, some other specimens are also reminiscent of crocodile swim tracks (Vila et al., 2014).

In general terms, the heterogeneity of trace fossils/producers can be attributed to a range of factors, such as food resources, shelter, or breeding opportunities, typical of a lacustrine shoreline (Cohen, 2003). Therefore, vertebrate tracks help in the delineation of cycles of expansion and contraction of water bodies (Lockley, 1986).

#### 7.1.2. Playa-lake zone (PL)

**7.1.2.1. Description and characteristics.** The term *playa-lake* used here is based in the criterion of the review by Briere (2000), after an original proposal by Motts (1972). Briere (2000) proposed to the *playa-lake* as a transitional category between *playa* and *lake*, essentially a “flooded *playa*”, and establishes that a *playa-lake* system is “an arid zone feature, transitional between *playa* and *lake*, neither dry more than 75% of the time nor wet more than 75% of the time”. This classification eliminates



the terms “continental sabkha” or “inland sabkha”, previously equivalents, and replaced them by “playa” (sensu Briere, 2000).

The PL zone is composed of the facies of mudstones–petee structures. The PL zone suggests a supratidal system of bodies of water that are dominated by sedimentation with very low energy, and with the establishment of coherent microbial mats in the substrate (Fig. 13). These bodies of water are adjacent to the perennial lagoon system but far from the direct influence of wave action (Fig. 13) (e.g., Persian Gulf Trucial coast model in Shinn, 1983). The PL zone was flooded during periods of maximum lake growth. During periods of maximal withdrawal, it is inferred that the bodies of water of the PL zone acquired characteristics of ephemeral ponds (e.g., dry mudflats of a lake margin in the tracksites of the Upper Cretaceous Jindong Formation (Korea); Paik et al., 2001), and may have formed a playa system sensu Briere (2000), as shown by the presence of gypsum. In this zone there are gamma petee type structures formed by the decay of microbial mats as a result of desiccation (sensu Reineck et al., 1990). These structures are frequent in sabkha type settings, salt flats and peritidal zones *s.l.* (e.g., Andros Island and Inagua Island (both in Bahamas), Shinn, 1983; Sleaford Mere, Eyre Peninsula and Coorong Lagoon (south Australia), de Deckker, 1988; Gavish Sabkha and Gulf of Aqaba (both in Egypt), Lanzarote and Canary Islands (both in Spain), Reineck et al., 1990; Mumbai (India), Eriksson et al., 2007). In general sense, petee environments range between subtidal and highest supratidal areas, whereas gamma–petees rather indicate intertidal and lower supratidal exposure (Reineck et al., 1990). Also, a similar environmental setting have been observed in the upper section of the El Molino Formation (Maastrichtian–Paleocene) of Bolivia, deposited in ephemeral lakes or playa lakes with microbialites fringed by dry mudflats (Camoin et al., 1997). As it has already been mentioned, the El Molino Formation is analogous in facies and chronostratigraphy with the Yacoraite Formation (see Introduction).

The microbial mats have played a special role in the tracks' preservation. Kvale et al. (2001) reported two Middle Jurassic dinosaur tracksites from the Sandance and Gypsum Spring formations (Bighorn Basin), northern Wyoming (USA). The palaeoenvironmental context of these tracksites belongs to an upper intertidal to supratidal system, with sediments deposited under at least seasonally arid conditions. After comparison with the modern intertidal zone of Pine Island (Cape Coral), Florida, Kvale et al. (2001) assumed that preservation of the Jurassic tracks were improved following the microbial stabilization and early cementation of substrate, which is related with tidal cyclicity. In the same sense, Marty et al. (2009) elucidate about the importance of microbial mats in the preservation of human footprints in several different peritidal environments [e.g., Ambergris Caye (Belize), Eleuthera Island (Bahamas), southern Tunisia, and southern Sinai (Egypt)], and provided a model for comparison with similar geological records. Marty et al. (2009) have studied several subenvironments, such as intertidal flats, supratidal flats and marshes and sabkhas, and have observed that in thin moist mats, the mats were compressed by the foot, and shallow but well-defined prints have remained, with anatomical details of the toes that were formed. On the other hand, poorly defined footprints were produced in thin but dry mats. Regarding environmental issues, Marty et al. (2009) observed that footprints in microbial mats are only produced in wet conditions. During periods of drought, the mats consolidate rapidly, getting hard and rigid and making it almost impossible even for a heavy trackmaker to leave a footprint (Marty et al., 2009). Moreover, such consolidated microbial mats are difficult to disintegrate and even resist heavy rainfall, so new footprints can only be made once a new microbial community is in place after renewed wetting (Marty et al., 2009; Melchor, 2015).

Carvalho et al. (2013) presented the association of cracked biofilms and dinosaur tracks in the Sousa Basin (Lower Cretaceous) of Brazil, deposited in ephemeral saline lakes, where biofilms and mats would develop during wet seasons or wetter climate phases, due to cyclic floodings. In dry mats, generally poorly defined or no footprints are produced, while in saturated ones the imprints are well defined, sometimes

with well-defined displacement rims (Carvalho et al., 2013). de Deckker (1988) reported an interesting analogy in ephemeral lakes of south Australia (Frome and Eyre lakes), where there are footprints made by birds feeding on crustaceans – mainly brine shrimp and ostracodes – when water level was ~5–10 cm deep. In these ephemeral lakes, two main types of bird footprints can be preserved: tracks by small birds feeding on aquatic organisms such as brine shrimp and ostracodes, and tracks by a larger bird (i.e., emu, *Dromaius novaehollandiae*; de Deckker, 1988). In these Australian lakes, algal mats grow on the substrate only in wet phases, and in withdrawal phases mats suffer desiccation and cracking, forming petee structures (de Deckker, 1988). In the same sense, in recent years has been increased attention on the importance of microbial mats and matgrounds in trace fossils preservation (e.g., Carmona et al., 2011, 2012; Buatois and Mángano, 2012; Fernández and Pazos, 2013).

Biped dinosaur tracks are penecontemporaneous to the formation of the petee structures (Fig. 11d) which has been observed in current environments with analogous characteristics, such as the microbial mat muds of the Arabian Gulf in western Abu Dhabi (Diedrich, 2005). The deficient track preservation may be attributed to extreme conditions of the substrate (dry/moist), which prevented preservation of anatomical details, and have been observed in neoichnological analogous cases (e.g., Diedrich, 2005; Marty et al., 2009; Genise et al., 2009).

Therefore, the playa-lake zone is considered to constitute a limit to the zone of optimal track preservation in this environmental context. This does not imply a good preservation of tracks within the playa-lake zone. This concept is pointing out that the better chance of good track preservation is before the end of the playa-lake zone, where the substrate is too dry. In addition, as we discussed, in the playa-lake zone microbial mats have played a main role in the stabilization of substrate, accelerating early cementation.

**7.1.2.2. Ichnological composition.** Ichnodiversity is also low in the PL zone. The invertebrate traces are arranged in two suites: (I) *Lockeia siliquaria* and ?*Ptychoplasma* *isp.*, and (II) *Palaeophycus tubularis* and *Planolites cf. montanus* with avian tracks (*cf. Alaripeda* *isp.*, *Avipeda* *isp.*, *cf. Gruipeda* *isp.*, *cf. Yacoraitichnus avis*) and *indet.* biped dinosaur tracks. The suite *Lockeia*–?*Ptychoplasma* suggests the activity of bivalves that moved in the mud using a non-cleft wedge foot (Uchman et al., 2011). The ichnospecies *Lockeia siliquaria* has been interpreted as the basal part of a dwelling structure of suspension-feeding bivalves (Mángano et al., 1998). Bivalve traces in lacustrine settings can be interpreted in the same way, because their producers are also suspension feeders (Buatois and Mángano, 2011). With regard to settings with a certain analogy, *Lockeia* has been recorded as occurring abundantly in a carbonate lake shoreline where water was very shallow, and the sediment surface was intermittently subaerial (Lucas et al., 2010).

