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Rodríguez-de la Rosa, Rubén A.; Velasco-de León, María Patricia; Arellano-Gil, Javier; Lozano-Carmona, Diego Enrique

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Rubén A. **Rodríguez-de la Rosa**, María Patricia **Velasco-de León**, Javier **Arellano-Gil**, Diego Enrique **Lozano-Carmona**

Rubén A. Rodríguez-de la Rosa
ruben_raptor@yahoo.com
Unidad Académica de Ciencias Biológicas, Unidad Académica de Ciencias de la Tierra, Universidad Autónoma de Zacatecas, Campus II, Calzada Solidaridad, esq. Paseo de la Bufa s/n, C.P. 98060, Zacatecas, Mexico.

María Patricia Velasco-de León
Diego Enrique Lozano-Carmona
Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Campus II, Batalla 5 de mayo s/n esquina Fuerte de Loreto, Ejército de Oriente, Iztapalapa, C.P. 09230, CDMX, Mexico.

Javier Arellano-Gil
Facultad de Ingeniería, Universidad Nacional Autónoma de México, Av. Universidad 3000, Ciudad Universitaria, Coyoacán C.P. 04510, CDMX, Mexico.

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ABSTRACT

A track-bearing locality in one of the shores of the Ñumí River, near the City of Tlaxiaco, northwestern Oaxaca, southern Mexico, preserves the footprints of sauropod and theropod dinosaurs; it is located within the stratigraphic sequence of the Zorrillo-Taberna Indiferenciadas Formation, of Middle Jurassic (Bajocian) age. A well-preserved manus-pes set of ankylosaurian affinity (*Tetrapodosaurus*) is preserved on a rock block from this formation. These tracks are preserved as convex hyporeliefs. The pes impression is tetradactyl, with ventrally curved toe tips, suggesting that these were deeply impressed in the sediment. Manus impression is pentadactyl, with short and blunt digits. A curved structure preserved together with these footprints is herein interpreted to be a tail drag. The stratigraphic unit from whence this block came was identified and two additional ankylosaurian tracks, were found preserved *in situ* as natural sandstone casts. An isolated handprint, has the same features that fit the ankylosaurian hand morphology; however, some features such as a medio-lateral concavity are indicative of the presence of a well-developed palmar pad, and could suggest the functional mechanics of the ankylosaurian manus. The Zorrillo-Taberna Indiferenciadas Formation is a coal-bearing formation; after the global record, ankylosaur footprints are concentrated in coal-bearing and floodplain facies, thus suggesting, that at least the North American Ankylosauria were adapted to similar paleoecological conditions from Middle Jurassic to Early Cretaceous times. It represents the second report of ankylosaurian tracks from Mexico and the southernmost record of the ichnogenus *Tetrapodosaurus* in North America. In this way, it suggests a geographic *continuum* in the record of the Ankylosauria to southern North America during Middle Jurassic times. With their Middle Jurassic age, these footprints represent the oldest ankylosaurian ichnofossils known to date.

Keywords: Ankylosauria, *Tetrapodosaurus*, Ichnology, Middle Jurassic, Oaxaca, Mexico.

RESUMEN

Una localidad icnofosilífera en una de las orillas del Río Ñumí en las cercanías de la Ciudad de Tlaxiaco, noroeste de Oaxaca, al sur de México, conserva las huellas de dinosaurios saurópodos y terópodos; esta se localiza dentro de la secuencia estratigráfica de la Formación Zorrillo-Taberna Indiferenciadas, de edad Jurásico Medio (Bajociano). Se identificó un conjunto de pie-mano de afinidad anquilosauriana (Tetrapodosaurus) en un bloque de roca procedente de esta formación; las huellas se encuentran conservadas como hiporrelieves convexos. El pie es tetradáctilo, con las puntas de los dedos curvadas ventralmente, sugiriendo que éstas fueron impresas profundamente en el sedimento. La mano es pentadáctila, con dedos pequeños y romos. Una estructura curvada, conservada junto a las huellas, es interpretada aquí como un arrastre de cola. El estrato original de procedencia del bloque portador de las huellas, fue identificado y dos huellas adicionales de anquilosaurios fueron encontradas in situ, conservadas como rellenos naturales de arenisca. Un relleno natural de una mano fue encontrado de forma aislada; éste presenta los mismos caracteres morfológicos de la mano anquilosauriana; sin embargo, algunas características como la concavidad medio lateral de la zona palmar indica la presencia de un cojinete, y podría sugerir la mecánica funcional de la mano anquilosauriana. La Formación Zorrillo-Taberna Indiferenciadas es una formación con estratos de carbón; en otras secuencias sedimentarias las huellas de anquilosaurios se concentran en facies aluviales y portadoras de carbón, esto sugiere que al menos los Ankylosauria norteamericanos estaban adaptados a condiciones paleoecológicas similares, desde el Jurásico Medio al Cretácico Temprano. Este trabajo representa el segundo reporte de huellas de anquilosaurios en México, y el más sureño del icnogénero Tetrapodosaurus en Norte América; sugiriendo un continuum geográfico en el registro de Ankylosauria, hasta el sur de Norte América durante el Jurásico Medio. Además, son los icnofósiles más antiguos de anquilosaurios conocidos hasta este momento.

Palabras clave: Ankylosauria, Tetrapodosaurus, Icnología, Jurásico Medio, Oaxaca, México.

1. Introduction

During paleontological fieldwork in search for paleobotanical sites, one of the authors (MPVL) found a locality bearing dinosaur footprints in the Ñumí River, near the City of Tlaxiaco, northwestern Oaxaca, in southern Mexico (figures 1, 2). The locality preserves the footprints of sauropod and theropod dinosaurs (figures 3, 4) (Lozano-Carmona, 2012; Rodríguez-de la Rosa, 2014, 2015; Rodríguez-de la Rosa *et al.*, 2014); it is located within the stratigraphic sequence of the Zorrillo-Taberna Indiferenciadas Formation, of Middle Jurassic age (Carrasco-Ramírez, 1981; González-Torres, 1989; Corro-Ortiz and Ruíz-González, 2011). This geological formation preserves a notable record of fossil plants of Bennettitales, Caytoniales, Equisetales, Filicales, conifers and Ginkgoales (Silva-Pineda *et al.*, 2007; Lozano-Carmona, 2012; Velasco-de León *et al.*, 2013; Velasco-de León *et al.*, 2015; Lozano-Carmona and Velasco-de León, 2016). The study of this dinosaur tracksite started in a consecutive field season; however, it was noted that a fallen rock block in front of the main track-bearing surface (Figure 4) contained dinosaur tracks, preserved as natural casts in its underside. Among these tracks is a well-preserved manus-pes set of an ankylosaurian dinosaur.

