

Pentadactyl ankylosaurian manus tracks from the Lower Cretaceous of Galve (Teruel, Spain): first occurrence of *Tetrapodosaurus* in the Iberian Peninsula

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Abstract

Introduction This work is a detailed description of ankylosaurian natural casts found in Galve (Teruel, Spain), with the identification and classification of the major dynamic and static structures that depend on the phase of autopodial (hand) movement.

Geological setting Specimens come from the Lower Cretaceous (Barremian) of the eastern sector of the Iberian Range. The depositional environment is of continental coastal influence with both fluvial and tidal current structures.

Material and methods We studied the morphology and main features of approximately 50 manus casts of *Tetrapodosaurus*. The structures were correlated with the different stages of the movement during the formation of the print (footprint formation phases of Thulborn and Wade 1989).

Description We describe the prints, lithological composition and the features observed at the top, the base and the walls of the casts (striae, lineations, grooves and polygonal scales) for understand the autopodial shape, the response of the pads and the hand movement.

Comparative palaeoichnology Manus prints of sauropods, stegosaurs and ankylosaurs may show a similar morphology. However, the presence of five perfectly-distinct, protruding and separate digits in the Galve specimens make these ichnites incompatible with those of stegosaurs or with those of sauropods.

Discussion We examine the original definition and the diagnosis of *Tetrapodosaurus*, including other similar pentadactyl tracks; also the global distribution and palaeoenvironments of these ankylosaurian ichnites, and the possible affinities of the trackmaker.

Conclusions The first citation of *Tetrapodosaurus* in Galve (Spain) confirms the palaeontological importance of this area, due to the variety of sites and dinosaur fossil types found. Careful examination of the casts has allowed reconstruction of the kinds of joint and forelimb movements that are independent of, but consistent with, interpretations based on functional aspects of the forelimb skeleton. The structures observed in the walls and in the base of the casts indicate that the digital pads of the ankylosaur hands were flexible calluses.

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Keywords Ankylosauria · Tracks · Natural casts of Manus · *Tetrapodosaurus* · Teruel · Iberia

Resumen

Introducción En este trabajo se describen los contramoldes encontrados en Galve (Teruel, España), con la identificación y clasificación de las estructuras dinámicas y

estáticas que dependen de la fase del movimiento del autopodio (mano).

Geología Los contramoldes son del Cretácico Inferior (Barremiense) del sector Este de la Cordillera Ibérica. El ambiente sedimentario es continental costero con influencia tanto de corrientes fluviales como de marea.

Material y métodos Estudiamos la forma y estructuras principales de unos 50 contramoldes de mano de *Tetrapodosaurus*. Las estructuras se ha correlacionado con los estados de movimiento durante la formación de la huella (fases de formación de la huella de Tulborn y Wade, 1989).

Descripción Describimos las huellas, la composición litológica del relleno y las estructuras observadas en el techo, base y paredes de los contramoldes (estrias, lineaciones, acanaladuras y escamas poligonales) para investigar la forma del autopodio, la respuesta de las almohadillas y el movimiento de la mano.

Paleoicnología comparada Las huellas de mano de saurópodos, estegosaurios y anquilosaurios pueden tener forma similar. No obstante las huellas de Galve tienen cinco dedos identificables que sobresalen y están perfectamente aislados y separados., lo que hace que estas icnitas sean incompatibles con las de estegosaurios o con las de saurópodos.

Discusión Examinamos la definición original y la diagnosis de *Tetrapodosaurus* junto con la de otras huellas pentadáctilas similares; también la distribución mundial y paleoambientes en las que están las huellas de anquilosaurios así como sus afinidades posibles de los autores.

Conclusiones Esta primera cita de *Tetrapodosaurus* en Galve (España) confirma la importancia paleontológica de la zona, debido a la variedad de yacimientos y tipos de dinosaurio encontrados allí. El examen cuidadoso de los contramoldes permite la reconstrucción del tipo de articulaciones y del movimiento de las extremidades delanteras, independientemente aunque coincidentes con las interpretaciones basadas en los aspectos funcionales del esqueleto. Las estructuras observadas en las paredes y en la base de los contramoldes indican que las almohadillas dactilares de las manos de los anquilosaurios con callosidades flexibles.

Palabras clave Ankylosauria · icnitas · contramoldes de mano · *Tetrapodosaurus* · Teruel · Península Ibérica

1 Introduction

The Galve syncline (Teruel) is a rich palaeontological area (Ruiz-Omeñaca et al. 2004) where a large amount of work on dinosaurs and their tracks has been published from a long time ago. The first publication on skeletal remains is that of Fernández-Galiano (1958), while the first on dinosaur tracks is the article of Casanovas et al. (1983). The

fossiliferous sites range from the Upper Jurassic (Higueruelas Formation) to the Lower Cretaceous (Artoles Formation). As trace fossils (indirect evidence), there is an extensive record of dinosaur footprints (Figs. 1, 2).

During the prospecting campaign of 2009 in the Galve area, we found natural casts (convex hyporeliefs) of sauripod dinosaurs (Pérez-Lorente and Herrero-Gascón 2009; Castanera et al. 2010), ornithopods (an *Iguanodontipus* trackway; Herrero Gascón and Pérez-Lorente 2009, 2013a), stegosaurs (isolated casts and two trackways assigned to *Deltapodus*; Herrero Gascón and Pérez-Lorente 2016) and ankylosaurs (*Tetrapodosaurus* casts; Pérez-Lorente and Herrero-Gascón 2009).

In this paper, we report on the ankylosaurian casts from the Lower Cretaceous of Galve, which are assigned to the *Tetrapodosaurus* ichnogenus. All casts have been found as isolated elements on the ground and are identified as manus tracks (pentadactyl casts). The main objectives of this work are a detailed description of ankylosaurian casts found in Galve, the identification and classification of the major dynamic and static structures that depend on the phase of autopodial (hand) movement, the discussion of the affinities of the trackmakers, and their parataxonomic assignment to *Tetrapodosaurus*.

2 Geological setting

The ichnites (natural casts) of ankylosaurs of Galve come from several Cretaceous sites (Fig. 2). We consider as casts (or natural casts) the hollow footprint as the actual print is filled in. Geologically, the sedimentary specimens are located in the Galve Sub-basin, part of the Cretaceous Maestrazgo Basin, in the eastern sector of the Iberian Range (Soria 1997; Soria et al. 2000; Salas et al. 2001). Some of these sites are located in the Camarillas Formation and others are part of the Artoles Formation. Their attributed age is Early Cretaceous (Barremian) and the depositional environment is of continental coastal influence with both fluvial and tidal current structure (Benito et al. 2015). In addition to these two formations, other dinosaur footprint casts have been found in the older geological units of Galve (Herrero Gascón and Pérez-Lorente 2016), such as El Castellar and El Villar del Arzobispo formations (Fig. 2).

The Camarillas Formation (Canérot 1974), redefined by Salas (1987), is a very thick series of red and versicolor clays with red and white interbedded sandstones and, to a lesser extent, gray limestone and marl. The lower limit of this unit is marked by a sharp lithological change while the upper limit is rather obscure.

According to the Díaz-Molina and Yébenes (1987) interpretation, the Camarillas Formation starts with

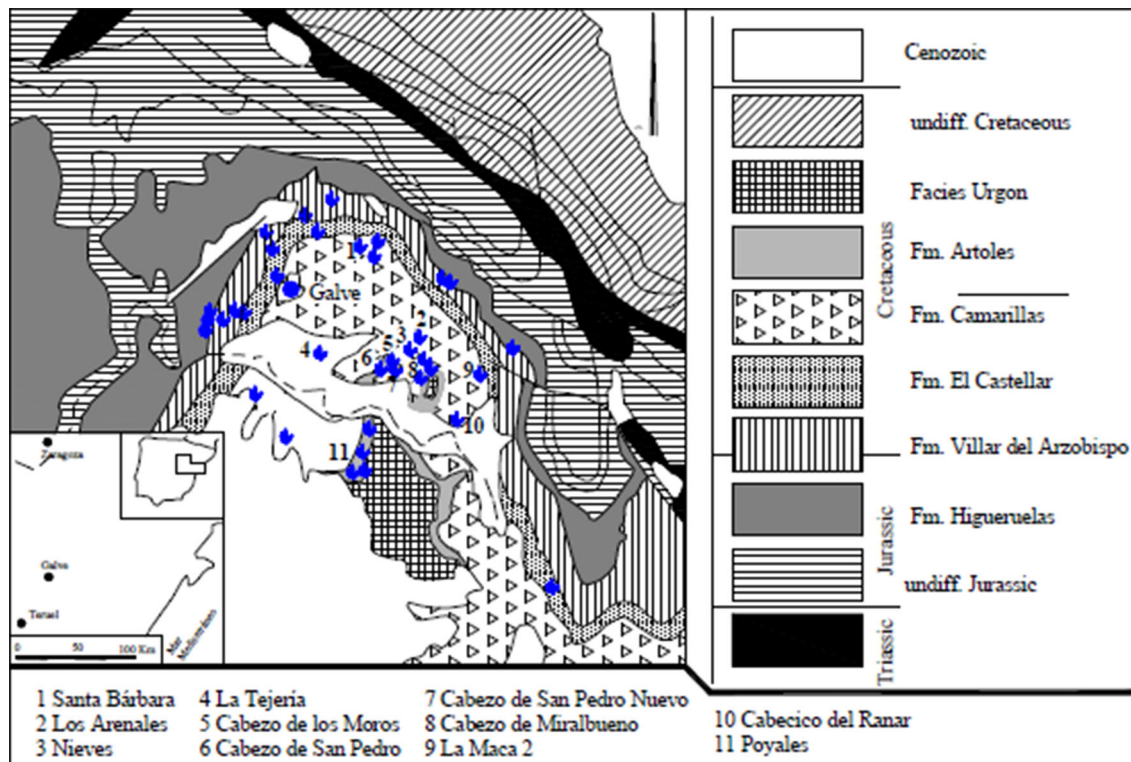


Fig. 1 Geographical and geological location of the 11 *Tetrapodosaurus* sites

wet alluvial fan sediments formed by a river channel system of low sinuosity and extensive lutitic plains. The upper part of the Camarillas Formation is interpreted as being deposited on a barrier island system lagoon (Navarrete et al. 2013), which implies the retreat of these river systems into an area influenced by tides.

The transition to the overlying formation, the marls and limestones of the Artoles Formation, is quite gradual, and the first significant marine interbedded sediments appear within the Cretaceous strata. The Artoles Formation consists essentially of marls and limestones, but at its base we can identify more detrital materials (silts, clays, sandstones and conglomerates).

The ankylosaurian casts described here generally have two types of filling: some show a brown–reddish sandy filler of variable grain size, sometimes with interbedded microconglomerates between the sandy sheets; and other microconglomerate of white to light gray color that usually have a great degree of bioclasts, mostly of which consist of ostreids.

Sandstone fills most casts, while carbonate is found in only four specimens (CSN10, CSP14, CSP15, POYY). Most fillers are siliceous sandstone, although the cement reacts with effervescence to attack with hydrochloric acid. They usually contain larger elements such as siliceous grains up to 5 mm, shell fragments (CBMLX) and very small bone fragments (CBLM3a). In several

casts, soft sediment clasts are placed either at the base of the cast, on the inside or on the top of the filling. Those casts filled with light and gray colored sediments are in the transition between Camarillas and Artoles Formations. At the bottom of the Artoles Formation, the casts are of marly composition with an abundance of bioclasts. In those casts of the Artoles Formation that are from the levels of shell accumulation of ostreids, the filling can also be of red siliceous sands and microconglomerates.

Although it is difficult to appreciate the type of sedimentary structures in the filling material, in sandy casts of the Camarillas Formation there are some diverse features. Some have flow structures, such as planar and hummocky cross stratification. Fining upward stratification (CSP13) and cross stratification have been observed in several samples of both Camarillas and Artoles formations (CSP9, CSP13, CSPF, POY10, POY13, POY17), one with curved laminites (Fig. 3). In the filling of CSP13 and POY12, casts are structures of invertebrate bioturbation.