Regarding suite II, *Planolites* is suggested as associated to the action of backfilling of a deposit-feeding animal; whereas *Palaeophycus* suggests passive sedimentation within an open dwelling burrow constructed by a predaceous or suspension-feeding animal (Pemberton and Frey, 1982). Be that as it may, the active/passive fill inference – as well as the “collapse” of these structures – should be employed cautiously in the inference of producers/ethology because it is a process which could be masked taphonomically (sensu Keighley and Pickerill, 1995). Moreover, active fill does not always imply “internal processing” of the material (Keighley and Pickerill, 1995). This ichnoassemblage composed of horizontal structures is consistent with the occupation of an ephemeral setting, where the trace fossil-bearing horizon represents a single event of deposition, which has been observed in other playa-lake systems and ephemeral ponds (e.g., Minter et al., 2007; de Gibert and Sáez, 2009). Melchor et al. (2006) have previously documented overbank settings with a high ichnodiversity belonging to a floodplain pond assemblage, typified by abundant avian-like footprints and several invertebrate trace fossils (*P. tubularis* and *T. barretti*, *R. carbonarius*, *Diplichnites* *isp.*,

*S. linearis*, *H. tenuis*). Regarding paleoecological interpretation, the occupation of the pond by different animals was probably immediate after the original sheetflooding event and accompanied the partial desiccation of the pond (Melchor et al., 2006). de Gibert and Sáez (2009) reported the association of avian tracks (*Gruipeda*) with invertebrate trace fossils (*Cochlichnus* and *Taenidium*) in lake shore/terminal lobe facies, suggesting a nearly saturated substrate, also suggesting a high water table preventing the penetration of air-breathing invertebrates.

In Maimará, the association of *Planolites-Palaeophycus* with avian and dinosaurian tracks suggests a pre-desiccation suite (sensu Melchor et al., 2006), with low diversity consistent with the stress of a hypersaline environment, also observed in analogous neoichnological cases (e.g., Scott et al., 2009). Although the presence of petee structures indicates desiccation of these ephemeral water bodies, the absence of a suite of desiccation trace fossils, with the presence of ornamented trace fossils (e.g., *Scoyenia*) may be due to taphonomic processes.

#### 7.2. Relation of the Maimará ichnoassemblages to the archetypal continental ichnofacies model

The Maimará trace fossils in their sedimentary context have enabled a distribution gradient in two environmental settings to be established

(Fig. 13): A) a subtidal-lower intertidal zone (S-LI), characterized by a moderate/high energy shoreline under wave and tide action, and B) a playa-lake zone (PL), a protected supratidal/eulittoral zone that characterizes low energy ephemeral bodies of water. Fig. 14 contains a summary of the palaeoecological reconstruction of the Maimará palaeoenvironments and tracemakers.

In general sense, track-bearing surfaces can be ascribed to the archetypal *Scoyenia* Ichnofacies. The *Scoyenia* Ichnofacies is typical of fluvial and lacustrine systems that are repeatedly exposed and submerged, although it may also occur in certain eolian subenvironments (Genise et al., 2010; Buatois and Mángano, 2011). In lacustrine complexes, this ichnofacies typically characterizes lake-margin deposits, being present in both open and closed lake basins, and in both ephemeral and perennial systems (Buatois and Mángano, 1998).

Originally, Cónsole-Gonella and Aceñolaza (2009, 2010) assigned the levels with *Skolithos* of the S-LI zone to the *Skolithos* Ichnofacies, without contradicting the general interpretation presented here, given that the *Skolithos* Ichnofacies is identified in moderate- to high-energy lacustrine environments, such as wave dominated shorelines and delta mouth-bars (Buatois and Mángano, 2004). The absence of trace assemblages enabling identification of the *Mermia* Ichnofacies is probably related to the hypersaline to brackish conditions of the depositional



**Fig. 14.** Palaeoecological and palaeoenvironmental reconstruction of the Maimará tracksite. Note at the left side a lagoonal shoreline (S-LI zone). The low tide is exposing domal stromatolites, “incipient” *Skolithos* burrows and a Pycnodontiform fish. At the right side there are ephemeral ponds that are part of an extensive playa lake system (PL zone). Birds are feeding in those ponds. Several sauropods and an ankylosaur are walking through the lagoon shoreline. In the frontside, theropods are stalking herbivore dinosaurs at the back view. Drawing by Jorge A. González.

environment (e.g., Ekdale et al., 1984; de Gibert et al., 2000; Cohen, 2003).

Regarding the Maimará record in the context of the emergent tetrapod ichnofacies model, a brief discussion is useful. The first intention of establishing vertebrate archetypal ichnofacies dates back to the work by Lockley et al. (1994), and the latest refinement to this proposal was contributed by Hunt and Lucas (2005, 2007a,b), Lockley (2007), and recently by Hunt and Lucas (2016).

The ichnofaunas of the S-LI zone could be assigned to the *Brontopodus* ichnofacies (after Hunt and Lucas, 2007), given the dominance of terrestrial herbivore tracks and lower number of carnivore tracks. Lockley et al. (1994) have already proposed this idea for the correlative El Molino Formation, whose ichnofauna and palaeoenvironmental settings are close to that of the Yacoraite Formation (see Table 2). The *Brontopodus* ichnofacies includes coastal plain-marine shoreline environments and some lacustrine shorelines, and ranges from Late Jurassic to Recent in age (Hunt and Lucas, 2016). Since the original approach by Lockley et al. (1994), it has been observed that almost all sauropod track ichnocenoses are recorded from carbonate and evaporitic facies associated with carbonate platform environments or from alkaline-saline carbonate lake deposits situated at low palaeolatitudes, suggesting a strong environment/tracemaker

relationship. Besides, sauropods may have had gregarious behavior with repetitive walks in environments previously used by their predecessors (sensu Thulborn, 2012).

Suite III with possible swim traces in the S-LI zone (Fig. 11), could be assigned to the *Characichnos* ichnofacies (i.e., medium diversity ichnofaunas composed of majority of swimming traces or parallel scratch marks and fish swimming trails or *Undichna*) which represents shallow lacustrine and tidal environments (Hunt and Lucas, 2016). It perhaps constitutes a new ichnocoenosis and extends its range – from the Early Jurassic – to the Upper Cretaceous.

The ichnofauna of the PL zone could be assigned a priori to the *Grallator* ichnofacies (Hunt and Lucas, 2007), chronostratigraphically referred to the Triassic–present time lapse. Hunt and Lucas (2007) claimed that this ichnofacies broadly characterizes lake margins with tracks of tridactyl avian and non-avian theropods (usually dominant) or other biped vertebrates. Suite II of the PL zone is characterized by a highly diverse avian ichnocoenosis and low diversity of invertebrate trace fossils, in a low-energy marginal lacustrine setting. This paleoecological requirement of low energy is fundamental, because it enables shorebirds to feed, which has been observed in analogous neoichnological cases (e.g., de Deckker, 1988; Martin, 2013).

**Table 2**

Vertebrate ichnological record and environments of Late Cretaceous of Central Andes.

Lithostratigraphic unit	Locality/country	Age	Ichnotaxa Name/inferred tracemaker	Environmental setting	References
Toro Toro, El Molino, and Chaunaca formations	Toro Toro (Potosí, Bolivia)	(Santonian?)–Upper Maastrichtian–Paleocene	<i>Ligabueichnium bolivianum</i> Theropod and sauropod tracks	Ceratopsid or ankylosaurid tracks	Leonardi (1984)
	Cal Ork'O (Sucre, Bolivia)		Medium-sized sauropod (titanosaurid) trackways. Large and small theropods trackways. Ankylosaurid isolated tracks and trackways. Small ornithopods trackways.	Perennial to ephemeral lacustrine shorelines	Meyer et al. (2001)
	Humaca (Chuquisaca, Bolivia)	Campanian?–Maastrichtian	Sauropod trackways	Perennial to ephemeral lacustrine shorelines	Lockley et al. (2002)
Santa Lucía Formation	Parotani (Cochabamba, Bolivia)	Upper Maastrichtian	“six biped dinosaur trackways bad preserved”		Leonardi (1981)
Yacoraite Formation	Valle del Tonco (San Carlos, Salta, Argentina)	Maastrichtian–Danian	<i>Hadrosaurichnus australis</i> <i>Taponichnus donottoi</i> <i>Telosichnus saltensis</i> <i>Yacoraitichnus avis</i> <i>Salfitichnus mentoor</i>	Hadrosaurids (?) Ornithopods (?) Birds Theropods (?)	Alonso (1980, 1989); Alonso and Marquillas (1986)
	Río Juramento (Coronel Moldes, Salta, Argentina)		Hadrosaurid (?) footprint		Marquillas et al. (2003)
	Quebrada de Acherai (Guachipas, Salta, Argentina)		<i>Acherailichnus leonardii</i>	Hadrosaurid (?)	Sánchez Rioja (2004)
	Maimará (Tilcara, Jujuy, Argentina)		<i>Hadrosauropodus</i> isp. <i>Alaripeda</i> isp. <i>Avipeda</i> isp., cf. <i>Gruipeda</i> isp., cf. <i>Yacoraitichnus avis</i> Titanosaur tracks. Ornithischian tracks. Biped dinosaur tracks. Didactyl (theropod?) tracks.	Lagoon shoreline associated with a playa lake system	Cónsole-Gonella et al. (2012a, 2012b, 2013); Díaz-Martínez et al. (2016); Cónsole-Gonella et al. (this work)