Ankylosaurian remains have been collected in Mexico, mainly from northern states such as Baja California, Chihuahua and Coahuila. Among the most common ankylosaur remains found in Mexico are teeth and osteoderms, an isolated vertebra, and a few limb elements have also been found (Rivera-Sylva and Espinosa-Chávez, 2006; Rivera-Sylva *et al.*, 2011; Martínez-Díaz and Montellano-Ballesteros, 2011). Kappus *et al.* (2011) mentions the presence of ankylosaur tracks near Ciudad Juárez, Chihuahua, northern Mexico. However, these authors present only illustrated outline drawings of the tracks, and do not specify which one of the illustrated specimens was found in Mexico, or if the specimen is available or lost as other specimens mentioned in their work. Furthermore, the ankylosaur tracks are referred to as "*Ankylosauripus*" and/or "*Tetrapodosauripus*" (Kappus *et al.*, 2011: 281), when both names are inexistent. Therefore, the purpose of this paper is to report these tracks, noting that due to their Middle Jurassic age, they represent the oldest ankylosaurian ichnofossils known to date.

2. Geological setting

The study area is located in the Tlaxiaco Basin, which is placed in the boundary between the Zapoteco and Mixteco terrains (Dávalos-Álvarez, 2006); both terrains in contact along the Caltepec lateral fault (Sedlock *et al.*, 1993). The late Aalenian (early Middle Jurassic) Ñumí Conglomerate (or Cualac Conglomerate) is the oldest unit within the local stratigraphic column (Corro-Ortiz and Ruíz-González, 2011). The Tecocoyunca Group is a very fossiliferous rich unit overlying the Ñumí Conglomerate, with an age that ranges from the Bajocian to Callovian (Erben, 1956; Sandoval and Westermann, 1986; Lozano-Carmona and Velasco-de León, 2016). According to Carrasco-Ramírez (1981) the Tecocoyunca Group is composed of four formations that, in ascending stratigraphic order are, the Zorrillo-Taberna Indiferanciadas Formation, Simón, Otatera, and Yucuñuti formations. Subsequently, González-Torres (1989) divided the Tecocoyunca Group into two subgroups: a lower unit comprising the Zorrillo-Taberna Indiferenciadas and Simón formations, and an upper unit comprising the Otatera and Yucuñuti formations (Figure 5). The youngest Jurassic unit outcropping in the area corresponds to a marine environment unit named Caliza con *Cidaris* (*Cidaris*-bearing limestone) of Oxfordian age (Carrasco-Ramírez, 1981). The only post-Jurassic formation outcropping in the area is the Albian-Cenomanian Teposcolula Formation of marine origin, composed of carbonate platform limestones (Pérez-Ibargüengoitia *et al.*, 1965).

The rock block containing the ankylosaurian footprints belongs to the Zorrillo-Taberna Indiferen-

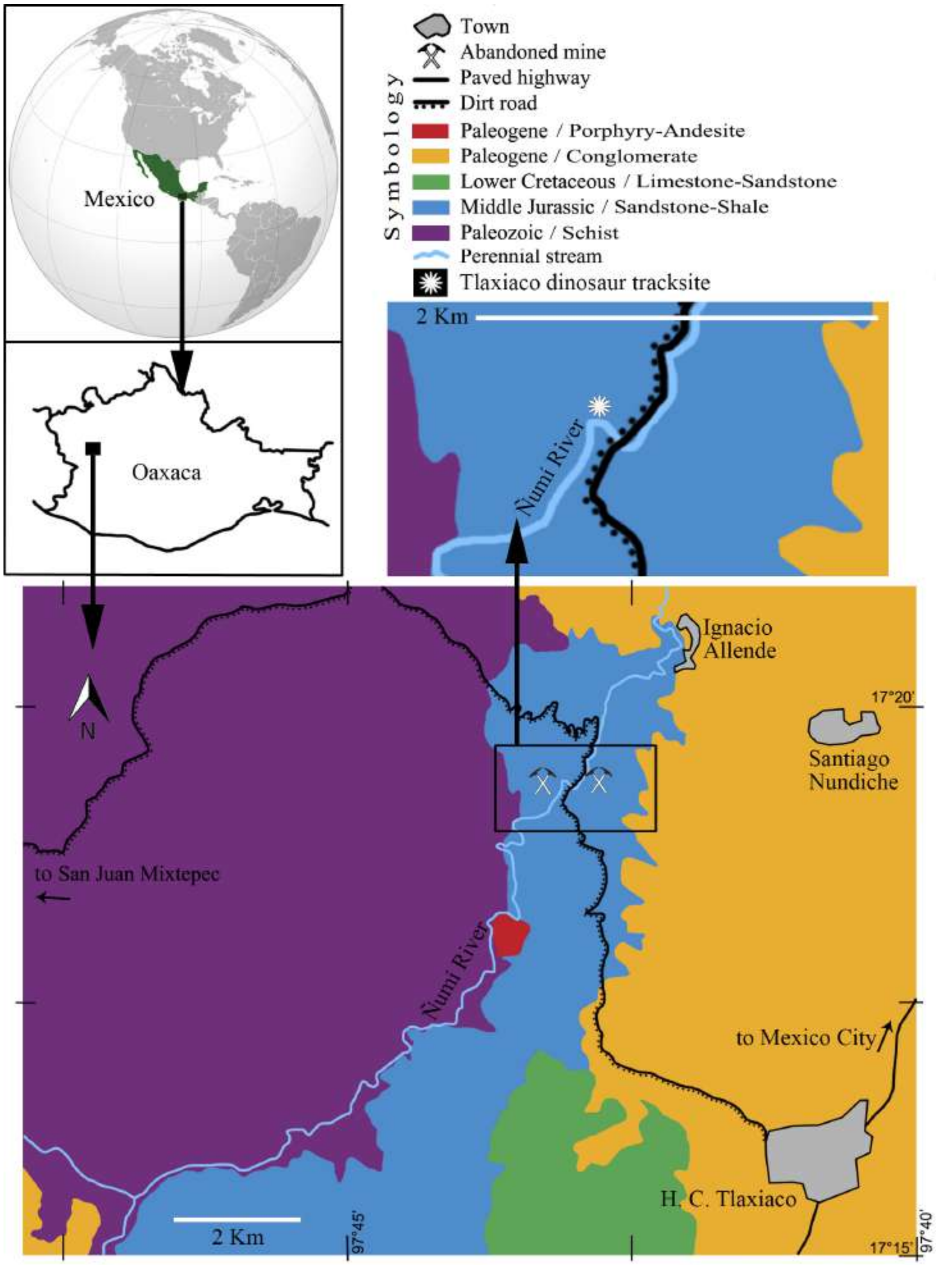

Figure 1 Regional map and geographic location of the Tlaxiaco tracksite (white asterisk), near the Ñumí River, northwest from the City of Tlaxiaco, western Oaxaca, southern Mexico.

ciadas Formation of Middle Jurassic (Bajocian) age. This age was determined due to its content of the ammonites: *Duashnoceras* Westermann, *Leptosphinctes* Buckman and *Parastrenoceras* Ochoterena from the Taberna Formation (Sandoval and Westermann, 1986). The Zorrillo-Taberna Indiferenciadas Formation is a succession of sandstones (subarkoses, litharenites and graywackes), shale, and thin coal beds. The shale layers are tabular-shaped and 10 – 40 cm in thickness; the sandstone layers are irregular and discontinuous with a thickness of 20 – 70 cm. In the case of the ankylosaurian tracks, these are preserved as natural casts or convex hyporeliefs in a sandstone layer, while the tracks and/or concave epireliefs were originally registered in a shale layer.

