



Nothosaur tracks from the Middle Triassic of Spain suggest a global distribution for distinctive swim track assemblages

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LETHAIA



The seas of the Mesozoic were remarkable for predatory marine reptiles, but the track record of these vertebrates is extremely scarce and morphologically distinct. In this paper, Middle Triassic seabed tracks made by the paddles of nothosaurs (Reptilia, Sauropterygia) from the Valdelcubo locality, Riba area, Guadalajara, Spain, are reported. The trackway occurs at the base of Cuesta del Castillo Sandstones Formation. The palaeoenvironment was a shallow near-coastal marine habitat. The tracks from Valdelcubo are broad, elliptical, with the claw marks locally differentiated, with double row imprints. The left tracks of the trackway are better recognized than the right ones. This record is interpreted as a trackway of a buoyant and punting tetrapod, using its forefeet only. The features of these tracks and trackway have a strong affinity with the ichnogenus *Dikoposichnus*. Nevertheless, some tracks from Valdelcubo are associated swim traces and claw marks, being tentatively classified as aff. *Dikoposichnus*. This finding adds new data to the little-known type of locomotion of nothosaurs. Additionally, this is the first Triassic record of subaqueously-registered paddle tracks attributed to sauropterygians outside China and enhances the information about its palaeobiogeographical distribution, suggesting a global distribution for distinctive swim track assemblages. □ Marine reptiles, Nothosaur tracks, Middle Triassic, Valdelcubo, Spain.

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The first marine reptiles are known from the late Early Triassic, including ichthyosaurs, nothosaurs and pachypleurosaur, while placodonts and thalattosaurs emerged soon after, in the early Middle Triassic (Chen *et al.* 2012; Liu *et al.* 2014). These marine reptiles swam in shallow seas around Pangaea, feeding generally on small to large prey ranging from crustaceans and other invertebrates to fishes. In addition, the larger marine reptiles, such as some ichthyosaurs, thalattosaurs and nothosaurs, may also have fed on smaller marine reptiles, while the placodonts specialized in browsing and crushing oysters (Motani 2009; Neenan *et al.* 2013; Liu *et al.* 2014; Scheyer *et al.* 2014). Reports of tracks or markings made by sauropterygians or ichthyosaurs are rare (Geister 1998; Manni *et al.* 1999) including the few Triassic tracks made by sauropterygians only known from the Middle Triassic

of China (Zhang *et al.* 2014; Xing *et al.* 2020). This is surprising, as fishes and tetrapods today commonly make markings on the seabed when they are foraging or moving, and indeed examples of sinusoid impressions produced by the ventral fins of fishes have been reported (e.g. Simon *et al.* 2003; Minter & Braddy 2006).

At the Valdelcubo locality in the Riba Anticline (Guadalajara, Spain), Middle Triassic (around 242 Myr ago) seabed tracks made by the paddles of a marine reptile have been recently discovered and the aim of this paper is to describe them to contribute new data to both the Iberian and global Triassic record of Sauropterygia. Implications for the palaeobiogeographical distribution presently known for these Middle Triassic marine reptiles are also considered.

Geographical and geological setting

The palaeontological sites of the Riba Anticline are located in the North-West of the Province of Guadalajara, Central-Eastern Spain (Fig. 1A). This area corresponds to the Riba Anticline, which comprises a series of sites close to Riba de Santiuste, Valdelcubo and Tordelrábano (Fig. 1B, C). The Valdelcubo reptile tracksite is located in the eastern flank of the anticline complex. The Riba anticline is composed of Triassic materials that include Buntsandstein, Muschelkalk and Keuper facies. It is an exceptional place due to the excellent preservation of the inorganic and organic structures and the information that they provide for the reconstruction of the Triassic sedimentary environments (Sánchez-Moya *et al.* 2015; Berrocal-Casero *et al.* 2018a).