The *Grallator* ichnofacies encompasses the “shorebird ichnofacies” of Lockley et al. (1994) in the criterion of Hunt and Lucas (2016). Doyle et al. (2000) and later Melchor et al. (2006) observed that it is preferable to retain the original “shorebird ichnofacies” designation by Lockley et al. (1994). The shorebird ichnofacies comprises ichnocoenoses of shorebirds attributable to Charadriiformes (waders and gulls), Anseriformes (ducks and geese) and Ciconiiformes (storks and herons), and has been interpreted as effectively a lacustrine ichnofacies, although potentially associated with playas, marine influenced lagoons or other lake types (Doyle et al., 2000). An ichnosubfacies may be considered as a group of trace fossils representing a subdivision in an ichnofacies (sensu Buatois and Mángano, 2011), or as assemblages of trace fossils that constitute “medium-scale ichnofacies”, which do not adhere to the archetypal model and which must demonstrate recurrence in time and space (sensu MacEachern et al., 2012). For this reason, we prefer to keep the shorebird as a sub-set (ichnosubfacies) within the *Scoyenia* Ichnofacies (Melchor et al., 2006; de Gibert and Sáez, 2009; Díaz-Martínez et al., 2016).

In the current state of knowledge, the extension of the ichnofacial model represented by tetrapod ichnofacies has received dissimilar consideration from the scientific community. From a critical standpoint, Santi and Nicosia (2008) question the validity of vertebrate ichnofacies, pointing out that the ichnocoenosis–sedimentary rock–palaeoenvironment relationship is poorly sustained in this model, wherefore its theoretical basis is inconsistent. With regard to factors controlling vertebrate ichnofacies distribution, MacEachern et al. (2012) analyze the subject in detail and recognize that although vertebrate ichnofacies have correspondence with certain sedimentary settings, their temporal – and sometimes even geographical – distribution is limited, as had already been observed by Melchor et al. (2006).

Although at first the proposal of vertebrate ichnofacies encompassed vertebrate and invertebrate ichnotaxa providing global occurrences (Lockley et al., 1994), refinements of this model have not delved deeply in the vertebrate–invertebrate tracemakers relationship, and only mentioned the environmental overlap between both approaches (Hunt and Lucas, 2007, 2016). In fact, Hunt and Lucas (2007: Fig. 1) pointed out that the *Grallator*, *Brontopodus* and *Batrachichnus* ichnofacies correspond to aspects of the *Scoyenia* Ichnofacies, and the *Characichnos* ichnofacies “overlaps” both the *Mermia* and *Skolithos* Ichnofacies, an idea supported by Buatois and Mángano (2011). In the opposite way, this question has been observed by Lockley (2007), who discussed that although invertebrate continental ichnofacies are well defined, they do not address the associated vertebrate traces to any significant degree.

In fact, it is possible that the disagreement regarding the validity of both paradigms is related to a misunderstanding of the role of the vertebrate ichnofacies model. Hunt and Lucas (2007, 2016) supported that the main difference in conception between these two models is that vertebrate ichnofacies are “biotaxonichnofacies” and all invertebrate ichnofacies are “ethoichnofacies”. This concept arises from the assumption that invertebrate ichnologists use an “ethological” approach to ichnology by describing and naming behavioral interactions between an organism and the substrate and vertebrate ichnologists use a “biotaxonomic” approach by attempting to relate tracks and traces to the taxonomy of the producer. Archetypal vertebrate ichnofacies are biotaxonomic in nature, and therefore, they are neither directly comparable nor subsumable within Seilacherian ethoichnofacies (Hunt and Lucas, 2016).

A further discussion on such aspects is beyond the scope of this paper. Moreover, many of the points assessed critically by Santi and Nicosia (2008) and MacEachern et al. (2012) have already been discussed by Hunt and Lucas (2016). Finally and regarding the discussion above, we assign the ichnofaunas of the S-LI zone to the *Scoyenia* and *Skolithos* Ichnofacies, and ichnofaunas of the PL zone to the shorebird ichnosubfacies, within the *Scoyenia* Ichnofacies. We also believe that redefining the *Brontopodus* ichnofacies is a promising topic for future contributions.

## 8. The Maimará locality in the context of Upper Cretaceous tracksites of Central Andes

Regarding the distribution of the vertebrate tracks in late Cretaceous units, a brief discussion is appropriate. As we mentioned, the Yacoraite Formation is homologous and correlative in chronostratigraphy and facies with units of Bolivia, Peru and northern Chile as result of the establishment of epeiric seas and extensive lacustrine basins (Gayet et al., 2001; Camoin et al., 1997; Marquillas et al., 2011). This correlation has a counterpart in vertebrate trace fossils (see Table 2). Concerning the palaeoenvironmental distribution of tracks, there is a strong control. Lockley et al. (1994, 2002) observed that sauropod and ankylosaurian tracks (sensu McCrea et al., 2001) ichnocoenoses are recorded from carbonate and evaporitic facies associated with carbonate platform environments. In carbonate-dominated lacustrine basins, the common sedimentary facies where the trace fossils occur are oolitic grainstones with cross-bedding and mudcracks, associated with micrites, stromatolites and shales (Genise et al., 2010). The palaeoenvironment is envisaged as a shallow-lacustrine, agitated and commonly vegetated littoral zone and associated mudflats (Genise et al., 2010). In terms of paleodiversity, Meyer et al. (2001) observed that the El Molino Formation is characterized by track-assemblages composed of several producers (titanosaur sauropods, theropods, ankylosaurs and ornithopods) (see Table 2) that suggests that there was no gradual decline in dinosaur diversity towards the end of the Cretaceous and it favours a drastic event at the K-Pg boundary. The Yacoraite and El Molino formations display the same tracemaker taxa (see Table 2), although the first one has yielded several avian footprints.

We support the concept that suggests that the El Molino and the Yacoraite formations are part of a “megatracksite” (sensu Meyer et al., 2001). A suggestive further step will be to establish within both units the K-Pg boundary in several sections. We believe that the Andean Basin can provide the key to understand the dinosaur diversity in late Cretaceous and their abrupt decline after the K-Pg event.

## 9. Conclusions

In the shoreline carbonate lagoon deposits of the Yacoraite Formation in Maimará, two distinct subenvironments were identified: A) the subtidal-lower intertidal zone (S-LI), a moderate/high energy shoreline under wave and tide action, and B) the playa-lake zone (PL), a protected supratidal/eulittoral zone, with low energy ephemeral bodies of water.

The invertebrate trace fossils in both zones display low ichnodiversity and are restricted to the shallow tier with substrate penetration of a few centimeters. This is characteristic of sedimentary systems whose palaeoenvironmental conditions (variations in salinity, energy and/or substrate desiccation) were unfavorable for the establishment of a permanent benthic community.

The dinosaur tracks and avian footprints have been preserved in an “optimal preservation area”, extending between the two zones. This means between the edge of the water body, where waves obliterate tracks and more distant zones, where the substrate is too dry to enable track formation.

In view of all the above discussed, in a parsimonious sense, we prefer to assign the ichnoassemblages of the S-LI zone to the *Scoyenia* and *Skolithos* Ichnofacies. However, and following the current knowledge, the ichnofaunas of the PL zone are assigned to the shorebird ichnosubfacies, keeping it as a sub-set within the *Scoyenia* Ichnofacies.

## 10. Acknowledgements

This research was supported by grants PICT 1665 (C. Cónsole-Gonella), PIP 0053 and PI UNRN 40-A-402 (S. de Valais), and CIUNSA 2043 from the Universidad Nacional de Salta (R. Marquillas).

We are grateful to colleagues P. Herrera, P. Machuca, D. Lizarraga and Miguel Griffin for their help in different stages of the fieldwork. Also



thanks to Cristhian Tannenbaum of the Rock Sample Preparation Laboratory of the National University of Salta for his outstanding help in preparing materials. The authors wish to thank the editor David Bottjer and especially Martin Lockley and two anonymous reviewers for their constructively critical reviews.