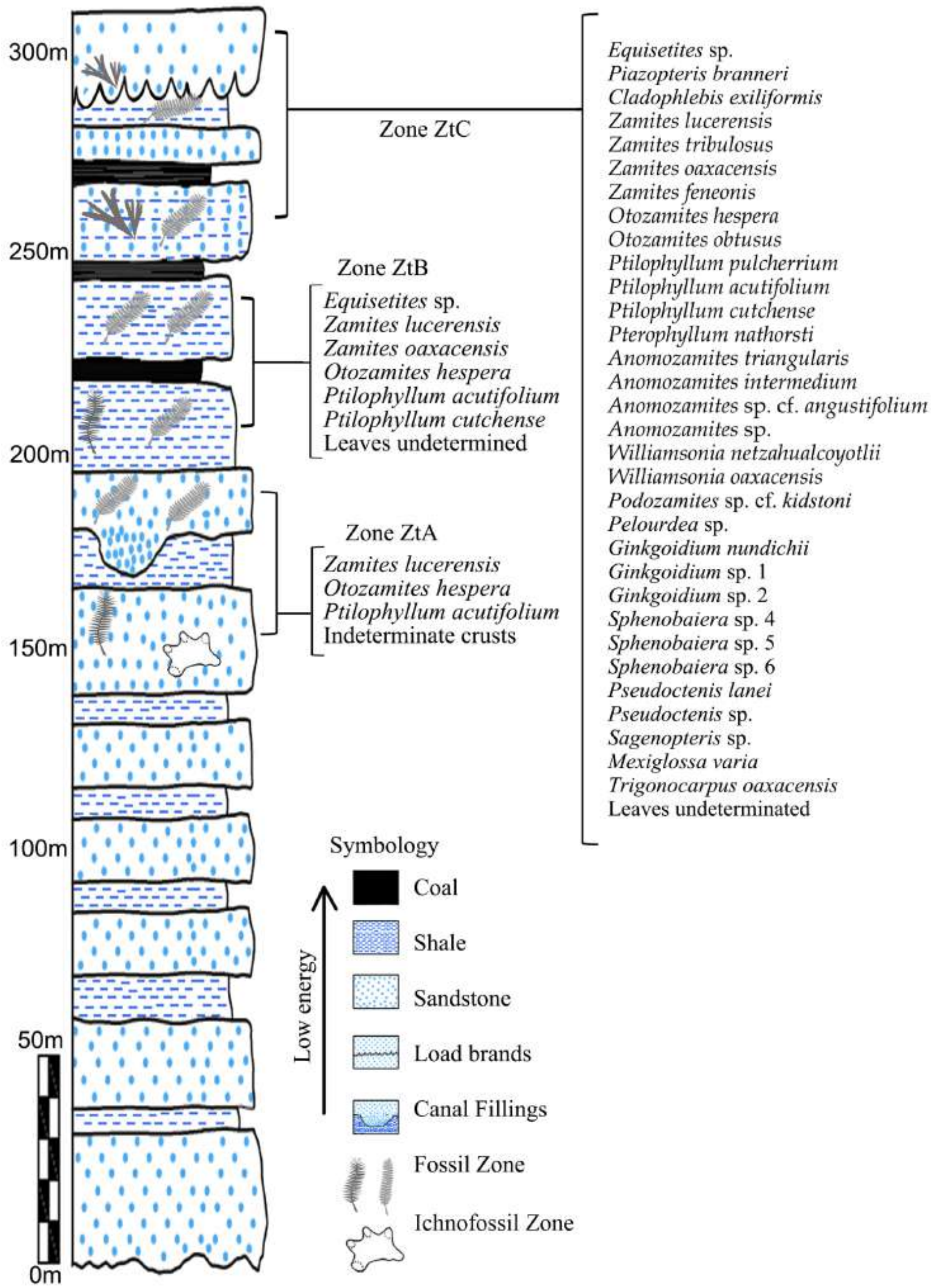

Figure 2 Stratigraphic column near Ñumí River, at 150 – 190 m footprints are indicated.

3. Material and methods

The outline of the ankylosaurian tracks was drawn on a plastic sheet using waterproof ink markers; additionally, silicon rubber molds and resin casts of the ankylosaur footprints were made. These, and other materials, are now housed at the Paleontological Collection of the Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México under the catalogue numbers: CFZ-Zt 305, ankylosaur manus and pes; and CFZ-Zt 306, an ankylosaur manus natural sand-

Figure 3 General view of the Tlaxiaco tracksite. Black arrows point to the two different footprint concentrations. To the left, badly-preserved footprints, these were left in a water-saturated sediment; to the right, well-preserved footprints of sauropod and theropod dinosaurs. The white arrowhead points to the rock block with the ankylosaur footprints. The site of provenance of this block is marked with the white asterisk.

stone cast. Measurements of the tracks were taken using standard metric tapes, a Vernier caliper and a conventional protractor.

4. Results

Systematic ichnology
Ichnofamily Tetrapodosauridae Sternberg, 1932
Ichnogenus *Tetrapodosaurus* Sternberg, 1932
Tetrapodosaurus isp.
(Figure 6)

4.1. MATERIAL

The fallen rock block bears at least three ankylosaurian tracks preserved as natural casts (convex hyporeliefs), as well as plant leaves (Figure 6A, B). In the case of the ankylosaurian tracks, a manus-pes set and a partial pes were recognized (Figure 6C); the block is composed of fine-grained sandstone; however, as mentioned above, the tracks were originally preserved in a carbonaceous shale layer. The catalogue codes are CFZ-Zt 305 for the ankylosaur manus and pes, and CFZ-Zt 306 for the ankylosaur manus natural sandstone cast.