All casts seem to have a similar genesis. The dinosaur stepped over an area of soft mud and then the hollows were filled. In those found in the Camarillas Formation, filling comes from streams, and in the top of the Formation they have some marine influence. The casts at the base of the Artoles Formation are filled by tidal currents that carry lots of bioclasts, mostly ostreids.

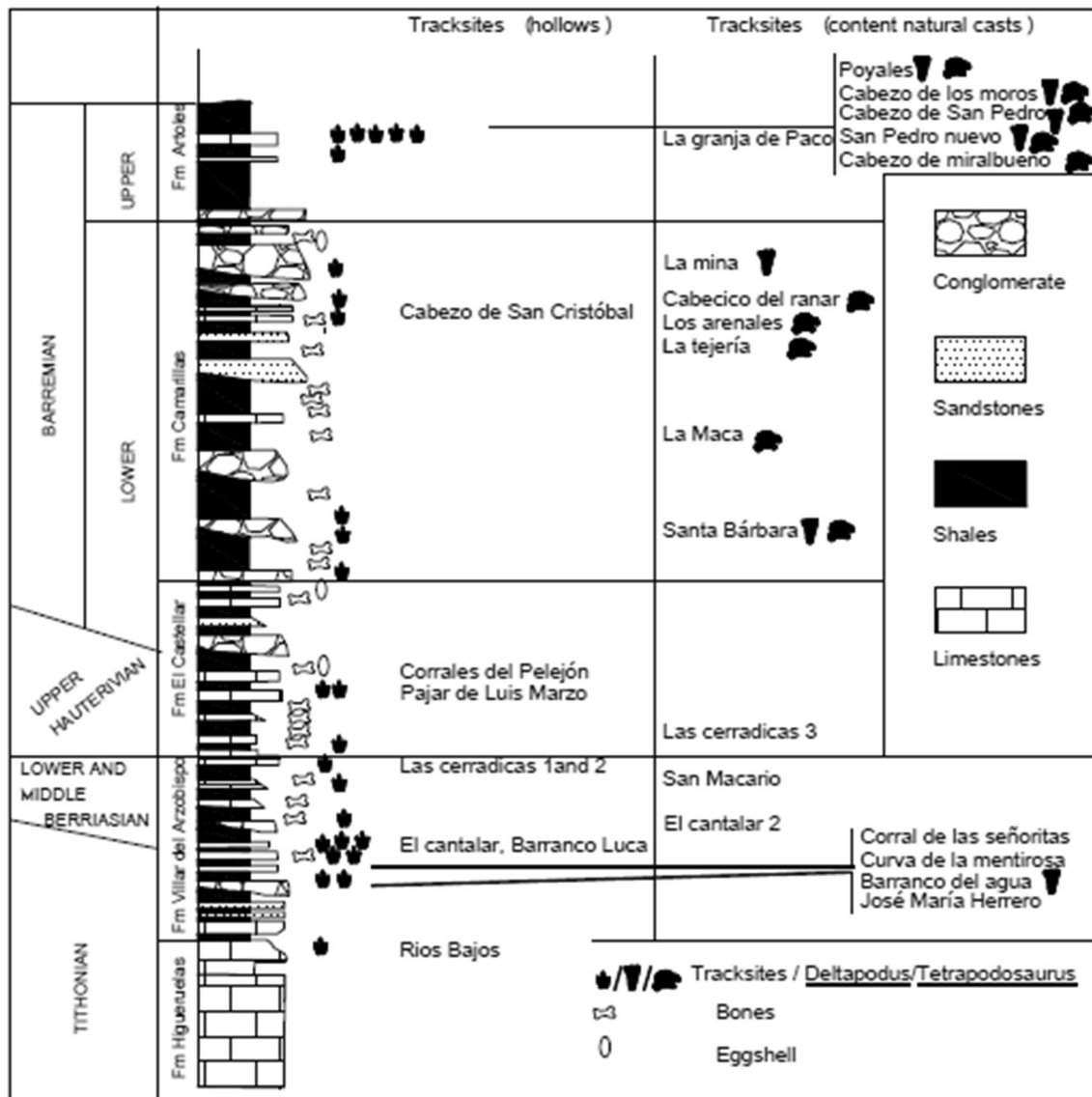


Fig. 2 Age and distribution of Galve palaeoichnological sites

Many of the casts have a ferruginous patina that envelops them whole or in part. Ferruginous minerals form crusts that do not permeate the interior. Crusts may be more than 5 mm thick and have a botryoidal structure. Many samples do not retain the continuous crust because in places they are broken.

A number of casts have a portion of the upper sandy layer attached that could be of syngenetic origin. Other casts have a flat or curved top, parallel to a lamination surface, where the separation between the sample and the upper sedimentary layer is sharp and occurs because the upper surface is erosional, or because immediately after print formation it was filled with sand, creating a discontinuity surface that now allows such separation. The remaining casts are totally or partially eroded or broken. In

some cases, the breaks of the top and base of the casts are parallel and form a tablet of pentagonal outline.

3 Materials and methods

We studied approximately 50 casts having the structures and morphology of ankylosaurian prints. The casts usually appear piled up at the edges of the cultivated fields and their embankments or slopes, as a result of removal of stones by farmers.

The casts are not associated in trackways or in manus-pes pairs, but appear as individual elements. To-date, pes casts have not been found at Galve.



Fig. 3 CBLM1 cast. Cross stratification in sediments filling the hole. Scale bar 10 cm

Sedimentary structures are not easy to observe inside the casts. However, structures correlated with the different stages of the movement during the formation of the print are plentiful on the walls and bottom (footprint formation phases of Thulborn and Wade 1989: T [touch-down], W [weight-bearing] and K [kick-off]), and structures produced by digital pads and scales are distinguished very well.

Abbreviations: Most of the ichnological terms used are defined in the papers of Leonardi (1987), Allen (1997) and Pérez-Lorente (2015). The nomenclature of casts is the same that has been followed in the rest of ichnological studies done by our team in Galve, so that the identifying symbols of the sites are maintained. The designation consists of two parts: the first refers to the site (letter abbreviations, e.g. CBLM4), and the second refers the sample (numerals, e.g. CBLM4). In some cases, all characters are letters (e.g. CBLMX), which means that identification is provisional and lack assigning the sample number. Key to abbreviations: CBLM, Cabezo of the Moros; CBML, Cabezo de Miralbueno; CBR, Cabecico del Ranar; CSN, Cabezo de San Pedro (new); CSP, Cabezo de San Pedro; LM, La Maca; NIV, Nieves Herrero; POY, Poyales; STB, Santa Bárbara; TJR, The Tejería.

4 Description

4.1 Description of the natural casts

The outline of the casts studied in this work is wider than long, and has a curved shape that is somewhat flattened in

an anteroposterior direction. The casts have five projections that radiate outward, but are asymmetrically positioned with respect to the fore-aft axis of the print (Figs. 4, 5).

The anteroposterior length of the casts, as measured at their tops (upper surface of the filled tracks) and bases (lower surface of the filled tracks), ranges 19–57 cm, and the width ranges 22–70 cm (Table 1). The average of length values is a maximum of 27% for casts ranging in length from 26 to 30 cm, and 26% for those ranging between 36 and 40 cm. The width of almost half the casts ranges between 36 and 45 cm (Fig. 6). The percentage in which the width of all the tracks (a) is greater than its length (l) is 38%. The average of variation of the length relative to the width ($(l-a)/a$) is -0.27 , which is classified as a wide footprint (Perez-Lorente 2001, 2015).

Print depth is variable and does not depend on the size of the footprint or the lithology of the cast. The maximum cast depth is 60 cm, while the shallowest is 12 cm. The degree to which erosion has cut off the tops of casts is unknown.

The description of the casts that follows in this paper has been divided into four sections: (1) the top or upper part of the cast; (2) the outline; (3) the walls or penetration zone of the foot, which is the limit of the hole or shaft footprint; and (4) the base, which is generally the lowest and deepest part of the cast.

4.1.1 Top of the casts

In unbroken casts, the top is presented in several ways:

- (a) Some casts are attached to a sandy fragment of the overlying rock layer of which the cast was once a part. The grain size and composition of sand from the cast is identical to that of the rest of the overlying rock layer. Apparently there is no unconformity between the top of the cast and the upper level, but even being syngenetic (cast and upper layer), it is very likely that the base level erodes part of the top of the footprint hollow (isolated samples, sharp upper surface of cast, grain size of detrital filling), such that the current depth of the cast is less than it originally would have been.
- (b) The top of other casts is a flat or undulating surface that should correspond to a sedimentary structure that allowed separation from the rest of the overlying layer, either because there was a greater sand content in the fill than in the rest of the overlying rock layer, or because the top of the cast corresponds to some of the laminations (generated by sandy filling of the cast or by deposition at the base of the upper level). There are casts whose top shows mud clasts or curved cross stratification (Fig. 3). These surfaces