## References

- Alonso, R.N., 1978. Icnitas de dinosaurio de la Formación Yacoraite (Cretácico superior). Su importancia paleozoogeográfica y cronoestratigráfica. Facultad de Ciencias Naturales, Universidad Nacional de Salta (Professional Thesis).
- Alonso, R.N., 1980. Icnitas de dinosaurios (Ornithopoda, Hadrosauridae) en el Cretácico Superior del norte de Argentina. *Acta Geologica Lilloana* 15, 55–63.
- Alonso, R.N., 1989. Late Cretaceous dinosaur trackways in Northern Argentina. In: Gillette, D., Lockley, M. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Nueva York, pp. 223–228.
- Alonso, R.N., 2007. Dinosaurios salteños y argentinos: un fascinante capítulo en la historia de la Tierra: Salta, Argentina. Crisol Ediciones-UNSA-CONICET (180 p).
- Alonso, R.N., Marquillas, R.A., 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de huellas de aves en la Formación Yacoraite (Maastrichtiano) del Norte Argentino. Abstracts 4<sup>o</sup> Congreso Argentino de Paleontología y Bioestratigrafía 2, 33–41.
- Alpert, S.P., 1974. Systematic review of the genus *Skolithos*. *J. Paleontol.* 48, 661–669.
- Andres, M.S., Reid, R.P., 2006. Growth morphologies of modern marine stromatolites: a case study from Highborne Cay, Bahamas. *Sediment. Geol.* 185, 319–328.
- Apesteegüa, S., de Valais, S., Ríos Cordero, G., Medina Ramírez, O., 2011. First record of dromaeosaurid tracks in South America from the Toro Toro Formation (late Campanian) at Toro Toro (Potosí, Bolivia). *Ameghiniana* 48, 662–667.
- Assereto, R.L.A.M., Kendall, C.G.S.C., 1977. Nature, origin and classification of peritidal tepee structures and related breccias. *Sedimentology* 24 (153–2), 10.
- Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., Uchman, A., 2006. Names for trace fossils: a uniform approach. *Lethaia* 39, 265–286.
- Bohacs, K.M., Carroll, A.R., Neal, J.E., Mankiewicz, P.J., 2000. Lake-basin type, source potential, and hydrocarbon character: an integrated sequence stratigraphic–geochemical framework. In: Gierlowski-Kordesch, E., Kelts, K. (Eds.), *Lake Basins Through Space and Time: American Association of Petroleum Geologists Studies in Geology*. Vol. 46, pp. 3–37.
- Bosac, T., Knoll, A.H., Petroff, A.P., 2013. The meaning of stromatolites. *Annu. Rev. Earth Planet. Sci.* 41, 21–44.
- Braithwaite, C., 2005. *Carbonate Sediments and Rocks*. Whittles Publishing, Dunbeath, Scotland, A Manual for Earth Scientists and Engineers (164 pp).
- Briere, P.R., 2000. Playa, playa lake, sabkha: proposed definitions for old terms. *J. Arid Environ.* 45, 1–7.
- Bromley, R.G., 1981. Concepts in ichnology illustrated by small round holes in shells. *Acta Geol. Hisp.* 16, 55–64.
- Buatois, L.A., Mángano, M.G., 1998. Trace fossil analysis of lacustrine facies and basins. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 140, 367–382.
- Buatois, L.A., Mángano, M.G., 2004. Animal–substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. In: McIlroy, D. (Ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. Geological Society Special Publication Vol. 228, pp. 311–333.
- Buatois, L.A., Mángano, M.G., 2012. The trace-fossil record of organism–matground interactions in space and time. In *Microbial mats in Siliciclastic Sediments*. SEPM Spec. Publ. 101, 15–28 (2011).
- Buatois, L.A., Mángano, M.G., 2011. *Ichnology: Organism–Substrate Interactions in Space and Time*. Cambridge University Press, New York (358 pp.).
- Buatois, L.A., Mángano, M., 2013. Ichnodiversity and ichnodisparity: significance and caveats. *Lethaia* 46, 281–292.
- Camoin, G., Casanova, J., Rouchy, J.M., Blanc-Valleron, M.M., Deconinck, J.F., 1997. Environmental controls on perennial and ephemeral carbonate lakes: the Central Palaeo-Andean Basin of Bolivia during Late Cretaceous to early Tertiary times. *Sediment. Geol.* 113, 1–26.
- Carmona, N.B., Bournod, C.N., Ponce, J.J., Cuadrado, D.G., 2011. The role of microbial mats in the preservation of bird footprints: a case study from the mesotidal Bahía Blanca estuary (Argentina). *SEPM Special Publication No. 101. Microbial Mats in Siliciclastic Depositional Systems Through Time*. pp. 37–45.
- Carmona, N.B., Ponce, J.J., Wetzel, A., Bournod, C.N., Cuadrado, D.G., 2012. Microbially induced sedimentary structures in Neogene tidal flats from Argentina: paleoenvironmental, stratigraphic and taphonomic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 353–355, 1–9.
- Carroll, A.R., Bohacs, K.M., 2001. Lake-type controls on petroleum source rock potential in nonmarine basins. *Am. Assoc. Pet. Geol. Bull.* 85, 1033–1053.
- Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. *Cretac. Res.* 44, 112–121.
- Catuneanu, O., 2006. *Principles of Sequence Stratigraphy*. Elsevier, Amsterdam (386 pp.).
- Cione, A.L., Pereira, S.M., 1985. Los peces de la Formación Yacoraite (Cretácico tardio-Terciario?, Noroeste argentino) como indicadores de Salinidad. *Rev. Asoc. Geol. Argent.* 40, 83–88.
- Clebsch, C.A., 1991. *The Geological Evolution of the Paraguayan Chaco*. PhD Thesis. Texas Tech University.
- Cohen, A.S., 2003. *Paleolimnology: The History and Evolution of Lake Systems*. Oxford University Press, New York (528 pp.).
- Cohen, A.S., Lockley, M., Halfpenny, J., Michel, A.E., 1991. Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *PALAIOS* 6, 371–389.
- Cohen, A.S., Halfpenny, J., Lockley, M.G., Michel, E., 1993. Modern vertebrate tracks from Lake Manyara, Tanzania and their paleobiological implications. *Paleobiology* 19, 433–458.
- Cónsole-Gonella, C.A., Aceñolaza, F.G., 2009. Icnología de la Formación Yacoraite (Maastrichtiano-Daniano) al sur de la localidad de Maimará, Cordillera Oriental de Jujuy, Argentina. *Acta Geológica Lilloana* 21, 100–110.
- Cónsole-Gonella, C.A., Aceñolaza, F.G., 2010. Tafofacies e icnofacies de los niveles maastrichtianos-danianos correspondientes a la Formación Yacoraite, Cordillera Oriental de la provincia de Jujuy, Argentina. *Bol. Soc. Geol. Mex.* 62, 221–231.
- Cónsole-Gonella, C.A., de Valais, S., Sánchez, M.C., Marquillas, R., 2012a. Nuevo registro de huellas de vertebrados en la Formación Yacoraite (Maastrichtiano-Daniano), Maimará, Cordillera Oriental argentina. *Ameghiniana* 49, R141.
- Cónsole-Gonella, C.A., Griffin, M., Cione, A., Gouric Cavalli, S., Aceñolaza, F.G., 2012b. Paleontología de la Formación Yacoraite (Maastrichtiano-Daniano) en el ámbito de la Subcuenca de Tres Cruces, Cordillera Oriental de la provincia de Jujuy, Argentina. In: Marquillas, R., Salfity, J., y Sánchez, M.C. (Eds.), *Aportes Sedimentológicos a la Geología del Noroeste Argentino* (45–56 pp.).
- Cónsole-Gonella, C., de Valais, S., Sánchez, M.C., Marquillas, R.A., Herrera Oviedo, P., 2013. Icnocenos de vertebrados e invertebrados en el Subgrupo Balbuena (Maastrichtiano-Daniano), Quebrada de Humahuaca, noroeste argentino. *II Simposio Latinoamericano de Icnología*, Santa Rosa, La Pampa, p. 34.
- Coombs Jr., W.R., 1980. Swimming ability of carnivorous dinosaurs. *Science* 207, 1198–1200.
- Cornish, F.G., 1986. The trace-fossil Diplocraterion: evidence of animal–sediment interactions in Cambrian tidal deposits. *PALAIOS* 1, 478–491.
- D'Alessandro, A., Bromley, R.G., 1987. Meniscate trace fossils and the *Muensteria-Taenidium* problem. *Palaeontology* 320, 743–763.
- de Deckker, P., 1988. Biological and sedimentary facies of Australian salt lakes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 62, 237–270.
- de Valais, S., Melchor, R.N., 2008. Ichnotaxonomy of bird-like footprints: an example from the Late Triassic–Early Jurassic of Northwest Argentina. *J. Vertebr. Paleontol.* 28, 145–159.
- de Gibert, J.M., Ekdale, A.A., 1999. Trace fossil assemblages reflecting stressed environments in the Middle Jurassic Carmel Seaway of Central Utah. *J. Paleontol.* 73, 711–720.
- de Gibert, J.M., Sáez, A., 2009. Paleohydrological significance of trace fossil distribution in Oligocene fluvial–fan–to-lacustrine systems of the Ebro Basin (Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 272, 162–175.
- de Gibert, J.M., Fregenal-Martínez, M.A., Buatois, L.A., Mángano, M.G., 2000. Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 156, 89–101.
- Díaz-Martínez, I., Suárez-Hernando, O., Martínez-García, B., Hernández, J.M., García Fernández, S., Pérez-Lorente, F., Murelaga, X., 2015. Early Miocene shorebird-like footprints from the Ebro Basin, La Rioja, Spain: palaeoecological and paleoenvironmental significance. *PALAIOS* 30, 424–431.
- Díaz-Martínez, I., de Valais, S., Cónsole-Gonella, C., 2016. First evidence of *Hadrosauropodus* in Gondwana (Yacoraite Formation, Maastrichtian-Danian), northwestern Argentina. *J. Afr. Earth Sci.* 122, 79–87.
- Diedrich, C., 2005. Actupalaeontological trackway experiments with *iguana* on intertidal flat carbonates of the Arabian Gulf – a comparison to fossil *Rhynchosauroides* tracks of Triassic carbonate tidal flat megatracksites in the European Germanic Basin. *Senckenberg. Marit.* 35, 203–220.
- Donato, S.V., Reinhardt, E.G., Boyce, J.I., Pilarczyk, J.E., Jupp, B.P., 2009. Particle-size distribution of inferred tsunami deposits in Sur Lagoon, Sultanate of Oman. *Mar. Geol.* 257, 54–64.
- Doyle, P., Wood, J.L., George, G.T., 2000. The shorebird ichnofacies: an example from the Miocene of southern Spain. *Geol. Mag.* 137, 517–536.
- Duke, W.L., 1984. Paleohydrological analysis of hummocky crossstratified sands indicates equivalence with wave-formed flatbeds: Pleistocene Lake Bonneville deposits, northern Utah. *Am. Assoc. Pet. Geol. Bull.* 68, 472–473.
- Duke, W.L., 1985. Hummocky cross stratification, tropical hurricanes, and intense winter storms. *Sedimentology* 32, 167–194.
- Dunham, R.J., 1962. Classification of carbonate rocks according to depositional texture. *Am. Assoc. Petr. Geol. Mem.* 1, 108–121 (AAPG, Tulsa).
- Ekdale, A.A., Bromley, R.G., 2001. A day and a night in the life of a cleft-foot clam: *Protovirgularia-Lockeia-Lophoctenium*. *Lethaia* 34, 119–124.
- Ekdale, A.A., Bromley, R.G., Pemberton, S.G., 1984. Ichnology: The use of trace fossils in sedimentology and stratigraphy. *SEPM Publication*, Tulsa, Oklahoma (317 pp).
- Eriksson, P.G., Porada, H., Banerjee, S., Bouougri, E., Sarkar, S., Bumby, A.J., 2007. Mat-destroyer features. Chapter 4. In: Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, S., Altermann, W., Catuneanu, O. (Eds.), *Atlas of microbial mat features preserved within the siliciclastic rock record*. Elsevier, Amsterdam, pp. 76–105.
- Eyles, N., Clark, B.M., 1986. Significance of hummocky and swaley cross-stratification in late Pleistocene lacustrine sediments of the Ontario basin, Canada. *Geology* 14, 679–682.
- Ezquerro, R., Doublet, S., Costeur, L., Galton, P.M., Pérez-Lorente, F., 2007. Were non-avian theropod dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* 35, 507–510.
- Fairchild, I., Herrington, P., 1989. A tempestite-stromatolite- evaporite association (late Vendian, East Greenland): A shoreface-lagoon model. *Precambrian Res.* 43: 101–127. [http://dx.doi.org/10.1016/0301-9268\(89\)90007-7](http://dx.doi.org/10.1016/0301-9268(89)90007-7).
- Fariás, M.E., Poiré, D.G., Arrouy, M.G., Albarracín, V.H., 2011. Modern stromatolite ecosystems at alkaline and hypersaline high-altitude lakes in the Argentinean Puna. In:

- Tewari, V., Seckbach, J. (Eds.), *Stromatolites: Interaction of Microbes with Sediments*. Elsevier, Amsterdam, pp. 427–441.
- Fernández, D.E., Pazos, P.J., 2013. Xiphosurid trackways in a Lower Cretaceous tidal flat in Patagonia: palaeoecological implications and the involvement of microbial mats in trace-fossil preservation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 375, 16–29.
- Filho, A.T., Mizusaki, A.M.P., Milani, E.J., Cesero, P., 2000. Rifting and magmatism associated with the South America and Africa break up. *Rev. Bras. Geosci.* 30, 17–19.
- Fillion, D., Pickerill, R.K., 1990. Ichnology of the Lower Ordovician Bell Island and Wabana Groups of eastern Newfoundland. *Palaeontogr. Can.* 7, 1–119.
- Fink, R.J., 2002. Sedimentology and stratigraphy of the Upper Cretaceous–Paleocene El Molino Formation, Eastern Cordillera and Altiplano, central Andes, Bolivia: Implications for the tectonic development of the Central Andes. Louisiana State University (USA) and Agricultural and Mechanical College (116 pp). (Master of Sciences Thesis).
- Fleming, J., 1822. *The Philosophy of Zoology, or A General View of the Structure, Functions, and Classification of Animals*. Vol. 2 (491 pp).
- Flügel, E., 2004. *Microfacies of carbonate rocks. Analysis, interpretation and application*. Springer-Verlag, Berlin-Heidelberg (976 pp).
- Frey, R.W., Pemberton, S.G., Fagerstrom, J.A., 1984. Morphological, ethological and environmental significance of the ichnogenus *Scoyenia* and *Ancorichnus*. *J. Paleontol.* 58, 511–528.
- García Raguél, M., Cuevas González, I., Díaz-Martínez, I., Pérez-Lorente, F., 2009. Fragmentos de roca con huellas de aves en el Terciario de Alcanadre (La Rioja). Descripción, estructuras y problemas de identificación. *Zubia*. 27 pp. 81–158.
- Gavish, E., Krumbein, W.E., Halevy, J., 1985. Geomorphology, mineralogy and ground water geochemistry as factors of the hydrodynamic system of Gavish sabkha. In: Friedman, G.M., Krumbein, W.E. (Eds.), *The Gavish sabkha. Ecological studies* 53. Springer, Verlag, Berlin, pp. 186–217.
- Gayet, M., Marshall, L.G., Sempere, T., Meunier, F.J., Cappetta, H., Rage, J.C., 2001. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecological and palaeobiogeographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 169, 39–68.
- Gebelein, C.D., 1969. Distribution, morphology, and accretion rate of recent subtidal algal stromatolites, Bermuda. *J. Sediment. Petrol.* 39, 49–69.
- Gehling, J.G., 1999. Microbial Mats in Terminal Proterozoic Siliciclastics: Ediacaran Death Masks. *PALAIOS* 14 (1):40–57. <http://dx.doi.org/10.2307/3515360>.
- Genise, J.F., Melchor, R.N., Archangelsky, M., Bala, L.O., de Valais, S., 2009. Application of neochronological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 272, 143–161.
- Genise, J.F., Melchor, R.N., Bellosi, E.S., Verde, M., 2010. Invertebrate and vertebrate Trace Fossils from Continental Carbonates. In: Alonso-Zarza, A.M., Tanner, L.H. (Eds.), *Carbonates in continental Settings. Developments in Sedimentology* Vol. 61, pp. 319–369.
- Hall, J., 1847. *Palaeontology of New York: Volume I. Containing Descriptions of the Organic Remains of the Lower Division of the New York System, (Equivalent of the Lower Silurian Rocks of Europe)*. C. van Benthuysen, Albany, 338 pp.
- Haldeman, S.S., 1840. Supplement to number one of “A monograph of the Limniades, and other fresh water univalve shells of North America”, containing descriptions of apparently new animal in different classes, and the names and characters of the subgenera in *Paludina* and *Anculosa* Philadelphia. 3 pp.
- Hallam, A., 1991. Relative importance of regional tectonics and eustasy for the Mesozoic of the Andes. In: Mac Donald, I.M., (Ed.), *Sedimentation, tectonics and eustasy. Sea level changes at active margins*. Int. Assoc. Sedimentol. Spec. Publ. 12, 189–200.
- Häntzschel, W., 1975. Trace fossils and problematica. In: Teichert, C. (Ed.), *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement I*. Geological Society of America, Boulder and University of Kansas, Lawrence (W1–W269).
- Hobday, D.K., 1978. Geological evolution and geomorphology of the Zululand coastal plain. In: Allanson, B.R. (Ed.), *Ecology and biogeography of Lake Sibaya*. The Hague, Junk, pp. 1–20.
- Hunt, A.P., Lucas, S.G., 2005. Tetrapod ichnofacies and their utility in the Paleozoic. In: Buta, R.J., Rindsberg, A.K., Kopaska-Merkel, D.C. (Eds.), *Pennsylvanian footprints in the Black Warrior basin of Alabama*. Alabama Paleontological Society Monograph Vol. 1, pp. 113–119.
- Hunt, A.P., Lucas, S.G., 2007. Tetrapod ichnofacies: a new paradigm. *Ichnos* 14, 59–68.
- Hunt, A.P., Lucas, S.G., 2016. The case for archetypal vertebrate ichnofacies. *Ichnos* 23, 237–247.
- Jahanert, R.J., Collins, L.B., 2011. Significance of subtidal microbial deposits in Shark Bay, Australia. *Mar. Geol.* 286, 106–111.
- Jahanert, R.J., Collins, L.B., 2012. Characteristics, distribution and morphogenesis of subtidal microbial systems in Shark Bay, Australia. *Mar. Geol.* 306, 115–136.
- Jaillard, E., Cappetta, J., Ellenberger, P., Feist, M., Grambast-Fessard, N., Lefranc, J.P., Sigé, B., 1993. Sedimentology, paleontology, biostratigraphy and correlation of the Late Cretaceous Vilquechico Group of Southern Peru. *Cretac. Res.* 14, 623–661.
- James, U.P., 1879. Descriptions of new species of fossils and remarks on some others from the Lower and Upper Silurian rocks of Ohio. *The Paleontologist* 3, 17–24.
- Johnson, K.R., 1986. Paleocene bird and amphibian tracks from the Fort Union Formation, Bighorn Basin, Wyoming. *Contrib. Geol.* 24, 1–10.
- Kah, L.C., Bartley, J.K., Frank, T.D., Lyons, T.W., 2006. Reconstructing sea-level change from the internal architecture of stromatolite reefs: an example from the Mesoproterozoic Sulky Formation, Dismal Lakes Group, arctic Canada. *Can. J. Earth Sci.* 43, 653–669.
- Keighley, D.G., Pickerill, R.K., 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology* 37, 305–337.
- Keighley, D.G., Pickerill, R.K., 1995. The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. *Ichnos* 3, 301–309.