The study area is situated at the conjunction of the Iberian Range and the Central System, a key region during the Middle Triassic, because this area constituted the western sector of the Tethys basin margin during that time. In the Riba Anticline, the Muschelkalk facies are composed by three successive formations defined by García Gil (1990): the Tramacastilla Dolostones Formation, the Cuesta del Castillo Sandstones Formation and the Royuela Marls and Siltstones Formation. The section begins with dolostones and dolomitic sandstones of around 10 m thick, which show microbial lamination, and corresponds to mixed tidal flat. This first sedimentary succession is known as the Tramacastilla Dolostones Formation. Some fossil remains are located in the overlapping sandstones and siltstones, reaching up to 12 m, showing well preserved sedimentary organic and inorganic structures, such as bioturbation, cross stratification, different types of ripple marks, flute casts, and fossil remains (plants, bivalves, brachiopods, fragmented vertebrates and vertebrate tracks). This unit corresponds to detrital-carbonate mixed deposits of coastal shallow marine palaeoenvironment (subtidal in the lower part) to supratidal environments with channels in the upper part and corresponds to Cuesta del Castillo Sandstones Formation. The uppermost part of the section (15 m) is composed of marls, dolostones, sandy dolostones, sandstones and shales and contains the richest diversity and fossil content (bivalves, brachiopods and vertebrate remains). Some levels show abundant bioturbation of ichnogenus *Rhizocorallium*. This unit was deposited in shallow marine environments and is called Royuela Marls and Siltstones Formation. A characteristic level of tepee structures is identified at the top of Muschelkalk facies in the section. The palaeoenvironment of this formation corresponds to shallow marine environments in

the lower part, and detrital-carbonate mixed deposits of coastal intertidal to supratidal environments at the upper part (see Berrocal-Casero *et al.* 2018a, for more detailed geological context).

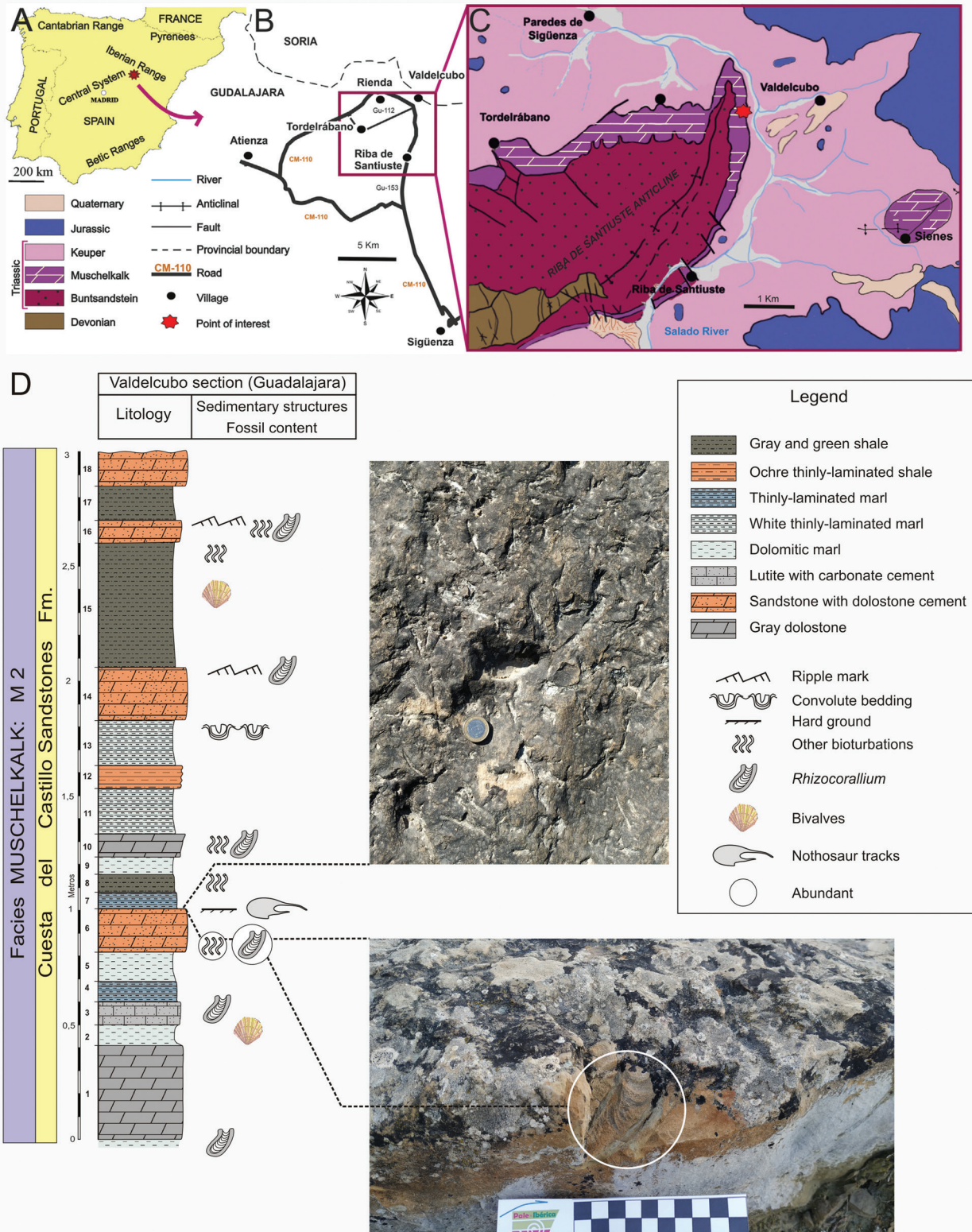
In detail, the track occurs at the base of Cuesta del Castillo Sandstones Formation (Fig. 1D, top of level 6). This detailed section shows an alternation of dolomite, thinly laminated marls and shales with levels of lutite and sandstones with dolomitic cement, and also some alternating dolostone levels. This sequence corresponds to a shallow subtidal environment. The level with the tracks corresponds to an approximately 20 cm thick of a mixed carbonate and terrigenous ochre and gray sandstone. It is very bioturbated by *Rhizocorallium* isp., especially at the top (Fig. 1D).