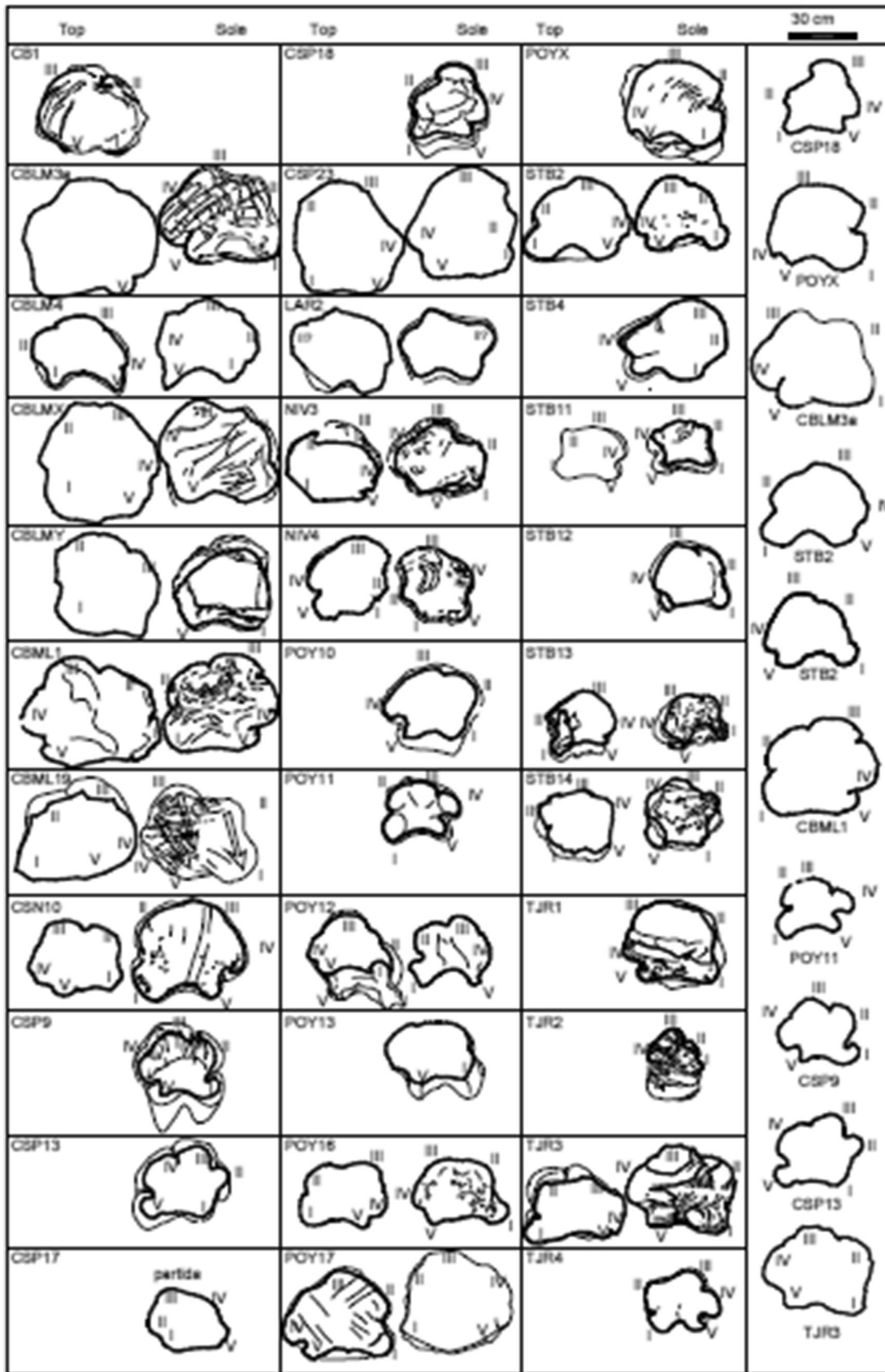


Fig. 4 Sole and top surfaces of some *Tetrapodosaurus* casts

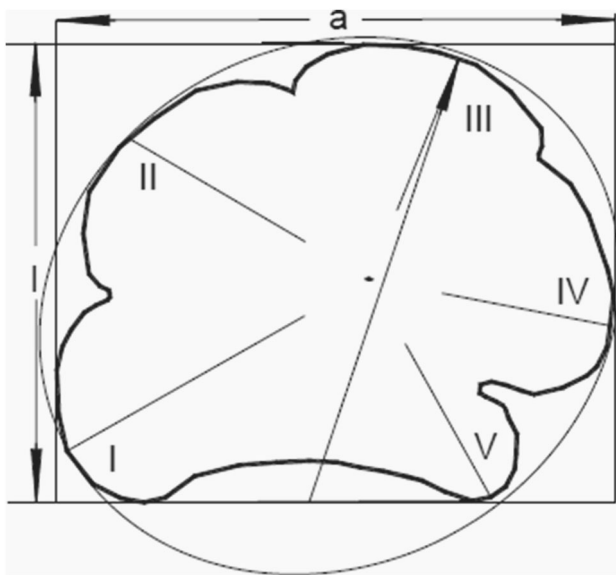


Fig. 5 Section of a *Tetrapodosaurus* cast. *l* manus print length; *a* manus print width; I, II, III, IV and V manus digits

(mud clasts, cross stratification) are not necessarily the top of the original fossil print but internal surfaces of the hollow filling.

4.1.2 Outline of the casts

The cast outline, what would correspond to the outline of a possible autopodium, consists of five radial lobes like a set of grouped columns, four of them of roughly equal size, that are regularly arranged around a central core (Figs. 4, 5). The core has no definite shape.

The protrusions differ from each other, so are numbered according to their order and characteristics from I to V (Fig. 5). It is supposed that they match autopodial digits, and on the assumption that the innermost digit was larger than the outermost, we interpret the pads of digits I and V as indicated in Fig. 5. Radii passing proximodistally through digits I and V point toward the back of the autopod, while digit IV is directed laterally, and digits II and III are directly more or less in an anterior direction. Digit V is noticeably the smallest lobe in all casts, but the relative sizes of the other digits is variable, and lacking a consistent pattern. All projections are close together and separated from each other by an incision of variable size. The gap separating digits I and V is a smooth, shallow, concave curve. In contrast, digits IV and V are separated by the deepest, most clearly marked notch. In some casts, digits III and IV are separated by a shallow incision, but in others the two pad marks are fully conjoined. The incisions separating digits I from II, and digits II from III, are well marked (Figs. 4, 5; CBML1, CSN10, CSP9, POY11, POY12, TJR4).

When the protrusions are sufficiently distinct, they display rounded, oval shapes (Figs. 4, 5; CSN10, POY11, TJR4). The major axis of the ovals is parallel to tangent of the confining curve except in digits I and V that penetrate inside that curve.

4.1.3 Cast walls

Foot penetration of dinosaurs in the muddy ground does not depend only on the body mass of the dinosaur but basically on the physical state of trodden mud (Pérez-Lorente 2015). In Galve, there are casts whose bases are of similar area, but which penetrate to different depths. The better conservation of spherical casts allows that the deepest footprints best preserved are the equidimensional samples. This means that there may be an undetermined number of wide shallow footprints, or narrow and deep ones, because which are more easily fragmented and destroyed. In this regard, it should be noted that most, if not all, casts studied have been uprooted by tractors to plow and placed at the edges of cultivated fields.

The substrate should, in addition to being fluid enough (low viscosity) to allow the entry of autopods, be cohesive enough to maintain vertical walls without collapse, and limited in stickiness, as indicated by the lack of drag features created by mud stuck to the skin.

In general, the response of mud varies depending on the thickness, composition and moisture content (Pérez-Lorente 2001, 2015). The autopod reaches a depth where the soil resistance equals the penetration force. Because the substrate may or may not be homogeneous, the autopod passes through layers that are either uniform or variable in viscosity.

Cast walls are usually vertical, or perpendicular to the top and the base surfaces. In lateral aspect some casts (CSPF, STB2) presents as a set of grouped, fluted columns (Fig. 7), in which the various lobes are continuous from bottom to top. The walls are usually vertical and their outline is like that of the mullions of windows. The columns are sometimes so widely separated that they are more like a group of contacting tubes. Vertical columnar or tubular structures are the most prominent features of autopodial penetration.

Many of the casts show straight, parallel, distinct and well-spaced striae, with a hexagonal shape at the base of the columns. The overall appearance is of bands separated by well-spaced, parallel grooves that run along the column from the top to the base, where the polygonal marks are located (Fig. 8). Both types of marks are attributed to skin flakes, imprinted during penetration of the foot into the substrate (T phase) and resting on the ground (W phase). In many specimens, the bands terminate in a tip that would be left by the scale at the end of phase T and the start of phase W.

Table 1 Measurements, composition and polygonal scale observations from 44 *Tetrapodosaurus* samples

Site	Sample (manus)		Cast size and dimensions (cm)				Composition (fr) ferruginous patina	Polygonal scales and scale dimensions	
	Left	Right	l_t/l_m	a_t/a_m	$(1-a)/a$	Depth			
Cabecico del Ranar	CBR1		///35	///45	−0.22	45	g	lw 1,6-1,9	
	CBR2						mc		
	CBR3						mc		
Cabezo de los Moros	CBLM3a		52///45	60///54	−0.15	33	f-g	so	
	CBLM4		34///38	44///45	−0.19	20	f,g,cb (fr)		
		CBLMX	57///49	70///54	−0.14	50	m,cb		
		CBLMY	46///38	54///42	−0.12	35?	f-m		
Cabezo de Miralbueno		CBML1	49///42	59///51	−0.17	37	f	f,b 0,9-1,6	
		CBML9	30///40	40///50	−0.22	60	g (fr)		
Cabezo de San Pedro nuevo	CSN10		34///41	40///51	−0.22		clz	so 1,1-1,5	
Cabezo de San Pedro	CSP7		///36	///45	−0.20	23	f-m (fr)	lw 0,7-0,9	
			CSP9	38///27	40///39	−0.18	15		g (fr)
			CSP13	37///32	43///39	−0.24	17		g-cb (fr)
			CSP17	26	34	−0.16			mc,cb (fr)
		CSP18		43///33	36///32	0.23	35	mc-g (fr)	
		CSP23		55///48	50///49	0.04		mc,cb	
		CSP27							
		CSP29							
		CSP30							
		CSP31							
	CSPF					f-g (fr)	lw-so 1-1,6		
Nieves	NIV2					50	fm	up, in f 1	
			NIV3	37///34	43///40	−0.14	40	f,m	up, in, lw 1
		NIV4	28///29	31///30	−0.07	20	f	up, in, lw, so 0,5-0,8	
		NIV5	///51	///54	−0.06	40	m,g		
		POY10	40///32	45/41	−0.16	16	mc-g		
Poayales	POY11		29///28	37///33	−0.19	12	g	up, in, lw 0,5-1,4	
			POY12	///31	36///37	−0.99			¿m? (fr)
		POY13	36///27	42///38	−0.21	20	¿m? (fr)	¿so?	
		POY16	30///30	30///42	−0.17	22	m-g (fr)		
		POY17	45///39	38///48	−0.02		(fr)		
		POY18				45?	m-mc	¿up? ¿in? lw	
		POYX	///37	///44	−0.16		m	lw 1, 2–1, 7	
		POYY					clz		
Santa Bárbara		STB2	37///33	47///41	−0.20	30	f-m	lw, so 0, 8–1,6	
		STB4					f	¿lw?	
		STB11	24///19	39///25	−0.33	12	g		
		STB12	30///30	38///22	0	25	f	up, in, lw, so 0,9-1,5	
		STB13	24///20	30///27	−0.23	20	f	lw, so	
		STB14	28///30	33///31	−0.09	25	m	lw, so 0,8-1,1	
Tejería		TJR1	///35	///43	−0.19	30	f (fr)	lw, so 1,7-2,1	
		TJR2	¿24?///	///26	−0.08		f-g	in, lw	
		TJR3	25///37	44///47	−0.32	33	g	lw 1,1-1,3	
		TJR4	///27	///32	−0.16	27	g	in,so	

Irregular and non identified casts: CSN5, CSN6, CSN7, CSN14, CSN15, CSP3, CSP10, CSP11, CSP12, CSP14, CSP15, CSP16, CSP19, CSP28, CSPE, LAR2 (Los Arenales site), POY1, POY2, POY3, POY4, POY8, POY9

g coarse sandstone, m medium sandstone, f fine sandstone, clz limestone, mc microconglomerate, cb mud clasts, r red sandstone, s cast sole surface, t cast upper surface, fr ferruginous patina. Polygonal scales located in: up the upper part of the lateral striae, lw the lower part of the striae, in the intermediate zone, so the sole of the cast. cm measurements in cm

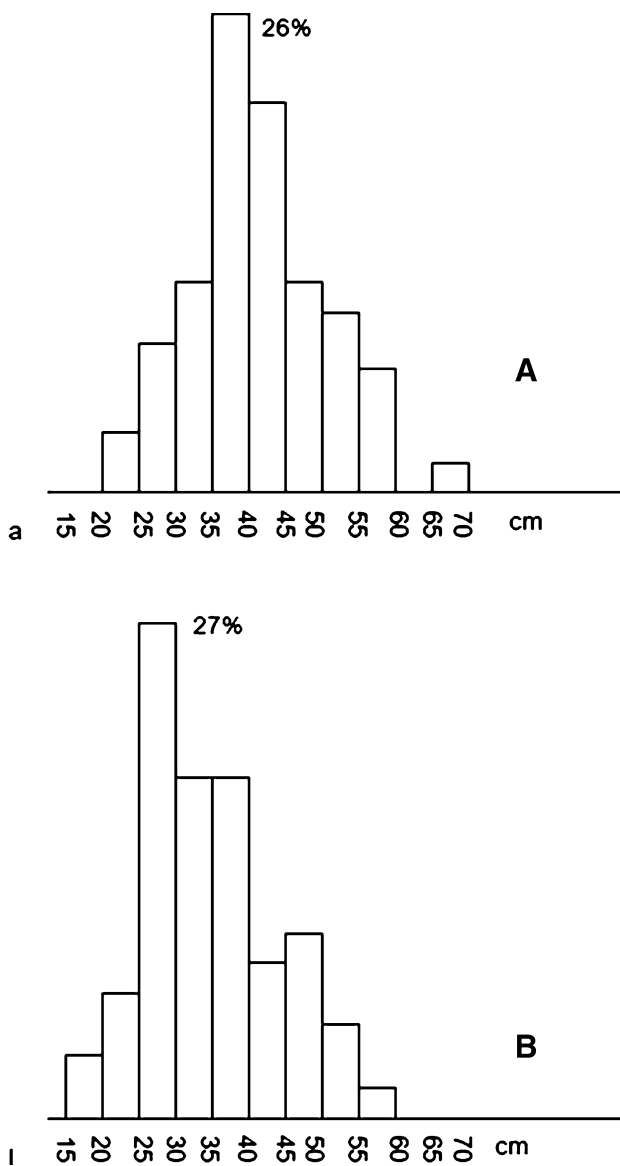


Fig. 6 Size-frequency distribution of manual print dimensions; *a* print width (a); *l* print length (b)

Two casts (POY12, CBLM4) have hollow walls oblique to the penetration grooves. In CBLM4, the striations form between them an angle of less than 30°. Penetration and sliding marks cannot be distinguished from each other in either of the two samples because no area of overlap is preserved between the two kinds of marks, and there are no criteria to identify their movement (entry or exit). The syngenetic striations of the K phase are called slide striations to separate them from penetration striations (the latter created during phase T).