4.2. DESCRIPTION

Pes impression is tetradactyl (Figure 6C); this impression presents a well-defined rounded heel, short and stout digits I and II, digits III, and IV slightly elongated, with faintly acuminated tips; these are curved and show an outward orientation. Additionally, digits III and IV preserve ventrally curved toe tips, suggesting that these were deeper impressed in the sediment. Pes impression measures 33 cm in maximum antero-posterior length and 26 cm in maximum medio-lateral width. The interdigital angles are of 22º for digits I – II, 41.5º for digits II – III, and of 25.5º for digits III – IV; thus, the digit total divarication is of 89º (digits I – IV). The distance between the toe tips is 9 cm for

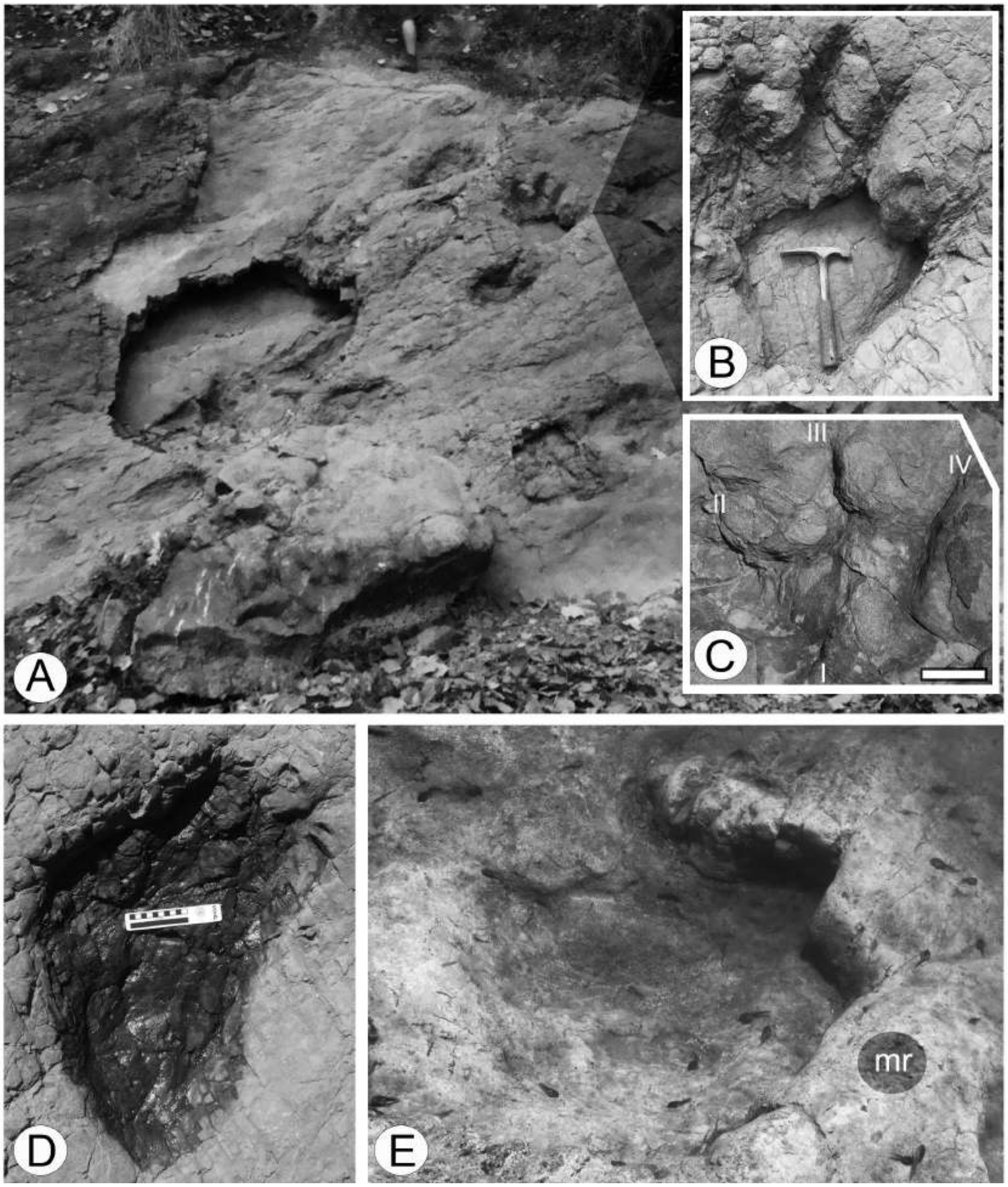

Figure 4 Dinosaur footprints at the Tlaxiaco tracksite. A. General view of the outcrop; B. Sauropod footprint, partially overstepped by a large theropod; C. Collapsed theropod footprint, note the hallux impression (I), and digits II to IV; D. Sauropod footprint, with digits rotated to the right; E. Sauropod footprint, this footprint is not in direct association with the ones above mentioned, instead it was discovered under the water of Ñumí River, note the well-defined claws, mudrim (mr) and tadpoles that arrive to the footprint after it was cleaned. Hammer for scale in B, the scale in C and D equals 10 cm.

digits I – II, 17.5 cm for digits II – III, and 10.2 cm for digits III – IV. The anterior portion of a second pes impression is preserved in one of the block ridges, thus it is possible that it forms a single step, 63.5 cm in length, with the pes impression previously described (Figure 6C).

Manus impression is pentadactyl and fits the outline of a rough pentagon (Figure 6C); it is clear that a manual pad is present; it is wider than long, being 21 cm and 16 cm, respectively; digit V is observed as a small bump located posterolaterally, while the other digits are short and blunt (Figure

6C). The angles between digits is 55.5º between digits I – II, 33º between digits II – III, 55.5º between digits III – IV, and 55º between digits I – V. Thus, the digit total divarication is 199º (digits I – V).

A curved structure is preserved together with these footprints. It is slightly elongate, forming an arch, with an acute posterior end and a wider anterior portion; it is here presumed to be a tail drag (Figure 6A).

4.3. COMMENTS

In spite of these tracks representing a manus-pes set, the manus track represents a right one and pes track represents a left one (Figure 7C). It implies that the manus-pes set belongs to a single individual organism and/or that the footprints had a distribution due to a particular mode of locomotion. A third possibility is that these tracks represent overstepping of two individuals traveling in the same direction.

The original level containing the ankylosaurian tracks was identified through petrographic slides through the track-bearing rock block and associated rock layer (Figure 3), both being litarenite. In addition to this, two other ankylosaurian tracks were identified *in situ* (Figure 8). These are preserved as natural sandstone casts; although weathered, it is possible to note one hand impression (Figure 8).