Material and methods

At the Valdelcubo tracksite, there is a trackway with seven tracks preserved as concave epireliefs on a carbonate-siliciclastic single bedding plane. The footprints have been photographed under natural light conditions using Olympus digital camera (Olympus EM5 Mark 2, 4608 × 3456). These tracks have been measured to describe them using the classic approach (*e.g.* Leonardi 1987) and following Xing *et al.* (2020) due to the necessity to adapt the measures to trackways made by floating tetrapods that put their limbs on the seabed to get the propulsion needed to move through the water. Therefore, as pace length and stride length cannot be used considering the original definition (Leonardi 1987), the measurement 'D', the distance between successive impressions on the same side of the trackway, have been adopted. The term 'stride length' is applied here to refer the measurement D, the distance between successive tracks made by the same limb as the animal moved forward. We also measured the trackway width (Tw), the distance between the outer tips of the left and right series of prints. In each impression the longest axis (TW – track width) and the shorter axis (TL – track length) have been measured perpendicular to each other (Fig. 2). All the measurements were taken in the field at the track level. The term 'track' has been used only in broadly descriptive portions of the paper, when it refers in a general sense to the individual front limb prints and the trackway as a sequence of marks.

Middle Triassic biota of the Riba Anticline

The existence of invertebrate and vertebrate remains in the Muschelklak facies of the Riba anticline was