In some casts, the indentation separating the rear pads (I and V) is less steeply inclined than others (Fig. 9), and is usually not accompanied by striations. In these casts, the walls of digits I and V have two inclinations, one with a



Fig. 7 Mullion or grouped columns structure. CBLM9 cast

shallow slope (made during penetration), and the other vertical (created during the W phase), parallel to the front digital pads. In some casts, the autopod entry starts with two large and gently sloping rear grooves corresponding to digital pads I and V (Fig. 9) that later become vertical. This is attributed to the fact that entry into the mud of the substrate is not strictly vertical, but at least the rear part of the autopod slides forward before the manus supports the animal. In digits II, III and IV, there is no indication of this kind of movement, so that, if these toes were pushed along the ground, these structures that they made in the substrate were deleted by the same autopod. It is possible that marks of the three central digits were formed at the real top of the hollow of many footprints, but subsequent erosion that accompanied sedimentation of the filling sand may have eroded them.

In almost all casts there are very clear and relatively wide grooves, which run along the columnar structures. The end of the T phase is indicated by the polygonal marks of the tip of the striae (scales that left slide marks). If the end of the movement is not instantaneous, elongated polygons in the direction of movement are formed.

The pattern of straight, lateral, columnar structures with polygonal marks at the base does not apply to all the casts. The most common modifications are: basal thickening, globular shapes, folds and squashing of the tubes, discontinuous striae and various levels with polygonal marks.

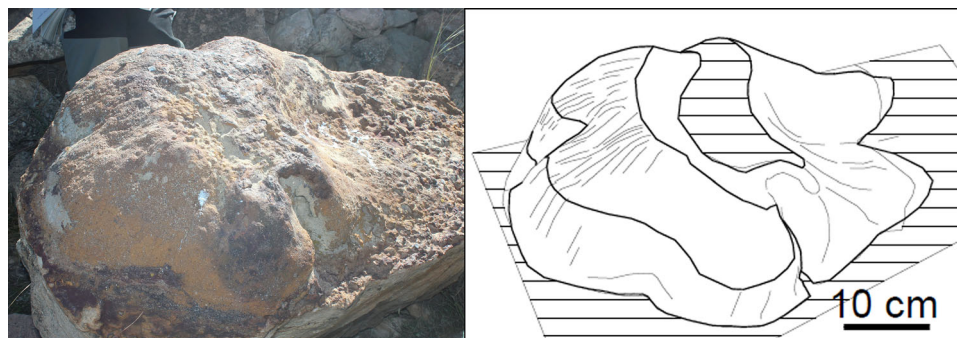
Some tubular or columnar structures become thicker at the base; there may be one or more of these (Fig. 10). In some tracks, the shape of the tubes at or near the base expands in a balloon-like manner, sometimes with curved grooves (Figs. 10b, 11).

In many casts, there are polygonal marks not just at the base of the columns, but also at their tops and at different position along their heights (Fig. 12). When the striae are not continuous along the tubular structure, longitudinal



Fig. 8 Lateral striation and polygonal marks in the base of columns. CSPF, CBML1 and POY18 casts

Fig. 9 Little slope of ground penetration walls of the rear digits. CSP9 cast



strips of column with parallel striations are separated by transverse discontinuities. The transverse discontinuities are broken lines or narrow bands with complete or incomplete polygonal marks (Fig. 12).

In sample NIV1 (Fig. 13), the tubular structures are bent as if they had a plastic regime. In POY18 (Fig. 14), the tubular structures are crushed, so that the walls of the columns come closer and touch.

The wall of many casts is uniform in all around its margin. However, in some ichnites, the wall depth varies around the periphery of the cast (Fig. 15). This could be due to collapse of the back-wall, but other causes can also be invoked (different autopodial penetration, different erosion of the top, among others) that have not been verified. In all ichnites, the narrowest column and the one with most irregularities along its length is that of digit V. No similar tendency toward variable thickness is seen among the other digital columns.

4.1.4 Cast bases

Cast bases have a variable shape. Some have flat bases (a), while in others six different shapes (b) have been distinguished. The flat bases are as follows:

- (a1) Smooth bases (Fig. 16) represent a neutral layer (“dead” region; Allen 1997) or are the sedimentary fillings of a flat bottom of the print. Some retain the sunken ellipsoidal digital pads (Fig. 17). Sometimes the casts have broken the flat bottom along

present day fractures associated with some unconformity. It is considered that the neutral layer or the “dead” region, embedded in the background during the T phase, terminates the process of entry into the W phase.

- (a2) The polygonal marks of the base, like those of the walls, are very distinct, especially on the outside of the base (Fig. 8). Some examples show polygonal marks, distributed haphazardly in different sectors of the sole (Fig. 17a, b). The polygon size is similar in all cases and similar to that of the polygons on the walls.
- (a3) The contour of the base usually is identical to, or at least very similar to, the walls of the cast. There are five protrusions, in three of which the ellipsoidal contour is distinguished (II, III, IV) and two that are only ellipsoidal in the best-preserved shapes (digits I, V). The orientation of the axes of the ellipsoids is described in Sect. 4.1.2.

On the other hand, irregular bases are of various types and can be defined as follows: bristly structures, transverse lineations, brecciated base, undulations, cones and horizontal basal tubular structures.

- (b1) The bristly structures are composed of marks similar to the blunt teeth of a saw, pointing to the rear of the casts that penetrate the ground more deeply than the sole of the autopod. These marks are located mainly in the area of digital pads II, III

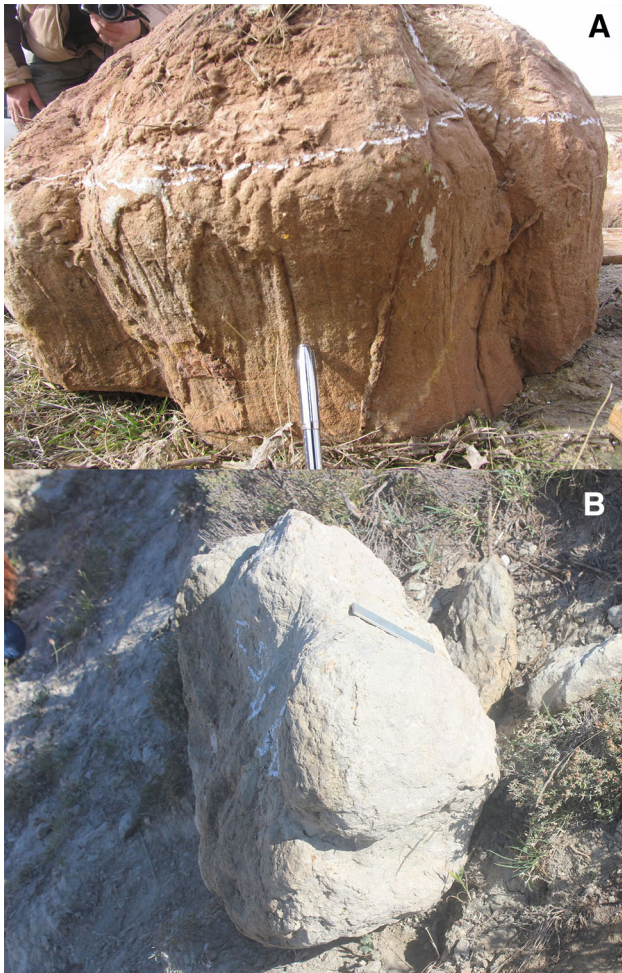


Fig. 10 Thickened columns in the base of the casts. CBML1 (a) and CSN10 (b) casts. Scale (b) 10 × 2 cm

and IV. They consist of two or more anteriorly located, denticulate rows, or they may cover much of the base (Fig. 18). The anteriormost jagged row

Fig. 11 Ballon and drop shaped structures. TJR1 and TJR4 casts



Fig. 12 Lateral striation with transverse discontinuities. NIV4 cast. Scale 10 × 2 cm



Fig. 13 Folding structures of the striated columns. NIV5 cast. Scaler 10 × 2 cm

is parallel to the edge of the column or tube with which it must be associated. The anterior margin is curved and smooth where it connects with the columnar structures (above) and jagged at its

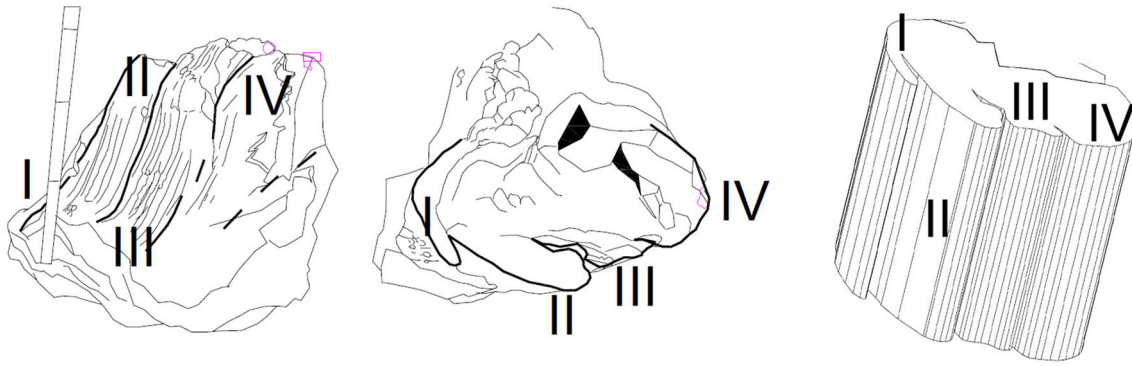


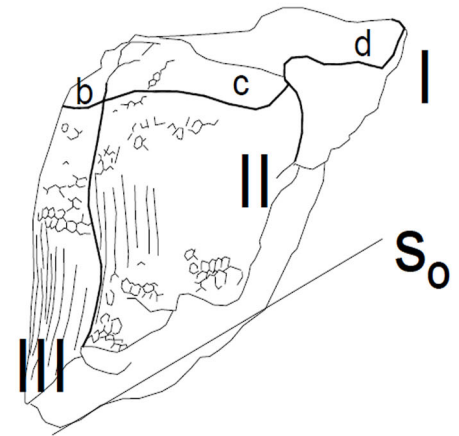
Fig. 14 Crushed columnar structures. POY18 and figuration

Fig. 15 Variation of the wall depth in POY12 cast. S_0 stratification surface (top); b, d, c surface of the cast sole (base)



Fig. 16 Base structures. Neutral or dead surface in the sole of the CBLMY cast

deepest part. The denticulations are similar in size to the polygonal scales. Towards the interior of the base, no order is observed. The serrated edges are comparable in size to the polygonal marks. We interpret this structure as forming as the front end of the autopod that penetrates the substrate, creating marks of the tip or the edges of the polygonal



scales, causing striations of penetration and polygonal marks on the cast. The formation of jagged projections and the bristly area of the sole of the footprint occurs when the foot begins to lift at the rear (K phase), rotating the scales of the sole so that they do not impress a flat polygonal mark on the ground, but rather an inclined one. We consider that the K phase begins when any part of the sole stops exerting pressure on the ground as the autopod begins to lift.