- Kim, J.Y., 1994. A unique occurrence of *Lockeia* from the Yeongheung Formation (Middle Ordovician), Yeongweol, Korea. *Ichnos* 3, 219–225.
- Kim, K.S., Lockley, M.G., Kim, J.Y., Seo, S.J., 2012. The smallest dinosaur tracks in the world: occurrences and significance of *Minisauripus* from East Asia. *Ichnos* 19, 66–74.
- Krapovickas, V., Ciccioli, P.L., Mángano, M.G., Marsicano, C., Limarino, C.O., 2009. Paleobiology and paleoecology of an arid–semiarid Miocene South American ichnofauna in anastomosing fluvial deposits. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 284, 129–152.
- Krapovickas, V., Mancuso, A.C., Arcucci, A., Caselli, A., 2010. Fluvial and eolian ichnofaunas from the Lower Permian of South America. *Geol. Acta* 8, 449–462.
- Kvale, E.P., Johnson, G.D., Michelson, D.L., Keller, K., Furer, L.C., Archer, A.W., 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. *PALAIOS* 16, 233–254.
- Laporte, L.F., Behrensmeier, A.K., 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. *J. Sediment. Res.* 50, 1337–1346.
- Leanza, A.F., 1969. Sistema de Salta. Su edad, sus peces voladores, su asincronismo con el Horizonte Calcáreo-Dolomítico y con las Calizas de Miraflores y la hibridez del Sistema Subandino. *Rev. Asoc. Geol. Argent.* 24, 393–407.
- Leonardi, G., 1981. As localidades con rastros fósiles de tetrapódos na América Latina. II Congreso Latinoamericano de Paleontología. *Anais* 2, 929–940.
- Leonardi, G., 1984. Le impronte fossili di dinosauri. In: Bonaparte, J.F., Colbert, E.H., Currie, P.J., de Ricqlès, A., Kielan-Jaworowska, Z., Leonardi, G., Morello, N., Taquet, P. (Eds.), *Sulle orme dei dinosauri*, pp. 165–186 (Venice).
- Lockley, M.G., 1986. The paleobiological and paleoenvironmental importance of dinosaur footprints. *PALAIOS* 1, 37–47.
- Lockley, M.G., 2007. A tale of two ichnologies: the different goals and missions of invertebrate and vertebrate ichnotaxonomy and how they relate in ichnofacies analysis. *Ichnos* 14, 39–57.
- Lockley, M.G., Harris, J., 2010. On the trail of early birds: a review of the fossil footprint records of avian morphological and behavioral evolution. In: Ulrich, P.K., Willetts, J.H. (Eds.), *Trends in Ornithology Research*. Nova Publishers, Hauppauge, pp. 1–63.
- Lockley, M.G., Milner, A.R.C., 2006. Tetrapod tracksites from the Shinarump Formation (Chinle Group, Upper Triassic) of Southwestern Utah. *N. M. Mus. Nat. Hist. Sci. Bull.* 37, 257–262.
- Lockley, M.G., Hunt, A., Meyer, C., 1994. Vertebrate tracks and the ichnofacies concept: implications for palaeoecology and palichnostratigraphy. In: Donovan, S.K. (Ed.), *The Paleobiology of Trace Fossils*. John Wiley and Sons, Chichester, pp. 241–268.
- Lockley, M., Schulp, A.S., Meyer, C.A., Leonardi, G., Mamani, D.K., 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretac. Res.* 23, 383–400.
- Lockley, M.G., Nadon, G., Currie, P.J., 2003. A diverse dinosaur–bird footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: implications for ichnotaxonomy. *Ichnos* 11, 229–249.
- Logan, B.W., 1961. Cryptozoon and associate stromatolites from the recent, Shark Bay, Western Australia. *J. Geol.* 69, 517–533.
- Logan, B.W., Rezak, R., Ginsburg, R.N., 1964. Classification and environmental significance of algal stromatolites. *J. Geol.* 72, 68–83.
- Lucas, S.G., Spielmann, J.A., Klein, H., Lerner, A.J., 2010. Ichnology of the Upper Triassic (Apachean) Redonda Formation, east-central New Mexico. *N. M. Mus. Nat. Hist. Sci. Bull.* 47, 1–75.
- McCrea, R.T., Lockley, M.G., Meyer, C.A., 2001. Global distribution of purported track occurrences. In: Carpenter, K. (Ed.), *The armored dinosaurs*. Indiana University Press, Bloomington and Indianapolis, pp. 413–454.
- MacEachern, J.A., Pemberton, S.G., Gingras, M.K., Bann, K.L., 2007. The ichnofacies paradigm, a fifty year retrospective. In: Miller III, W. (Ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, pp. 50–75.
- MacEachern, J.A., Bann, K.L., Gingras, M.K., Zonneveld, J.K., Dashtgard, S.E., Pemberton, S.G., 2012. The ichnofacies paradigm. In: Knaust, D., Bromley, R. (Eds.), *Developments in Sedimentology, 64, Trace Fossils as Indicators of Sedimentary Environments*, pp. 103–138.
- Mackenzie, D.B., 1975. Tidal sand flat deposits in Lower Cretaceous Dakota Group near Denver, Colorado. In: Ginsburg, R.N. (Ed.), *Tidal Deposits*. Springer-Verlag, New York, pp. 117–125.
- Mángano, M.G., Buatois, L.A., 2004. Reconstructing Early Phanerozoic intertidal ecosystems: ichnology of the Cambrian Campanario Formation in northwest Argentina. In: Trace Fossils in Evolutionary Palaeoecology. In: Webby, B.D., Mángano, M.G., Buatois, L.A. (Eds.), *Fossils Strata*. 51, pp. 17–38.
- Mángano, M.G., Buatois, L.A., Aceñolaza, G.F., 1996. Trace fossils and sedimentary facies from an Early Ordovician tide-dominated shelf (Santa Rosita Formation, northwest Argentina): implications for ichnofacies models of shallow marine successions. *Ichnos* 5, 53–88.
- Mángano, M.G., Buatois, L.A., West, R.R., Maples, C.G., 1998. Contrasting behavioral and feeding strategies recorded by tidal-flat at bivalve trace fossils from the Upper Carboniferous of eastern Kansas. *PALAIOS* 13, 335–351.
- Mansilla, H., de Valais, S., Stinnesbeck, W., Varela, N., Leppe, M., 2012. New avian tracks from the Upper Paleocene to Lower Eocene at Fossil Hill, King George Island, Antarctica. *Antarct. Sci.* 24, 500–506.
- Marquillas, R.A., 1985. Estratigrafía, sedimentología y paleoambientes de la Formación Yacoraita (Cretácico Superior) en el tramo austral de la cuenca, norte argentino. (Tesis Doctoral). Universidad Nacional de Salta, pp. 1–139.
- Marquillas, R.A., del Papa, C., Sabino, I.F., Heredia, J., 2003. Prospección del límite K/T en la cuenca del Noroeste, Argentina. *Rev. Asoc. Geol. Argent.* 2, 271–274.
- Marquillas, R.A., del Papa, C., Sabino, I.F., 2005. Sedimentary aspects and paleoenvironmental evolution of a rift basin: Salta Group (Cretaceous–Paleogene), northwestern Argentina. *Int. J. Earth Sci.* 94, 94–113.
- Marquillas, R.A., Sabino, I., Nóbrega Sial, A., del Papa, C., Ferreira, V., Matthews, S., 2007. Carbon and oxygen isotopes of Maastrichtian–Danian shallow marine