Additionally, an isolated sandstone cast of a hand was found, as an eroded footprint-bearing layer (Figure 7). This natural cast presents the same morphological features as the hand impression described above; it suggests the presence of a palmar pad in these ankylosaur tracks, in having small and rounded digital impressions (Figure 7A, B). It is wider than long, being 26.3 cm and 16 cm, respectively; digit V is observed as a small bump located posterolaterally, while the other digits are short and blunt (Figure 7A, B; compare with Figure 6C). The angles between digits is 55º between digits I – II, 42º between digits II – III, 30º between digits III – IV, and 58º between digits IV – V. Thus, the total digit divarication is 185º (digits I – V). An additional interesting feature of this natural cast is that it preserves a palmar surface with a medium-lateral concavity (Figure 7C); suggesting that the original footprint was not homogeneously impressed in the sediment; this feature is, perhaps, indicative of the functional mechanics of the ankylosaurian manus (Figure 7C, D). Small patches of faint skin impressions are preserved in some areas of this hand natural cast (Figure 7E). A photograph of the palmar view of the nodosaurid *Edmontonia* hand was digitally superimposed to this cast, the fit was remarkable (Figure 7D).

5. Discussion

5.1. PRODUCER OF THE TRACKS

The Tlaxiaco tracks contain obvious features such as tetradactyl pes and pentadactyl manus; the general features of these tracks allow the comparison with those of ankylosaurs and ceratopsians (McCrea *et al.*, 2001). McCrea *et al.* (2001), refer to some morphological criteria that help to discriminate between ceratopsian and ankylosaur footprints. For this purpose, the authors compared the general morphology of two ichnogenera, *Tetrapodosaurus* and *Ceratopsipes*, which represent the tracks of ankylosaurs and ceratopsians, respectively (Carpenter, 1984; Lockley and Hunt, 1995; McCrea *et al.*, 2001). Although *Tetrapodosaurus* and *Ceratopsipes* have a pentadactyl manus, it is small in proportion to the pes size in *Ceratopsipes* and larger in proportion to the pes size in *Tetrapodosaurus* (McCrea *et al.*, 2001). One of the most conspicuous differences is that digits are better defined in *Tetrapodosaurus* than in *Ceratopsipes* (McCrea *et al.*, 2001). The pes in both ichnogenera are tetradactyl; however, *Ceratopsipes* pes is roughly symmetrical in outline (Lockley and Hunt, 1995), it has shorter toe impressions (*i.e.*, with more enclosing flesh), and the inner digit (digit I) is larger than in *Tetrapodosaurus* (McCrea *et al.*, 2001). *Tetrapodosaurs* bears an asymmetrical pes and longer toe impressions (*i.e.*, with less enclosing flesh) and a shorter inner digit or digit I (McCrea *et al.*, 2001). Based on these features, the Tlaxiaco

ERA	PERIOD	EPOCH	AGE	MIXTECO TERRANE			
				Otlaltepec B.	Ayuquila B.	Tezoatlán B.	Tlaxiaco B.
MESOZOIC	JURASSIC	UPPER	TITHONIAN		F. Mapache		
			KIMERIDG.		F. Mapache / F. Chimeco		
			OXFORDIAN		F. Chimeco		
		MIDDLE	CALLOVIAN	F. Otlaltepec	F. Tecomazúchil	G. Tecocoyunca: F. Yucuñuti, F. Otatera	G. Tecocoyunca: F. Yucuñuti, F. Otatera
			BATHONIAN	F. Otlaltepec	F. Ayuquila	G. Tecocoyunca: F. Simón, F. Taberna	G. Tecocoyunca: F. Simón, F. Z-T I
			BAJOCIAN	F. Otlaltepec	F. Ayuquila	G. Tecocoyunca: F. Zorrillo	G. Tecocoyunca: F. Z-T I
			AALENIAN	F. Piedra Hueca		Cg. Cualac	Cg. Ñumi/Cg. Cualac
		LOWER	TOARCIAN			F. Rosario	
			PLIENSBACH.			F. Rosario	
			SINEMURIAN				
			HETTANGIAN			U. Diquiyú	
	TRIASSIC					U. Diquiyú	

Figure 5 Comparative table of the Jurassic outcropping lithographs in the Mixteco Terrane. F. Z-T I, means Zorrillo-Taberna Indiferenciadas Formation.

tracks are undisputable, ankylosaurian in origin.
McCrea *et al.* (2001) reviewed the global record of ankylosaur tracks; these authors summarized the ichnogenera considered as produced from ankylosaurian dinosaurs and included *Tetrapodosaurus* Sternberg, 1932; *Deltapodus* Whyte and Romano, 1994; *Macropodosaurus* Zakharov, 1964; *Metatetrapous* Nopcsa, 1923, and *Ligabueichnium* Leonardi, 1984.

Initially, the ichnogenus *Macropodosaurus* was considered as produced from a theropod dinosaur (Zakharov, 1964); however, McCrea *et al.* (2001), based the similarity of the pes impressions and compared this ichnogenus to *Metatetrapous*, originally considered as produced by an ankylosaur by Haubold (1971). However, some authors still relate the ichnogenus *Macropodosaurus* to segnosaurian theropods (Sennikov, 2006).

Ligabueichnium, was established by Leonardi (1984) for a trackway from the El Molino Formation (Potosí Group), in Bolivia; the author suggested a possible relationship with a ceratopsid or an ankylosaur; however, in a subsequent work, he mentioned that "*Ligabueichnium bolivianum* may be attributed to an unusually large Ankylosauria" (Leonardi, 1994: 39) and it is now considered as ankylosaurian in origin by several authors (McCrea *et al.*, 2001). In regard to *Deltapodus*, Whyte and Romano (1994) reported this ichnotaxon from the Middle Jurassic of Yorkshire, England; they interpreted it, as made by a sauropod dinosaur. Lockley *et al.* (1994) subsequently reinterpreted these tracks as produced by a thyreophoran dinosaur; currently, *Deltapodus* is widely considered as an ichnotaxon made by stegosaurian dinosaurs (*e.g.*, Milàn and Chiappe, 2009; Mateus *et al.*, 2011).

The ichnogenus *Tetrapodosaurus* was established by Sternberg (1932), based on a trackway found in sediments of the Lower Cretaceous Gething Formation in British Columbia, Canada. Although, it was initially interpreted as ceratopsian in origin, it is now attributed with confidence to nodosaurid ankylosaurs (McCrea *et al.*, 2001). In addition to a tetradactyl pes with well-developed heel and pentadactyl manus, the general morphology of the Tlaxiaco tracks strongly resembles that of *Tetrapodosaurus*.