- (b2) Transverse lineations constitute a series of steps, more or less angular, and nearly perpendicular to the longitudinal axis of the sole (Fig. 19). The most conspicuous such feature is the step corresponding to digital pad III, whose rear edge is either straight (Fig. 19a), or curved and plastered with mud pushed back (Fig. 19b, c). Sometimes the steps are not completely parallel, or even intersect. In this case, they are signs of mud extrusion between the front pads, especially in space separating digits II–III. In addition to the angular transversal lineations, there are also others with sinuous appearance (undulations). They curve along their

Fig. 17 Ellipsoidal shaped digital pads and polygonal (scale) marks. CSN10 cast (a, b). POY10 cast (c, d). Grid 5 × 5 cm

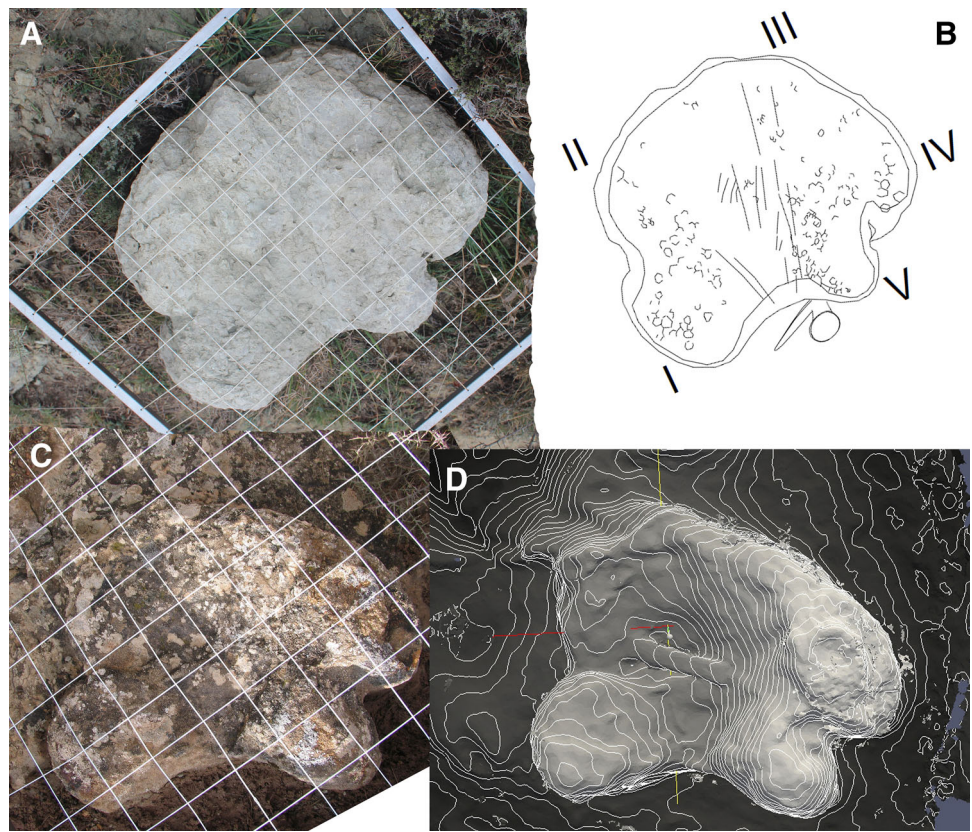


Fig. 18 Denticulate and bristly structures. Casts: a TJR1; b TJR2; and c NIV1

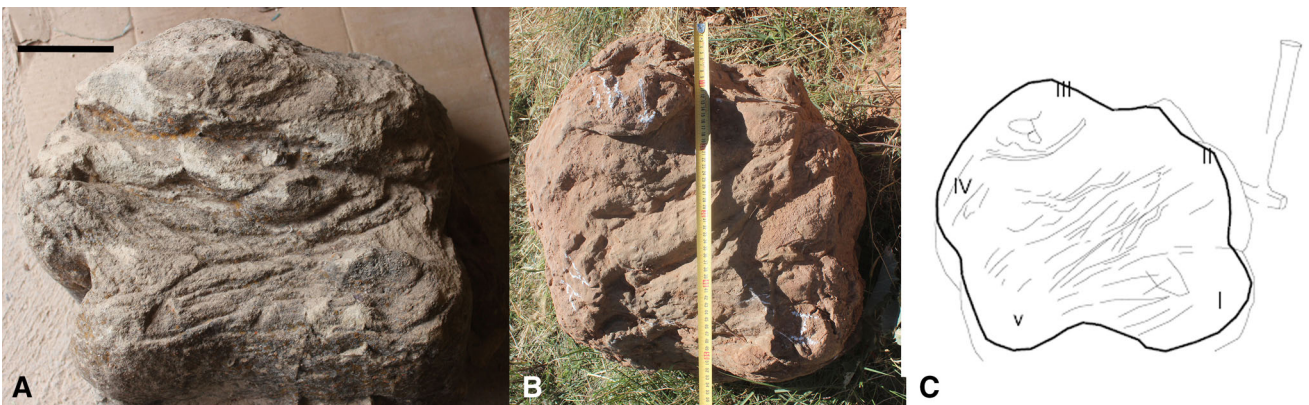


Fig. 19 Transverse lineations. Cast: a TJR1 (scale bar 10 cm); b and c CBLMX



Fig. 20 Brecciated base structure. CBLM3 cast

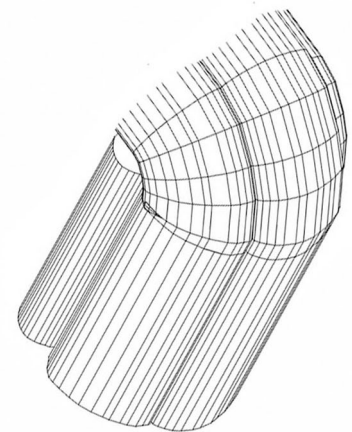
lengths, and have no sharp edges but are rounded in cross-section; the mark for digit III stands out in these cases as the geometric center of the lineation. The lineations (steps and undulations) transverse to the base must also be produced by the thrust of the foot in the K phase, as they are perpendicular to the direction of travel indicated by the shape of the autopod. In these structures, the sector corresponding to digit III is more distinct (being more depressed) and seems to be the center, or at the onset of the deformation.

- (b3) The base may have a partly or totally brecciated structure (Fig. 20). This may be due to more fragile behavior of the substrate, and is a result of its fracturing during phase W. We assume that the

brecciated, acute and curved shapes of the base steps depend on the physical condition of the mud, whether more crumbly or more fluid.

- (b4) One way the columnar structures made by digits II, III and IV end is by a gradual decrease in size of the tubular sections (Fig. 11), forming three cones whose vertices may or may not have a jagged appearance. The axes of the cones are below the vertical axes of the columns.
- (b5) Sometimes the end of cones are joined (K phase) to create a deeper and more projecting ridge in the middle, with the ends curving backward, forming the shape of a croissant (Fig. 9) or a conical ridge that may or may not be serrated, related to the placement of the center of digits II, III and IV. The central ridge starts at the front edge or at the center of the base, in an area usually marked with polygonal scales. In some bases (Fig. 9), the crest has very little topography, and has grooves in its front edge. The grooves are oriented in an antero-posterior manner.
- (b6) If the columnar structures associated with the marks of digits II, III and IV are fairly long, the straight tubes that extend from the roof fold at the bottom of the wall of the cast and continue as more or less horizontal pipes at the base. The length of the tubes after bending is usually small. In the extreme case of autopodial sliding, the columnar structures of digits II, III and IV curve to become horizontal and continue along the base of the cast and parallel to the base. In this case, the tubes pass below columns of digits I and V (Fig. 21). The three middle digits first punched down in (phase T), and then in the K phase, slid along the bottom of the track. In CBML9 (Fig. 21), the tubes extend beyond the bases of digits I and V, which are not involved in the creation. The basal torsion of the

Fig. 21 Folded columns structure. CBLM9 cast



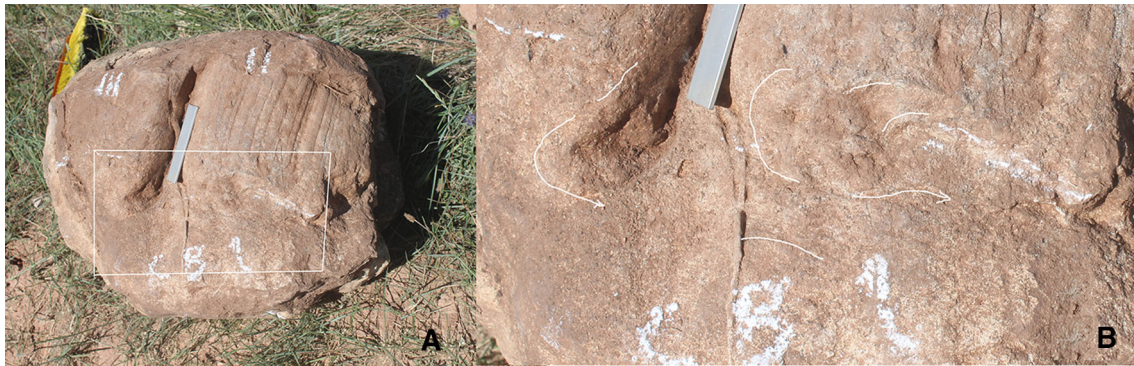


Fig. 22 Other slide structures on the base of cast CB1. Scale 10×2 cm

tubes indicates that, with digital pads I and V raised, the autopod slides backward. Digits II, III and IV sink and drag through the mud at the bottom, because of the viscosity of the mud. In this case, the vertical columnar structures of digits II, III and IV are not interrupted at the end of the T phase, but continue horizontally below the mark of the autopodial sole during the W phase.

There are also other bending features on the base of the casts (Fig. 22), which are formed without fracturing the walls of the cast.

Finally, there may be anteroposterior striations and grooves that start from one or more of the front digital pads (II, III, IV) and traverse part or all of the base of the cast (Figs. 9, 17a, b). They can be clearly distinguished in some flat surfaces and are formed in K phase when the autopodial tip presses and moves backward. The striations are sometimes very distinct. In other casts, whose bases also show polygonal marks, these lineations are less distinct, shallower and less abundant.

In all of the structures described here (jagged overhangs, bristly bases, ramps, cones and bent pipes), digits II, III and IV are involved making shapes that sink more than the sole. These shapes range from simple imprints of the front edge of the autopod that enter deeply into the substrate before the sliding of the three digits in the mud at the bottom. That is, in the K phase the autopodial tip presses and moves backward, probably to push the body of the animal forward.

The structures of the K phase indicate movement and sliding of the autopod from the front of the cast (digits II–III–IV) to the rear. The direction of the structures (lineations, ridges, grooves) shows that the direction of movement is anteroposterior, perpendicular to the rear edge of the cast (tangent to the marks of digits I–V), or slightly oblique and possibly directed toward digit I. That is, it would be consistent with negative rotation of the manus print.

4.1.5 Other structures: intermediate polygonal marks

Polygonal marks do not occur only at the ends of the columnar structures and the cast bases. Such marks are also present at various heights along the columnar structures, usually in sections where the continuity of the penetration grooves is interrupted. The interruption area is a horizontal band perpendicular to the striae, with polygonal marks of the scales. The maximum width of the band does not usually exceed three scales. These marks imply that contact between the skin and the footprint wall is static in such places. This can be interpreted in two ways. One possibility is that the autopod momentarily interrupted its penetration, at that moment impressing polygonal marks. Alternatively, the skin segment that touched the wall momentarily gripped the sediment, even while the manus as a whole continued its penetration. Either explanation serves to interpret this anomaly. The development of the longitudinal grooves is variable, and related to the amount of sliding. That is, polygonal structures were printed when the autopod was not moving or when the skin is temporarily attached to the wall; short grooves, or elongated polygonal structures (Fig. 8) are produced if the displacement is minimal. As the displacement (or dynamic range) increased, the striations became more elongate.

4.1.6 Structures created subsequent to the K phase

Some structures in casts are due to movement of mud after removal of the autopod, and so are not related to movement of the hand. The flattening of one wall has been detected and two types of wall collapse. In both cases, the final hole of the cast is modified:

- (a) Tubular structures deform: by flattening (Fig. 14) or by folding (Fig. 13);
- (b) Partially closed hollow by rear wall dropping, which retains the tubular projections of digits I and V.