- carbonates: Yacoraita Formation, northwestern Argentina. *J. S. Am. Earth Sci.* 23, 304–320.
- Marquillas, R.A., Salfity, J.A., Matthews, S.J., Matteini, M., Dantas, E., 2011. U-Pb zircon age of the Yacoraita Formation and its significance to the Cretaceous-Tertiary boundary in the Salta basin, Argentina. In: Salfity, J.A., Marquillas, R.A. (Eds.), *Cenozoic geology of the Central Andes of Argentina*. SCS Publisher, Salta, pp. 227–246.
- Marsicano, C.A., Mancuso, A.C., Palma, R.M., Krapovickas, V., 2010. Tetrapod tracks in a marginal lacustrine setting (Middle Triassic, Argentina): taphonomy and significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 291, 388–399.
- Martin, A.J., 2013. *Life traces of the Georgia coast. Revealing the unseen lives of plants and animals*. Indiana University Press, Indiana (692 pp.).
- Marty, D., Strasser, A., Meyer, C.A., 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* 16, 127–142.
- Melchor, R.N., 2015. Application of vertebrate trace fossils to palaeoenvironmental analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 439:79–96. <http://dx.doi.org/10.1016/j.palaeo.2015.03.028>.
- Melchor, R.N., Bedatou, E., de Valais, S., Genise, J.F., 2006. Lithofacies distribution of invertebrate and vertebrate trace fossil assemblages in an Early Mesozoic ephemeral fluvial system: implications for the Scoyenia ichnofacies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239, 253–285.
- Meyer, C.A., Hippler, D., Lockley, M.G., 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia—facts and implications. VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires. Asociación Paleontológica Argentina, Publicación Especial. Vol. 7, pp. 133–138.
- Milner, A.R.C., Lockley, M.C., Kirkland, J.I., 2006. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. *N. M. Mus. Nat. Hist. Sci. Bull.* 37, 315–328.
- Minter, N.J., Krainer, K., Lucas, S.G., 2007. Paleogeology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 246, 390–423.
- Moroni, A.M., 1984. *Mtchedilshvilia saltenia* n. sp. en sedimentitas del Grupo Salta, provincia de Salta. Abstracts Congreso Argentino de Paleontología y Biostratigrafía, Corrientes. Vol. 3 pp. 129–139.
- Motts, W.S., 1972. Some hydrologic and geologic processes influencing playa development in Western United States. In: Reeves Jr., C.C. (Ed.), *Playa Lake Symposium*, 89–106. ICASALS Publication no. Lubbock, TX, p. 4.
- Nicholson, H.A., 1873. Contributions to the study of the errant annelids of the older Paleozoic rocks. *Proceedings of the Royal Society of London* 21, 90–288.
- Netto, R.G., 2007. Skolithos-dominated piperock in non-marine environments: an example from the Triassic Catarruta Formation, southern Brazil. In: Bromley, R.G., Buatois, L.A., Mángano, M.G., Genise, J.F., Melchor, R.N. (Eds.), *Sediment–Organism Interactions: a Multifaceted Ichnology*. SEPM Spec. Publ. 88.
- Netto, R.G., Rossetti, D.F., 2003. Ichnology and salinity fluctuations: a case study in the Early Miocene (Lower Barreiras Succession) of São Luís Basin, Maranhão, Brazil. *Revista Brasileira de Paleontologia* 6, 5–18.
- Osgood, R.G., 1970. Trace fossils of the Cincinnati area. *Palaeontogr. Am.* 6, 281–444.
- Ostrom, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* 30, 1–165.
- Paik, I.S., Kim, H.J., Lee, Y.I., 2001. Dinosaur track-bearing deposits in the Cretaceous Jindong Formation, Korea: occurrence, palaeoenvironments and preservation. *Cretac. Res.* 22, 79–92.
- Paik, I.S., Huh, M., Park, K.H., Hwang, K.G., Kim, K.S., Kim, H.J., 2006. Yeosu dinosaur track sites of Korea: the youngest dinosaur track records in Asia. *J. Asian Earth Sci.* 28, 457–468.
- Panin, N., Avram, E., 1962. Noe urme de vertebrate in Miocenul Subcarpaților rominești. *Studii și Cercetări de Geologie* 7, 455–484.
- Pazos, P.J., Lazo, D.G., Tunik, M., Marsicano, C.A., Fernández, D.E., Aguirre Urreta, M.B., 2012. Palaeoenvironmental framework of dinosaur tracksites and other ichnofossils in the Early Cretaceous mixed siliciclastic-carbonate deposits in the Neuquén Basin, northern Patagonia (Argentina). *Gondwana Res.* 22, 1110–1124.
- Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma. *J. Paleontol.* 56, 843–881.
- Pereda-Suberbiola, X., Galton, P.M., Mallison, H., Novas, F., 2012. A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation. *Alcheringa. An Australas. J. Paleontol.* <http://dx.doi.org/10.1080/03115518.2012.702531>.
- Plička, M., Uhrová, J., 1990. New trace fossils from the Outer Carpathian flysch (Czechoslovakia). *Acta Musei Moraviae, Scientiae Naturales* 75, 53–59.
- Poyato-Ariza, F.J., Wenz, S., 2002. A new insight into pycnodontiform fishes. *Geodiversitas* 24, 139–248.
- Quattrocchio, M., Ruiz, L., Volkheimer, W., 2000. Palynological zonation of the Paleogene of the Colorado and Salta Group basin, Argentina. *Rev. Esp. Micropaleontol.* 32, 61–78.
- Raskovsky, M.A., 1968. Relevamiento geológico del sector sur del yacimiento “Los Berthos”. Seminario II. Universidad Nacional de Tucumán. Facultad de Ciencias Naturales, Salta. (41 pp.) Unpublished.
- Reineck, H.E., Gerdes, G., Claes, M., Dunajtschik, K., Riege, H., Krumbein, W.E., 1990. Microbial modification of sedimentary surface structures. In: Heling, D., Rothe, P., Förstner, U., Stoffers, P. (Eds.), *Sediments and Environmental Geochemistry Selected Aspects and Case Histories*, pp. 254–276.
- Reyes, F.C., 1972. Correlaciones en el Cretácico de la cuenca andina de Bolivia, Perú y Chile. *Revista Técnica de Y.P.F. Bolivianos* 1, 101–104.
- Richter, R., 1937. Marken und Spuren aus allen Zeiten. I–II. *Senckenbergiana* 19, 150–169.
- Rindsberg, A.K., 2012. Ichnotaxonomy: finding patterns in a welter of information. In: Knaust, D., Bromley, R. (Eds.), *Trace Fossils as Indicators of Sedimentary Environments. Development in Sedimentology* Vol. 6, pp. 45–78.
- Sabino, I., 2002. *Geología del Subgrupo Pírgua (Cretácico) del noroeste argentino*. Universidad Nacional de Salta, Salta, Doctoral thesis (261 pp.).
- Salfity, J.A., 1980. *Estratigrafía de la Formación Lecho (Cretácico) en la Cuenca Andina del Norte Argentino*. Universidad Nacional de Salta, Salta, Doctoral thesis (91 pp.).