Regarding a possible ceratopsian origin for the Tlaxiaco tracks, it is necessary to mention that the earliest record of ceratopsians are teeth collected in late Early Cretaceous sediments of the Arundel and Cedar Mountain formations in U.S.A. (Chin-

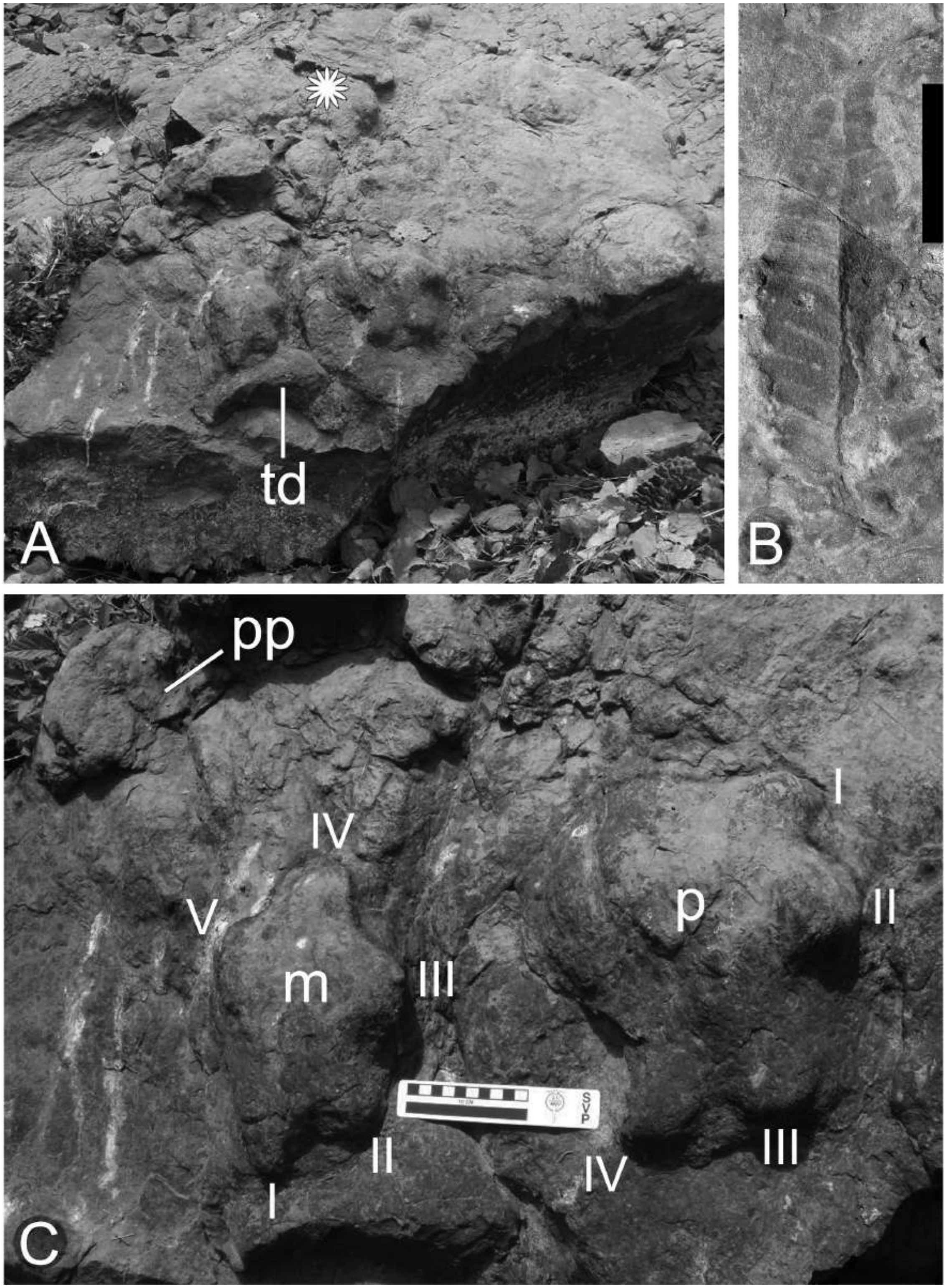

Figure 6 Ankylosaur footprints in the rock block. A. General view of the block, note the ankylosaur footprints (*Tetrapodosaurus*) at the center of the photograph and the supposed impression of a tail drag (td), the white asterisk is in the place of a well-preserved *Zamites lucerensis* leaf detailed in B; C. Ankylosaur footprints (*Tetrapodosaurus*), note the pentadactyl manus (m, digits I – V) and the tetradactyl pes (p, digits I – IV). Note the ventrally impressed digits II to IV of the pes (p) and a partial pes (pp) at the upper-left of the photograph. Scale for B equals 2 cm, scale in C equals 10 cm.