4.2 Autopodial shape and deduced movement of the structures of the casts

The shape of the casts indicates that the autopod was pentadactyl and consisted of a central part to which five side pads were attached. The side pads protrude from the central sector, because in the casts they leave totally independent columns that run along its shaft. The shape of the pads is ellipsoidal. The major axes of the ellipsoidal imprints of digits II, III and IV are tangent to the contour of the cast, while those of digits I and V intersect the curve (Fig. 5). These pads of digits I and V are directed backwards (Fig. 17). The III and IV digital pads are conjoined in all ichnites, albeit with a very slight incision partly separating them. The separation between digits V and IV is the most clearly marked. The pads do not consistently differ in size, except that digit V is always the smallest.

If the tangent line between digits I–V is the back of the autopod, the most anterior part of the ichnite is the mark of digit III. A line from the midpoint of tangent line of digits I–V to the front of digit III forms an angle with tangent of digits I–V, which is acute with respect to the impression of digit V (Fig. 3).

There are no claw marks at the edges or on the sole of the digital pads, but simply polygonal skin marks. The nails or hooves of *Tetrapodosaurus* hands neither touched the ground nor brushed against the walls, so they should be, if present, on the dorsal of the digits or perhaps a mere strip of harder material at the periphery of the digit (J. Farlow, pers. comm.).

4.3 Response of the pads

The pads create columns or tubes having the same section along their length. On some tracks, the tube expands at the base, which has been attributed on numerous occasions to the crushing of the digital pads (Romano and Whyte 2012; Herrero-Gascón and Pérez-Lorente 2013). This is due to support in the W phase of the greater weight in the formation of the footprint cycle, indicating that they are flexible.

If dermal scales leave striations during movement and polygonal marks during stops, it follows that polygonal marks at various heights of the column must imply times of stopping, or at least interrupting the movement of the skin area in contact with the wall. An explanation is based on the flexibility of the pads that may, even with continuous movement of the autopod, vary the segment of skin that brushes against the wall. Striations continue below the polygonal structure, but are displaced laterally with respect to the upper ones. The striations are interrupted when the scales that cause them are stuck to the wall, which does not mean that the downward movement of the internal part of

the autopod stops, but only that the scales interrupt its movement. Below the horizontal band, the scales marking striations are not the same as those of the upper part (where the upper striae end) but are made by others located below.

The globular shapes with curved grooves of the cones could also be explained on the basis of the high flexibility of the digital pads.

Columnar or tubular structures are the result of the entry of an object consisting of a central element with five (digits I, II, III, IV, V) projecting protrusions of elliptical section. Although they are very close (except for digits I–V), all are well separated (except digits III and IV, which are joined, or separated by only a small intervening notch). The interface between some (digits IV–V, I–II and II–III) is greater than the minor radius of the ellipse, as they leave very deep and convex incisions.

4.4 Hand movement

Before the supporting stage (phase T), the hand, with its anterior end slightly raised, drags the two rear pads on the ground. The subsequent support and penetration are perpendicular to the ground. The pads leave striated tubes perpendicular to the tracking surface. During the time of maximum support, depending on the soil resistance, the pads expand.

The autopod rotates and moves the tips of the digital pads II, III and IV back, pushing the dinosaur forward. The digits do not come together or separate in this movement, but remain in the same position they had during penetration of and resting on the ground. There is no indication of pressure digits I and V or metapodial support on the edge of the shaft, so the dinosaur must turn the autopod in the metacarpal–carpal joint and in this way drive the body forward. The forward end of the hand not only serves to support, but must also function as a propelling mechanism of the animal during phase K, perhaps downplaying the importance of the hindlimbs.

4.5 Architecture and function of forelimb of ankylosaurs

The humerus of ankylosaurs has a well-developed deltopectoral crest for the insertion of various muscles involved in locomotion (Coombs 1978b). The olecranon of the ulna is well developed and offers a height lever for elbow extensor muscles.

Maidment and Barrett's (2012) reconstruction of the position and function of the ankylosaur scapular muscles suggested that the forelegs of these dinosaurs operated differently during locomotion than in stegosaurs and ceratopsids. In ankylosaurs, the weight is distributed evenly between the fingers, a conclusion supported by our track

casts, in which all digits penetrated to the same depth. Although the hand of ankylosaurs is not well known (see Pereda-Suberbiola et al. 2005; Currie et al. 2011), it seems that all digits end in hoof-like, weight-bearing ungual phalanges. According to Maryańska (1977: “*these were not fossorial limbs*”) and Coombs (1978b), the hand of the ankylosaurs was not adapted for digging. Maidment et al. (2013), on the other hand, argued that the position of various arm muscles favored the transmission of considerable force to the hands, which would allow ankylosaurs to engage in this activity.

In accordance with the above, Burns et al. (2015) indicated that the forelimbs of ankylosaurs are more robust than hindlimbs, at least in the early stages of growth. Maryańska (1977: “*modification of the scapulocoracoid... may also point to similar fossorial tendencies in all Ankylosauria*”) suggested that they were capable of burrowing. Coombs (1978a), in contrast, thought that these limbs were mainly for weight bearing. The forelimbs are shorter than the columnar hind limbs, and held in a flexed stance. Consequently, the entire weight of the presacral part of the body of ankylosaurs rested on the forelimbs.

Senter (2010, 2011) reconstructed the metacarpal bones of ankylosaurs in a semi-tubular position, as in stegosaurs and in some sauropod dinosaurs. It is possible that the semi-tubular arrangement of the metacarpals was adapted to support most of the weight of these animals, or to increase power during the progression. According to Currie et al. (2011), who excavated fossilized ankylosaurs hands in life position, the metacarpals “*are almost the same length, the length increase... from metacarpal I*”, but their diameter is variable: metacarpal III is the longest and those located laterally are shorter; metacarpal I is the widest and the narrowest is V. These results confirm Senter’s (2010) hypothesis that the metacarpals are arranged vertically, as in stegosaurs and sauropods. The proximal articular surfaces fit together such that, when assembled, the distal joint surfaces at ground level form a radiating arc. The phalanges of all digits become smaller distally. The distal ends of the ungual phalanges expand medially and laterally, so that the distal end of each phalanx is broader than its proximal end. Many of the joints are hinge-like or trochlear, allowing sagittal movement relative to the longitudinal digital plane. The first phalanx of digit V is much narrower than the first phalanx of any other finger. The ungual phalanges of the first three fingers are hoof-like (digit I > II > III). The metacarpal bones would support the main weight.

5 Comparative palaeoichnology

The forelimbs of sauropods, stegosaurs and ankylosaurs are characterized by the vertical half-tube forming their metacarpal bones, which is reflected in the shape of the

manus prints of these dinosaurs (Senter 2010, 2011). According to this author, if the metacarpals were inclined, so as not to touch the ground, there should be a pad that could hold this structure. Thus, the closed-arc shape of the footprints reflects the metacarpal semi-tubular structure. Maryańska (1977) suggested that, in ankylosaurian specimens with articulated metacarpal bones, these bones are parallel and not divergent, so that they form an arc, with metacarpal V displaced towards the rear.

Senter (2010) thought that the manual digits in both sauropods and stegosaurs are not needed for locomotion, and so in these dinosaurs they were vestigial or lost. Ankylosaurs have several phalanges (2: 3: 3: 3: 2 [*Talarurus*] or 2: 3: 4: 3: 2 [*Sauropelta* and probably *Pinnacosaurus*]; see Thulborn 1990; Currie et al. 2011) and all digits end in an ungual phalanx. The digits, according to Senter (2011: “*... so that with a vertical metacarpus the finger is perpendicular to the metacarpal and parallel to the ground*”) are arranged radially, which would produce a relatively wider autopod than in the case of sauropods and stegosaurs.

The shape of the manus print in *Deltapodus* (regarded as stegosaurian) is easily confused with that of sauropod manus prints because (Whyte and Romano 2001; Herrero Gascón and Pérez-Lorente 2016):

- It is plano-convex or concavo-convex, concavely backward;
- Digit I is medially or posteromedially directed;
- It is wider than long and probably entaxonic, consistent with the tubular metacarpal placement (Senter 2011)
- The sole has a pad that includes the digits, similar to that of sauropods, in which there is no different structure of protruding digits except for digit I (see Castanera et al. 2016).
- The callosity that includes the digits thickens when the animal exerts maximum pressure on the sole, as in the hands of sauropods described by Romano and Whyte (2012).

The lack of distinct digit imprints (apart from that of the pollex in some tracks) indicates a digitigrade manus with metacarpals arranged vertically (Wilson 2005, p. 415, Fig. 4b). The arrangement of the metacarpals would be reflected in the tightness of the arc in the print.

González-Riga (2011, Fig. 4) also noted the possible increase in foot, and consequently footprint length during the weight-bearing phase with an ‘elastic plantar pad’ on the pes. On this basis, Gonzalez-Riga (2011) estimated that the print length may vary by as much as 5%.

The mark of five perfectly-distinct, protruding and separate digits in the casts of Galve presented in this work make these ichnites incompatible with those of stegosaurs or with those of sauropods.

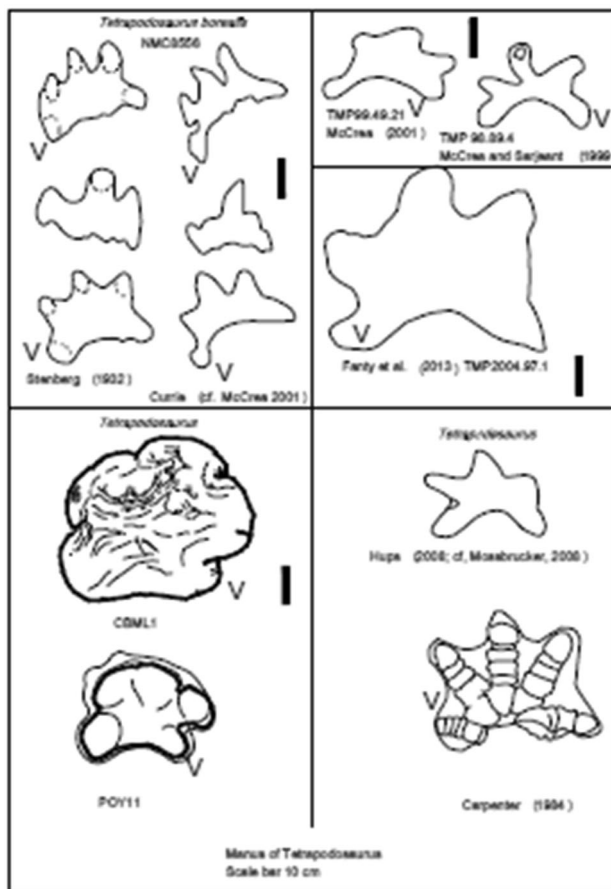


Fig. 23 Examples of described *Tetrapodosaurus* ichnites (manus)

Sternberg (1932) originally referred the ichnotaxon *Tetrapodosaurus borealis* to a ceratopsian trackmaker (see below). However, there are several criteria to differentiate ankylosaurian tracks from those of ceratopsians (McCrea et al. 2001; Fiorillo et al. 2010): for instance, prints of ceratopsian hands (*Ceratopsipes*) show a symmetrical distribution of digit impressions, which contrasts with the “outer digits (I and V) arranged, so that they almost completely project backward” in ankylosaurian manus prints (*Tetrapodosaurus*), with longer toe impressions; digit I in *Ceratopsipes* seems more prominently displayed than the other manual digits in *Tetrapodosaurus*, while digit I is shallow compared to digits II–IV. Manus prints are larger in proportion to the pes in ankylosaurian ichnites (about two-thirds the size of the pes in *Tetrapodosaurus*), while they are significantly smaller in ceratopsian ichnites (about half the size of the pes in *Ceratopsipes*; McCrea et al. 2001).

Given the morphological features of the casts studied in this work, their assignment to manus prints of ankylosaurs and, specifically, *Tetrapodosaurus* is consistent with the characters of this ichnogenus as described by previous authors (see Fig. 23). The manus impressions are wider

than long, with a concave posterior margin (McCrea 2000). There are five manual digits, which are short, blunt and widely divergent. Digit V is always the smallest one. The inner digits (II–IV) generally face forward while the outer digits (I and V) are directed laterally or posterolaterally.