- Salfity, J.A., 1982. *Evolución paleogeográfica del Grupo Salta (Cretácico-Eogénico)*, Argentina. Abstract 5th Congreso Latinoamericano de Geología 1, 11–25.
- Salfity, J., Zambrano, J.J., 1990. Cretácico. In: Bonaparte, J.F., Toselli, A.J., Aceñolaza, F.G. (Eds.), *Geología de América del Sur. Serie Correlación Geológica* Vol. 2, pp. 185–289.
- Salfity, J.A., Marquillas, R.A., Gardeweg, M.C., Ramírez, C., Davidson, J., 1985. Correlaciones en el Cretácico Superior del norte de Argentina y Chile. Abstracts 4th Congreso Geológico Chileno 4, 654–667.
- Sánchez, M.C., Marquillas, R.A., 2010. Facies y ambientes del Grupo Salta (Cretácico paleógeno) en Tumbaya, Quebrada de Humahuaca, Provincia de Jujuy. *Rev. Asoc. Geol. Argent.* 67, 383–391.
- Sánchez Rioja, H.S., 2004. *Estudio de las icnitas de dinosaurio de la Formación Yacoraita (Cretácico Superior), en la quebrada del Acheral (Salta): su implicancia paleobiológica y paleoambiental*. Universidad Nacional de Salta, Salta, Doctoral Thesis (78 pp.).
- Santi, G., Nicosia, H., 2008. The ichnofacies concept in vertebrate ichnology. *Studi trentini di scienze naturali. Acta Geol.* 83, 223–229.
- Sarjeant, W.A.S., Langston Jr., W., 1994. Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of Trans-Pecos Texas. *Texas Memorial Mus. Bull.* 36 (86 pp.).
- Sarjeant, W.A.S., Reynolds, R.E., 2001. Bird footprint from the Miocene of California. In: Reynolds, R.E. (Ed.), *The Changing Face of the East Mojave Desert*. Abstracts from the 2001 Desert Symposium, California, pp. 21–40.
- Schlirf, M., Uchman, A., Kümmel, M., 2001. Upper Triassic (Keuper) non-marine trace fossils from the Hassberge area (Franconia, southeastern Germany). *Paläontol. Z.* 75, 71–96.
- Schwab, K., 1984. Contribución al conocimiento del sector occidental de la cuenca sedimentaria del Grupo Salta (Cretácico-Eogénico) en el noroeste argentino. Abstract 9th Congreso Geológico Argentino 1, 586–604.
- Scott, J.J., Renaud, R.W., Owen, R.B., Buatois, L.A., 2009. Trace fossils in exhumed surfaces around saline lakes: an example from Lake Bogoria, Kenya Rift Valley. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 272, 176–198.
- Scott, J.J., Buatois, L.A., Mángano, M.G., 2012. Lacustrine environments. In: Knaust, D., Bromley, R. (Eds.), *Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology* Vol. 64, pp. 379–417.
- Scrivner, P.J., Bottjer, D.J., 1986. Neogene avian and mammalian tracks from Death Valley National Monument, California: their context, classification and preservation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 57, 285–331.
- Seilacher, A., 1953. *Studien zur Palichnologie II. Die fossilen Ruhespuren (Cubichnia)*. Neues Jahrb. Geol. Paläontol. Abh. 98, 87–124.
- Seilacher, A., Seilacher, E., 1994. Bivalvian trace fossils: a lesson from actiopaleontology. *Cour. Forschungsinst. Senck.* 169, 5–15.
- Sempere, T., Butler, R.F., Richards, D.R., Marshall, L.G., Sharp, W., Swisher, C.C., 1997. Stratigraphy and chronology of Upper Cretaceous–Lower Paleogene strata in Bolivia and northwest Argentina. *Geol. Soc. Am. Bull.* 109, 709–727.
- Shinn, E.A., 1983. Tidal flat environment. In: Scholle, P.A., Bebout, D.G., Moore, C.H. (Eds.), *Carbonate Depositional Environments*. AAPG Mem. Vol. 33, pp. 171–210.
- Sial, A.N., Ferreira, V.P., Toselli, A.J., Parada, M.A., Aceñolaza, F.G., Pimentel, M.M., Alonso, R.N., 2001. Carbon and oxygen isotope compositions of some Upper Cretaceous–Paleocene sequences in Argentina and Chile. *Int. Geol. Rev.* 43, 892–909.
- Thulborn, T., 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome sandstone (lower cretaceous), Western Australia. *PLoS One* 7, e36208. <http://dx.doi.org/10.1371/journal.pone.0036208>.
- Trotter, G., 1964. *Contribution à l'étude des Andes Nord-péruviennes*. Doctoral Thesis, University of Grenoble.
- Tucker, M.E., Wright, V.P., 1990. *Carbonate Sedimentology*. Blackwell Scientific Publications, Oxford (482 pp.).
- Uchman, A., Mikuláš, R., Rindsberg, A.K., 2011. Mollusc trace fossils *Ptychoplasma* Fenton and Fenton, 1937 and *Oravaichnium* Plicka and Uhrová, 1990: their type material and ichnospecies. *Geobios* 44, 387–397.
- Uliana, M.A., Biddle, K.T., Cerdán, J., 1988. Mesozoic extension and formation, Argentine sedimentary basins. In: Tankard, A., Balkwill, H.R. (Eds.), *Extensional Tectonics and Stratigraphy of the North Atlantic Margins*. American Association of Petroleum Geologists Memoirs Vol. 46, pp. 599–614.
- Van Dijk, D.E., Hobday, D.K., Tankard, A.J., 1978. Permo-Triassic lacustrine deposit in the eastern Karoo Basin, South Africa. In: Matter, A., Tucker, M.E. (Eds.), *Modern and ancientlake sediments; proceedings of a symposium*. Int. Assoc. Sedimentol. Spec. Publ. 2, pp. 225–239.
- Vialov, O.S., 1965. *Stratigrafiya neogenovix molass Predcarpatskogo progiba: Naukova Dumka (Kiev)*, Part K (191 pp.).
- Vila, B., Castanera, D., Marmi, J., Canudo, J.J., Galobart, A., 2014. Crocodile swim tracks from the latest Cretaceous of Europe. *Lethaia* 48, 256–266.
- Voigt, S., Lucas, S.G., Krainer, K., 2013. Coastal-plain origin of trace-fossil bearing red beds in the Early Permian of Southern New Mexico, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 369, 323–334.
- Vossler, S.M., Pemberton, S.G., 1988. Ichnology of the Cardium Formation (Pembina Oilfield): implications for depositional and sequence stratigraphic interpretations. In: James, N.P., Leckie, D.A. (Eds.), *Sequences, Stratigraphy, sedimentology: surface and subsurface*. Can. Soc. Petrol. Geol. Mem. 15, 237–254.

- Whyte, M.A., Romano, M., 1994. Probable sauropod footprints from the Middle Jurassic of Yorkshire, England. In: Lockley, M.G., Dos Santos, V.F., Meyer, C.A., Hunt, A.P. (Eds.), *Aspects of Sauropod Paleobiology*. Gaia Vol. 10, pp. 15–26.
- Whyte, M.A., Romano, M., 2001. A dinosaur ichnocoenosis from the Middle Jurassic of Yorkshire, UK. *Ichnos* 8, 223–234.
- Wigforss-Lange, J., 2007. Tidal facies in the Upper Silurian Öved-Ramsåsa Group of Scania, Sweden: linkages of radial and cerebroid ooids and evaporite tracers to subtidal, lagoonal environment. *GFF* 129, 7–16.
- Yang, S., 1984. Silurian trace fossils from the Yangzi Gorges and their significance to depositional environments. *Acta Palaeontol. Sin.* 23, 705–714.