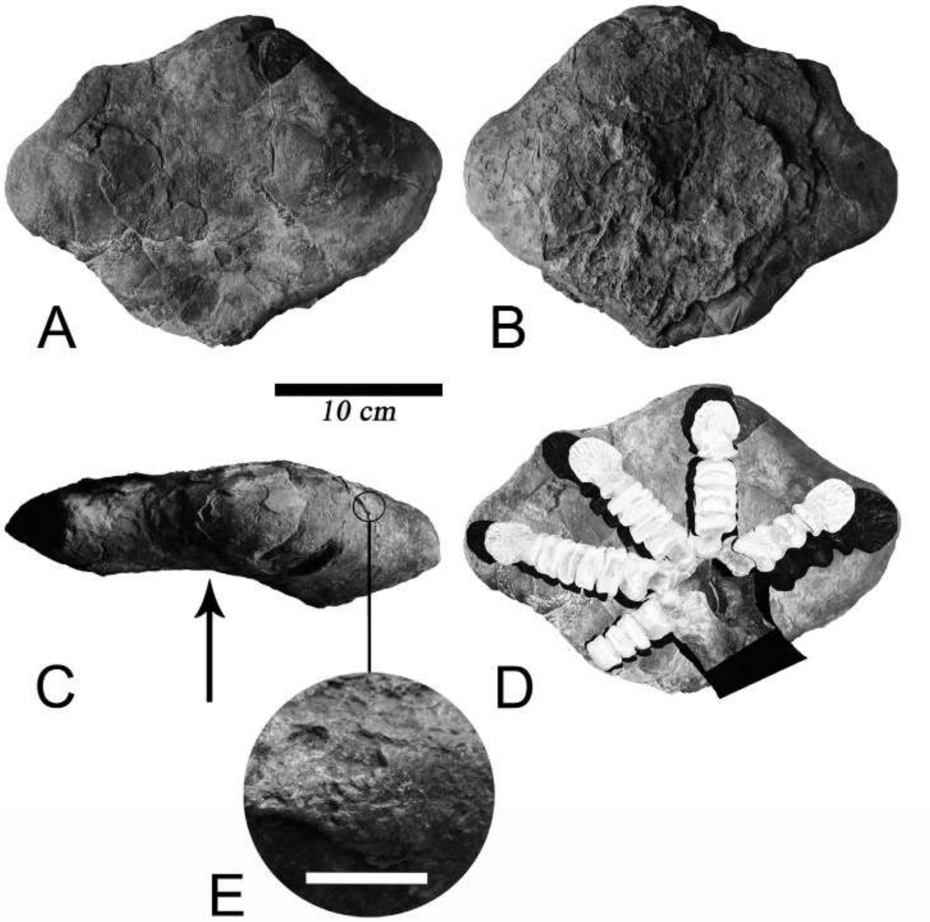

Figure 7 CFZ-Zt 306, ***Tetrapodosaurus*** **manus. It is a right manus natural sandstone cast. A. Palmar view; B. Dorsal view; C. Distal view; D. Palmar view of sandstone cast and superimposed skeletal manus elements of the nodosaur** ***Edmontonia*** **(in white color), the black color ones are modified to fit the digit position as suggested by the natural cast; E. Possible skin impressions. Scale in E equals 1cm.**

nery *et al.*, 1998). However, the earliest record of large ceratopsians is known from Turonian deposits of Moreno Hill Formation in New Mexico (Wolfe and Kirkland, 1998). In this way, being of Middle Jurassic age, ceratopsians are discarded as the trackmakers of the Tlaxiaco tracks. Ankylosaurian dinosaurs are known to occur since the Middle Jurassic in Europe and Asia (Galton, 1983; Zhiming, 1993; Carpenter *et al.*, 1998; Kirkland *et al.*, 1998). In North America, the earliest record of ankylosaurs comes from the Late Jurassic Morrison Formation (Kirkland and Carpenter, 1994; Carpenter *et al.*, 1998); in fact, the sediments of the Morrison Formation of Western Colorado have yielded the only ankylosaur track known from the Late Jurassic (Hups *et al.*, 2008). This track resembles the manus of *Tetrapodosaurus* and has been illustrated by Lockley *et al.* (2014).

The Tlaxiaco ankylosaur pes preserves the toe tips, digits III and IV, in such a form that indicates these were deeply impressed in the sediment. A similar situation has been mentioned by McCrea *et al.* (2001); these authors noted that some Cenomanian *Tetrapodosaurus* tracks from the Dunvegan Formation of British Columbia, Canada, preserve deeply impressed tip digits, and were impressed in rather dried sediment. In addition, McCrea *et al.* (2001) mention two ankylosaur trackways, from the Maastrichtian El Molino Formation of Bolivia; where the trackways "seem to suggest that the tracks were perhaps made on an overlying layer of sediment and represent the penetration of the distal portion of the toes into an under layer" (Mc Crea *et al.*, 2001: 442).

Findings from Canada and Bolivia together with the Tlaxiaco ankylosaur footprints, could yield insights into the mechanical function of the anklylosaur pes, at least suggesting a good subjection to the ground; perhaps for the use of the tail. Indeed, a similar condition could be suggested by the isolated natural cast of the hand from Tlaxiaco (Figure 7) that bears a well-developed palmar pad with a ventral medio-lateral concavity (Figure 7C). This suggests that the original footprint was not homogeneously impressed in the sediment; a feature suggesting, as well, part of the functional mechanics of the ankylosaurian manus. Some authors have suggested that a palmar pad is an unexpected feature for ankylosaurs (Senter, 2011); this based on track morphology of the hand impressions, as well as the ankylosaurian metacarpal configuration (Senter, 2011). However, the features of the three ankylosaur hand impressions from Tlaxiaco support the presence of a palmar pad.

Together with the tracks, a supposed tail drag is preserved; no tail impressions are known to occur associated to ankylosaur footprints. However, in regard to this, nodosaurid dinosaurs had a longer tail than that present in ankylosaurids (Carpenter, 1982, 1984). For example, the ankylosaurid *Euoplocephalus* had 21 caudal vertebrae; while it has been estimated 40 to 50 caudal vertebrae for nodosaurids, such as *Sauropelta* (Carpenter, 1982, 1984). It is thus possible that some nodosaurids left an occasional tail drag.

Most of the early members of Ankylosauria were small; forms such as *Mymoorapelta* and *Gargoyleosaurus* in North America, *Tianchisaurus* in Asia, and *Cryptodraco* and *Dracopelta* in Europe, were not longer than 3 m (Galton, 1983; Carpenter, 1984; Zhiming, 1993; Kirkland and Carpenter, 1994; Carpenter *et al.*, 1998). However, the nodosaur *Sauropelta*, which has been regarded as the trackmaker of the *Tetrapodosaurus* tracks (Carpenter, 1984; McCrea *et al.*, 2001), was an organism with a calculated length and weight of approximately 5.2 m and 1500 kg, respectively (Carpenter, 1984). When compared with the data raised from *Sauropelta* and *Tetrapodosaurus* footprint size (Carpenter, 1984; McCrea *et al.*, 2001; Sternberg, 1932), the Tlaxiaco *Tetrapodosaurus* tracks suggest an organism *ca.* 3.8 m in length and nearly 1 t in weight.

5.2. PALEOENVIRONMENTAL CONDITIONS

The plant macrofossils associated with the Tlaxiaco dinosaur footprints include Bennettitales, the most diverse order with 17 of the 34 species identified in the plant community; among these, *Zamites lucerensis* (Wieland) Person and Delevoryas, 1982 and *Otozamites hespera* Wieland, 1914, are abundant, while *Anomozamites triangularis* (Nathorst) Pott and McLoughlin, 2009; *Anomozamites* sp. cf. *intermedium* Antevs, 1919 as well as *Zamites* sp., are rather rare. Conifers are represented by *Podozamites* sp. cf. *kidstonii* Etheridge, in Jack and Etheridge, 1892. *Mexiglossa varia* Delevoryas and Person, 1975 and *Trigonocarpus oaxacensis* Wieland, 1914 are common and frequent respectively, however, both are of uncertain taxonomic position (Lozano-Carmona, 2012; Lozano-Carmona and Velasco-de León, 2016). The order Ginkgoales is represented by several new species within the genera *Ginkgoidium* and *Sphenobaiera* (Velasco-de León *et al.*, 2015). Ferns are important herbaceous elements and, together with Equisetales, have been associated to a climate with humid seasons (Van Konijnenburg-Van Citter, 2002; Rojas-Chávez, 2010); while the genera of conifers identified in the Jurassic of Mexico have been associated to a warm climate (Person and Delevoryas, 1982). However, the presence of Ginkgoales and Coniferales in the study area suggests a rough mountain relief, temperate and mesic conditions, as well as little variations in the local climate (Rees *et al.*, 2000; Wang *et al.*, 2005; Zhou, 2009).