Trackways with both manus and pes prints of *Tetrapodosaurus* have been cited by many authors: Sternberg (1932), Carpenter (1984), Ensom (1987, 1988), Thulborn (1990), McCrea and Sarjeant (1999), McCrea (2000), McCrea et al. (2001, 2014), Harington et al. (2005), Pond et al. (2014), Lockley and Gierliński (2014) and Weems and Bachman (2015). Pes prints are longer than those of the manus; the manus is approximately two-thirds the size of the pes. Described pes marks are tetradactyl and elongated. As noted by McCrea (2000), the lack of any pad or webbing enclosing the manual (and pedal) digits is likely the result of deformation of the substrate.

Ankylosaurian tracks have been assigned to several ichnospecies (see McCrea et al. 2001 for a review), but only two can be confidently attributed to this group (Petti et al. 2010): *T. borealis* and *Metatetrapous valdensis* Nopcsa (1923). The latter ichnotaxon comes from the Lower Cretaceous (Berriasian, lower part of the Bückeberg Formation) of Germany. Hornung and Reich (2014) noted a great similarity in pedal morphology to *Tetrapodosaurus*. The main difference is the tetradactyl manus of *Metatetrapous*, unlike the pentadactyl manus of *Tetrapodosaurus*. If correct, this feature is unique among ankylosaurian tracks (Hornung and Reich 2014). The manus of ankylosaurs generally retains the primitive pentadactyl condition (Pereda-Suberbiola et al. 2005; Currie et al. 2011), but a four-digit manus has been described for the enigmatic ankylosaur *Liaoningosaurus* from the Early Cretaceous of China (Xu et al. 2001).

The ankylosaurian affinities of other ichnotaxa, such as *Ligabueichnium bolivianum* Leonardi 1984 from the Late Cretaceous of Bolivia and *Qijiangpus sinensis* Xing et al. 2007 from the mid-Cretaceous of China, are still under debate (see McCrea et al. 2001; Apesteguía and Gallina 2011; Hornung and Reich 2014; Salisbury et al. 2016). The affinities of the ichnotaxa *Apulosauripus federicianus* Nicosia et al. 2000 from the Late Cretaceous of Italy and *Macropodosaurus gravis* Zakharov 1964 from the Late Cretaceous of Tajikistan are doubtfully ankylosaurian (see Petti et al. 2010).

6 Discussion

6.1 Definition of *Tetrapodosaurus*

Sternberg (1932) erected *T. borealis* for a type of ichnite attributed to ceratopsids. The manus prints were

pentadactyl and very open, with relatively close digits marks, except for the separation between digits I and V. Haubold (1971) redefined the ichnogenus based on the same footprints that Sternberg drew.

Carpenter (1984) attributed these ichnites to ankylosaurs and superimposed onto the ichnites the representation marks of the bones of the hands and feet of *Sauropelta* from the Early Cretaceous of North America. The manus print used is almost identical to those described in this paper. The digits are radial, digit V is the smallest of them, and digits I and V point sideways or backwards.

Thulborn (1990) recognized that the footprints of *Tetrapodosaurus* are comparable to traces of ankylosaurs. They have a pentadactyl hand, with stubby digits positioned radially and flat nails like spades. Digits II and III are the largest, and the smallest is the V. The manus prints are wider than long, with five short, rounded and divergent digits.

McCrea and Sarjeant (1999) reconstructed the manus and pes prints of *Tetrapodosaurus*. They are very narrow; the digits join together proximally without appearing to have a central pad. The manus is pentadactyl and the marks of the digits are radial, with digits I and V directed backwards.

McCrea (2000) reviewed the Sternberg (1932) diagnosis of *Tetrapodosaurus*: “footprints of a medium-large quadrupedal animal; manual and pedal digits are not enclosed in a pad or web; footprints that appear to have this morphology are likely the result of deformation of the substrate caused by the weight of the animal... The manus is wider than long with a concave posterior margin...”. In his diagnosis of *T. borealis*, Sternberg (1932) indicated that the manus prints generally show the impression of five digits. In the emended diagnosis, McCrea (2000) noted that “manual prints generally show the impression of five digits... they are not completely enclosed in a large fleshy pad. The inner digits (II–IV) generally face forward while the outer digits (I and V) are directed laterally... The divarication of manus prints is variable, but often quite high, from 100° to over 200°”. Hands point outward, i.e. positive orientation (sensu Leonardi 1987). Ankylosaurian fingers are quite free. Their hands and feet are wide to expand an area on which they rest.

McCrea et al. (2001) described the hand of *Sauropelta* (see Carpenter 1984; Carpenter and Kirkland 1998): it has five digits, three long (II, III and IV), digit I is shorter than the previous ones and digit V is the shortest of all. According to these authors, the manus print has to have very short finger marks.

Hornung and Reich (2014) synthesized diagnoses that characterise the traces of ankylosaurs as follows: moderate to large size; quadrupedal trackway; tetradactyl pes; relatively small metacarpal and metatarsal regions in relation

to the length of the free part of the digits; pentadactyl manus separate from the pes print without membranes; toe I much shorter than the second; asymmetric pes with digit IV clearly anterior to digit I; the width of the manus print reaches 60–80% of the foot; the manus trackway width is somewhat lower than the pes; strong divergence of the manus digits ($I \wedge V$ or $I \wedge IV$ between 180° and 250°).

It has been suggested that some sauropod manus tracks are similar in shape to those of *Tetrapodosaurus*, namely *Titanosaurimanus nana* Dalla Vecchia and Tarlao 2000, and *Brontopodus pentadactylus* Kim and Lockley 2012. Moratalla et al. (2003) described a trackway formed by 5 prints whose morphology is similar *Titanosaurimanus* from the Aptian of Los Cayos, in Cornago (La Rioja, Spain) (also cited by Castanera et al. 2016).

We consider that these tracks are different from those of Galve described in this work. Differences mainly concern the relative position of the digits with respect to the metatarsal bones, and the mobility of the lower joints of the forelimbs. The holotype specimen (SOLII-S5m, plastotype stored at the Museo Paleontologico Cittadino of Molfalcone, Gorizia, Italy) of *T. nana* is a manus print from the Albian of the Istrian Peninsula. It is different from all the other tracks of the same outcrop. SOLII-S5m is not associated with any trackway or pes print. Dalla Vecchia and Tarlao (2000) associated it with a group of “isolated prints”, which are unrelated since they do not form any trackway and have neither a similar size nor morphology. The site is complex and only a single sauropod track is identifiable. The criterion used by the authors does not currently serve to define a new ichnotaxon because there is not a sequence of at least five similar footprints in the same trackway or “a series of successive footprints or both, or all four, feet” (see Peabody 1955; Sarjeant 1989). Concerning the *Titanosaurimanus*-like track from the Los Cayos site, Moratalla et al. (2003) described only a complete manus ichnite, in this case associated with four more prints (i.e., two pes and two manus). Two manus prints are incomplete and the pes prints do not show diagnostic characters to identify the trackmaker among ornithischians or saurischians.

Kim and Lockley (2012) did not explain why they refer *B. pentadactylus* to a sauropod trackway. They stated that *B. pentadactylus* (a) “have distinctive pentadactyl manus traces”; (b) “represents the first sauropod ichnospecies named from Korea and provides new insight into sauropod manus morphology”; and (c) “the pentadactyl manus has some similarities to certain blunt-toed ankylosaur tracks. The authors concluded that “this alerts ichnologists to the possibility that isolated tracks may be misidentified”. With regard to the pes prints, Kim and Lockley (2012) noted that “no clear digit V trace is discerned as separate from the lateral margin of the rounded heel trace posterior to the

trace of digit IV”. In our opinion, this can be also considered as an ornithischian feature.

The hand anatomy of sauropod dinosaurs is incompatible with the *Tetrapodosaurus* tracks. Members of Eusauropoda had their hands in the form of a column without digits. According to Naish (2008), the digits in eusauropods did not extend of the metatarsus. The casts that we describe in this paper show separated digits that leave a free space between them. The axis of these digits forms a large angle, about 90°, with the corresponding metatarsal axis. The digits are protruding elements of a vertical metatarsal “cylinder”. In Galve, there are relatively deep casts in which the digit penetration marks are vertical and then become horizontal. This means that the palm of the hand is placed vertically, making this position difficult to justify in a sauropod. Despite this hand movement, the front wall of the casts remains vertical, which means that the rotation of the elements above the hand (if it exists) is negligible. The study of deep casts has showed that there is not an appreciable twisting motion between the digits, metacarpus and zeugopodium in the forelimbs of sauropods, and probably also of stegosaurs (Milàn et al. 2005; Romano and Whyte 2012; Herrero Gascón and Pérez-Lorente 2016).

Thus, it does not seem that the sauropod joints have this mobility. According to Tschopp et al. (2015), “together with the immobility of the wrist, it implies that the forefeet did not contribute much to the propulsion but that their main function was weight-bearing”. “Phalanx morphology is very similar among most sauropod taxa. With the exception of I-1, they are short and broad with flat proximal articular surfaces, which contribute to the restriction of movements against their corresponding metacarpal” (Tschopp et al. 2015).

6.2 Distribution of *Tetrapodosaurus*

The ichnotaxon *T. borealis* was originally described from a single quadrupedal trackway found in the Aptian–Albian Gething Formation of British Columbia, Canada (Sternberg 1932; also Harington et al. 2005). In recent years, similar quadrupedal tracksites have been discovered from the Albian Gates Formation (Grande Cache Member) of Alberta (McCrea and Currie 1998; McCrea et al. 2001), the upper Aptian Patuxent Formation of Virginia, USA (Weems and Bachman 2015), the Cenomanian Dunvegan Formation of Alberta and British Columbia (Currie 1989; McCrea et al. 2001, 2014), and the upper Cenomanian to middle Turonian Kaskapau Formation of British Columbia (McCrea 2003; McCrea et al. 2014) (Table 2). Moreover, a partial trackway of *Tetrapodosaurus* cf. *T. borealis* has been described from the Ross River Block of Yukon Territory (middle Albian–early Cenomanian), Alaska (Gangloff et al. 2004; McCrea et al. 2014). This area is the most

northern occurrence of the *Tetrapodosaurus* tracksites in North America.

In addition, tracks and trackways of *Tetrapodosaurus* isp. have been reported in North America from the Albian–Cenomanian Dakota Formation of Colorado, USA (Lockley et al. 2014b; McCrea et al. 2014), and the contemporaneous Nanushuk Formation of Alaska (May and Druckenmiller 2009; Gangloff 2012). Fanti et al. (2013) described an isolated manus print of *Tetrapodosaurus* isp. from the Campanian Wapiti Formation of Alberta. It is therefore the youngest *Tetrapodosaurus* track reported from North America.

McCrea et al. (2014) have referred to cf. *Tetrapodosaurus* isp. a number of tracks and trackways from the Berriasian–Valanginian Gorman Creek Formation, some of them of very large size, and from the upper Albian Pay-saten (?) Group, both of British Columbia. Tracks reminiscent of the *Tetrapodosaurus* prints are also known in the Albian–Cenomanian Chandler Formation of Alaska (McCrea et al. 2011; see Gangloff 1998).

The presence of *Tetrapodosaurus* in the Kimmeridgian–Tithonian Morrison Formation of Colorado is likely (Lockley et al. 2014a), but needs to be confirmed on the basis of additional tracks. If so, the temporal distribution of *Tetrapodosaurus* could be extended to the Upper Jurassic.

It has been suggested that *Tetrapodosaurus* was unique, even endemic to North America (Gierliński and Sabath 2008). However, recent discoveries indicate a more extensive geographic range, including Europe and probably Asia. In Europe, Pond et al. (2014) have described pes tracks of *Tetrapodosaurus* isp. from the Barremian–lower Aptian Wealden Group of the Isle of Wight, England. The natural casts from the Barremian of the Artoles and Camarillas formations of Galve (Teruel) in Spain extend the record of this ichnogenus to the Barremian of the Iberian Peninsula. The discovery of an ankylosaurian trackway in the Aptian Apulian Carbonate Platform of Puglia in southern Italy is worthy of consideration (Petti et al. 2010), as the tracks display some features in common with those of *Tetrapodosaurus* and could belong to this ichnotaxon. In any event, the trackmaker inhabited emergent areas of the Africa-derived Apulian microplate and should be regarded as having Gondwanan affinities.

In Asia, manus and pes prints from the Aptian Atotsuwaga Formation of Japan and the Campanian Djadokhta Formation of Mongolia, the latter poorly preserved, have been referred to cf. *Tetrapodosaurus* isp. (Fujita et al. 2003; Ishigaki et al. 2009). *Tetrapodosaurus* has also been reported from from the Barremian–Albian of the Jiaguan Formation of Sichuan, China, but this is a rare occurrence based on limited material (Xing and Lockley 2016).

Finally, the presence of *Tetrapodosaurus* in Australia was tentatively based on isolated tracks from the

Table 2 Distribution of the ichnotaxon *Tetrapodosaurus*

Ichnotaxon	Ichnites	Unit	Location	Age	References
<i>Tetrapodosaurus borealis</i>	A trackway with 14 prints, manus and pes (holotype)	Gething Formation	British Columbia, Canada	Aptian–Albian	Sternberg (1932), Harington et al. (2005)
<i>Tetrapodosaurus borealis</i>	Several trackways, manus and pes prints	Gates Fm	Alberta, Canada	Albian	McCrea and Currie (1998), McCrea et al. (2001)
<i>Tetrapodosaurus borealis</i>	Tracks and trackways, manus and pes prints	Patuxent Fm	Virginia, USA	Aptian	Weems and Bachman (2015)
<i>Tetrapodosaurus borealis</i>	Tracks and trackways, manus and pes prints ^a (skin impressions)	Dunvegan Fm.	Alberta and British Columbia, Canada	Cenomanian	Currie (1989), McCrea et al. (2001, 2014)
<i>Tetrapodosaurus borealis</i>	Tracks and trackways, manus and pes prints	Kaskapau Fm	British Columbia, Canada	Cenomanian–Turonian	McCrea (2003), McCrea et al. (2014)
<i>Tetrapodosaurus</i> cf. <i>T. borealis</i>	Tracks and a partial trackway, manus and pes prints ^a	Ross River Block	Yukon Territory, Alaska	Albian–Cenomanian	Gangloff et al. (2004), McCrea et al. (2014)
<i>Tetrapodosaurus</i> isp.	Tracks and trackways, manus and pes prints ^a	Dakota Fm.	Colorado, USA	Albian–Cenomanian	Lockley et al. (2014b)
<i>Tetrapodosaurus</i> isp.	Isolated manus print ^a	Wapiti Fm	Alberta, Canada	Campanian	Fanti et al. (2013)
<i>Tetrapodosaurus</i> isp.	Tracks, manus and pes prints ^a (skin impressions)	Nanushuk Fm	Alaska	Albian–Cenomanian	May and Druckenmiller (2009), Gangloff (2012)
<i>Tetrapodosaurus</i> isp.	Pes tracks ^a	Wessex and Vectis Fms	Isle of Wight, England	Barremian–Aptian	Pond et al. (2014)
<i>Tetrapodosaurus</i> isp.	Manus tracks ^a	Artoles and Camarillas Fms	Teruel, Spain	Barremian	This work
Cf. <i>Tetrapodosaurus</i> isp.	Tracks and trackways, manus and pes prints	Gorman Creek Fm	British Columbia, Canada	Berrisian–Valangian	McCrea et al. (2014)
Cf. <i>Tetrapodosaurus</i> isp.	Tracks and trackways, manus and pes prints	Pasayten (?) Group	British Columbia, Canada	Albian	McCrea et al. (2014)
Cf. <i>Tetrapodosaurus</i> isp.	Tracks and trackways, manus and pes prints ^a (skin impressions)	Chandler Fm	Alaska	Albian–Cenomanian	Gangloff (1998), McCrea et al. (2001)
Cf. <i>Tetrapodosaurus</i> isp.	Pes prints from a trackway (lost)	Dakota Fm	Utah, USA	Cenomanian	Loewen et al. (2013)
Cf. <i>Tetrapodosaurus</i> isp.	Isolated manus track ^a	Morrison Fm	Colorado, USA	Late Jurassic	Hups et al. (2008), Lockley et al. (2014a)
Cf. <i>Tetrapodosaurus</i> isp.	Manus and pes prints	Atotsuwaga Fm	Japan	Aptian	Fujita et al. (2003)
Cf. <i>Tetrapodosaurus</i> isp.	Manus and pes prints ^a (poorly preserved)	Djadoktha? Fm	Mongolia	Campanian	Ishigaki et al. (2009)
? <i>Tetrapodosaurus</i> isp.	“Limited material” (undescribed)	Jiaguan Fm	Sichuan, China	Barremian–Albian	Xing and Lockley (2016)

^a Including natural casts

Valanginian–Barremian Broome Sandstone of the Dampier Peninsula (McCrea et al. 2011). However, these tracks are assigned by Salisbury et al. (2016) to the new ichnotaxon *Garbina noerorum*, regarded by them as having likely stegosaurian affinities.

6.3 Affinities of the *Tetrapodosaurus* trackmaker

The trackmaker of *Tetrapodosaurus* appears to be an ankylosaur with a pentadactyl manus and a tetradactyl pes. Based on a comparison of the autopodial morphology with

that of the ichnites and also on biostratigraphical and geographical grounds, Carpenter (1984) suggested that the tracks of *T. borealis* are those of the nodosaurid *Sauropelta* (Aptian–Albian, USA). Late Cretaceous North American nodosaurids *Nodosaurus* (Cenomanian, USA) and *Nio-brarasaurus* (Coniacian–Campanian) also display a tetradactyl pes, but the manus is incomplete (Carpenter and Kirkland 1998; Carpenter et al. 1995). In the Early Cretaceous North American nodosaurid *Peloroplites* (Aptian–Albian, USA), the manus is pentadactyl but the pes is unknown (Carpenter et al. 2008). By contrast, the pes of the Late Cretaceous North American ankylosaurid *Euoplocephalus tutus* (Campanian, Canada) is tridactyl (Coombs 1986), and this excludes it as a possible trackmaker of *Tetrapodosaurus*.

Taking into account that the current geographic distribution of *Tetrapodosaurus* is not limited to North America, other ankylosaurian taxa with a pentadactyl manus and a tetradactyl pes may also be the producers of the ichnites. In Asia, the Late Cretaceous Mongolian ankylosaurids *Shamosaurus* (Aptian–Albian), *Talarurus* (Cenomanian–Santonian) and *Saichania* (Campanian) have a five-digit manus but the pes is either unknown or partially preserved (Maryńska 1977; Currie et al. 2011; ages sensu Arbour and Currie 2016). The Asian ankylosaurids *Pinacosaurus* (Campanian, Mongolia), ‘*Zhejiangosaurus*’ (Cenomanian, China) and *Liaoningosaurus* (Barremian, China) have tridactyl pedes (Currie et al. 2011).

In Europe, the only preserved ankylosaurian autopodium is the manus of *Dracopelta* from the Late Jurassic of Portugal, but the specimen is incomplete (Pereda-Suberbiola et al. 2005). No data are currently available about the hands and feet of Early Cretaceous European ankylosaurs. In Galve, isolated teeth and dermal scutes of a “polacanthid” have been found in the Barremian of the La Cantalera site (Canudo et al. 2004, 2010). The only ankylosaur known in the Barremian of Spain is *Polacanthus*, with osteological records in Burgos, Soria and Castellón (Pereda-Suberbiola et al. 1999, 2007; Gasulla et al. 2011). *Polacanthus* is a medium-large nodosaurid (body length 5–6 m), first described in the pencontemporaneous deposits of the Isle of Wight (see Pereda-Suberbiola 1994; Blows 2015 and references within). Although there is no direct evidence, *Polacanthus* may be a possible trackmaker of the Galve ichnites.

In summary, autopodial morphology and geological age suggest a nodosaurid as the best candidate trackmaker for the *Tetrapodosaurus* tracks, as hypothesized by Carpenter (1984). It cannot be definitively excluded that some of the ichnites assigned to *Tetrapodosaurus* have been produced by an ankylosaurid with a pentadactyl manus and a tetradactyl pes (but no taxon with these features is currently known in the fossil record).

6.4 Palaeoenvironment of *Tetrapodosaurus*

According to McCrea (2000), *Tetrapodosaurus* has wide hands and feet that expand on the area on which they rest. This foot type is ideal for supporting a lot of weight in soft and soaked substrates, which would have allowed ankylosaurs to eat without getting bogged down (the diet is soft plants). McCrea (2000) believed that *Tetrapodosaurus* may be traces of generalist animals with respect to the sedimentary environments, but skeletons of ankylosaurs have generally not been found in marine deposits perhaps because they prefer inland habitats: “ankylosaurs found in marine deposits... may have been transported by rivers or floods into the marine environment” (McCrea et al. 2001; see Arbour et al. 2016 for a discussion about the presence of ankylosaurs in marine depositional environments and its possible relation to habitat preferences). According to McCrea et al. (2014, 2015), the footprints of *Tetrapodosaurus* are associated with wetlands (low energy environments with plenty of water and abundant organic matter), such as coal swamps, coastal plains with abundant vegetation and lake shores. The ichnofaunas of these environments are dominated by quadruped dinosaurs, with a normally absence of bipedal forms (McCrea et al. 2014).

Although we have found associated theropod and ornithopod tracks, we do not know what ichnofauna is associated with *Tetrapodosaurus* in Galve because the natural casts are removed specimens. Where we find *Tetrapodosaurus* tracks, it seems that the quadrupedal dinosaurs (sauropods–*Deltapodus*–*Tetrapodosaurus*) are dominant relative to the bipedal forms (theropods–ornithopods) (Pérez-Lorente and Herrero-Gascón 2009). Nevertheless, it is still unknown in which way the tracks are distributed in the sedimentary levels. At first sight, *Tetrapodosaurus* does not seem to be the dominant ichnotaxon in Galve, unlike over 30 ichnocoenoses in western Canada that support the establishment of the *Tetrapodosaurus* ichnofacies (McCrea et al. 2014). Further research, including the discovery of trackways or manus-pes sets, is needed to test this hypothesis in the Galve syncline.

7 Conclusions

About fifty natural casts (convex hyporeliefs) of ankylosaurs are here reported from the Lower Cretaceous (Barremian, Camarillas and Artoles formations) of Galve, in Teruel (Spain). They are assigned to manus prints of the ichnotaxon *Tetrapodosaurus*. The ichnites are pentadactyl, wider than long, with a concave posterior margin. The digits are divergent, positioned radially, and are not enclosed in a pad. Digits II–IV face forward while digits I

and V are directed laterally or postero-laterally; digit V is the smallest of them.

The presence of *Tetrapodosaurus* in the Galve syncline (Teruel) confirms the importance of this area, due to the variety of sites and dinosaur fossil types found. Interest in this case is due to the fact that it is the first citation and description of this ichnogenus in Spain, extending its geographical and temporal distribution. Furthermore, this report demonstrates the importance of ichnology for detecting the presence of animals in places where the skeletal remains are to-date rather scarce (Canudo et al. 2004, 2010).

Careful examination of the casts has allowed reconstruction of the kinds of joint and forelimb movements that is independent of, but consistent with, interpretations based on functional aspects of the forelimb skeleton. Cast structures also depend on the relationship between the soft parts of the autopods and the ground. Direct structures (sensu Gatesy 2003) respond to the behavior of the soft parts of the hand that are in contact with the mud. The expansion structures of crush pads, the change of the sector of skin in contact with the walls, and the rotating scales in the base of the cast are factors indicating that digital pads of the ankylosaur hands were not rigid, but rather flexible calluses.

Our finding of only manus prints and none from the pes raises the question of whether ankylosaurs, like other four-legged dinosaurs, could produce manus-only trackways. With the data presently available, however, we cannot say anything about the behavior of these animals when they left this kind of trackway. The hypothesis of the conservation status of the footprints as a possible answer to the problem is pointed out.

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