The identified flora bears a high percentage of small leaves; in this case, 72% of the identified plants had microphyl leaves with an area between

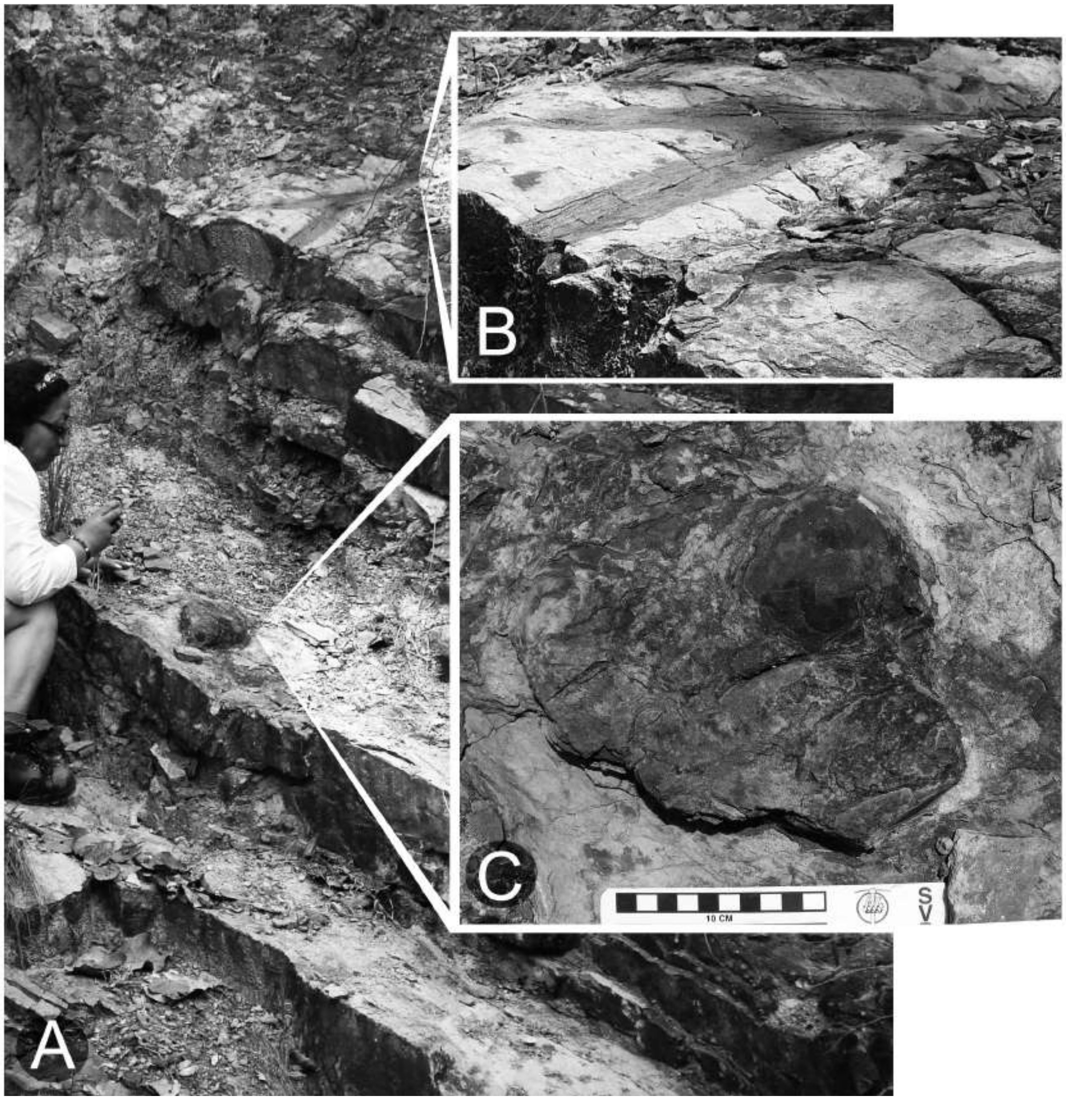

Figure 8 Location of provenance of the rock block bearing *Tetrapodosaurus* footprints. A. The site is marked with a white asterisk in Figure 3; B. Fossilized log; C. *In situ* manus sandstone cast in dorsal view (scale 10 cm).

0.08241 to 1.3660 cm^2 (Lozano-Carmona, 2012; microphyl 1 type *sensu* Ortiz-Martínez *et al.*, 2013). This feature indicates the dominance of a sub-warm, sub-humid climate, and with periods of low water circulation in the floodplain allowed the swamps establishment; these swamps accumulate a great amount of organic matter that formed the coal layers, 1.5 m thick, present in the Zorrillo-Taberna Indiferenciadas Formation. The paleobasin was subject to a continuous subsidence that permitted the homogeneous depositional and environmental conditions during its formation (Corro-Ortiz and Ruíz-González, 2011). The plant remains preserved in the Zorrillo-Taberna Indiferenciadas Formation surely were part of the diet of the Middle Jurassic herbivorous dinosaur communities present at the Tlaxiaco area, included is the nodosaurid ankylosaur, represented by these *Tetrapodosaurus* tracks.

In regard to the paleoecological conditions, the Tlaxiaco nodosaurid ankylosaur tracks were found in a coal-bearing formation, such as the Zorrillo-Taberna Indiferenciadas Formation. This observation agrees with that of McCrea *et al.* (2001);

these authors mention that ankylosaur footprints are concentrated in coal-bearing and floodplain facies. Also, ankylosaurs seem to have a preference for well-vegetated and well-watered lowlands (McCrea *et al.*, 2001). This environmental condition is supported by the great amount of coal and plant remains found in the Zorrillo-Taberna Indiferenciadas Formation (Lozano-Carmona, 2012; Velasco-de Léon *et al.*, 2013). Even more, well preserved *Zamites lucerensis* leaves were found preserved in the same surface of the *Tetrapodosaurus* footprints (Figure 6B).

The fact that the Tlaxiaco nodosaurid ankylosaur tracks are preserved in a coal-bearing formation, such as the Zorrillo-Taberna Indiferenciadas Formation, suggest that at least the North American Ankylosauria was adapted to similar paleoecological conditions since Middle Jurassic times.

6. Conclusions

The presence of *Tetrapodosaurus* tracks in the south of Mexico indicates the existence of a geographic *continuum* in the record of the Ankylosauria to southern North America during Middle Jurassic times. Also, these footprints represent the oldest ankylosaurian ichnofossils known to date. In this way, the ankylosaur diversity at the Middle Jurassic seems represented by at least two body sizes, small and medium, for these thyreophoran dinosaurs.

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