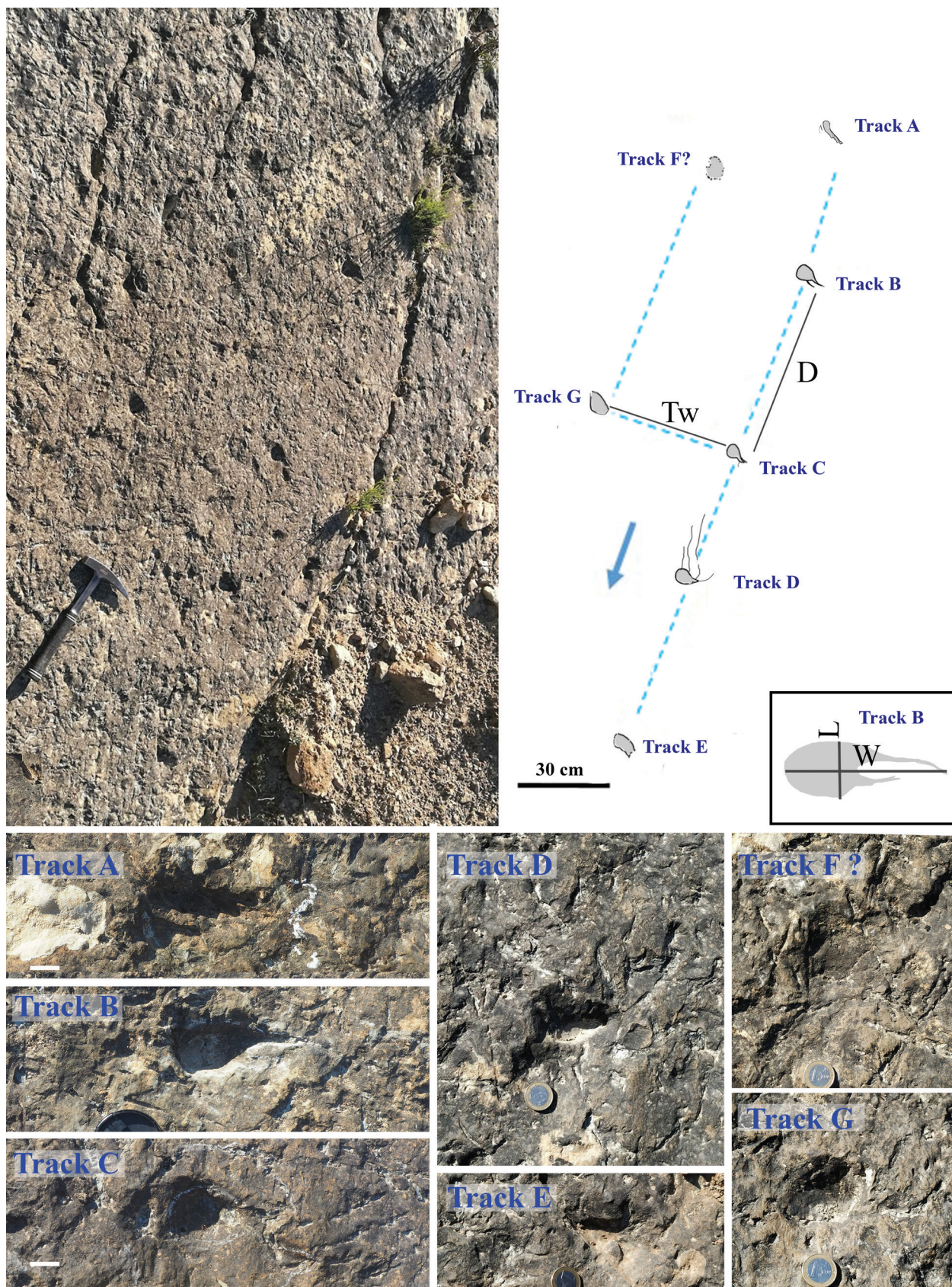


Fig. 2. Overview of the trackway aff. *Dikoposichnus* studied in Valdelcubo locality, in Riba Anticline (Guadalajara, Spain). Top left, photo of the trackway. Top right, draft of the trackway indicating the measurements taken. Below, detail of the different tracks. D: distance between successive impressions on the same side of the trackway. Tw: trackway width, the distance between the outer tips of the left and right series of prints. L: track length. W: track width. Arrow indicates the direction of movement. White scale bars: 2 cm.

observed by Sopena (1979), and García-Gil (1990, 1991, 1994). Sopena (1979) identified some palynomorphs, and García Gil (1990) identified bivalves (*Lyriomyophoria sublaevis*, *Unionites* sp.), foraminifera (Nodosaridae, Miliolidae), echinoderms, gastropods, green algae and ichnofossils (*Rhizocorallium*) at some levels of Cuesta del Castillo Formation. Márquez-Aliaga & García-Gil (1991) identified brachiopods (*Lingula tenuissima*) and bivalves (*Lyriomyophoria* cf. *sublaevis*, *Pseudocorbula gregaria*) in the Cuesta del Castillo and Royuela Formations. Sopena (1979) found a big nautiloid in the Upper part of the Muschelkalk facies of this area, in the Valdelcubo locality. Goy and Martínez (1996) classified this specimen to the new species of nautiloid *Picardiceras sopegnai*. Alafont (1999) described some invertebrates and several isolated sauropterygian fossil remains, and Fortuny *et al.* (2011) mentioned the presence of nothosaurs and placodonts in the Muschelkalk facies of the Riba Anticline. Berrocal-Casero and Castanhinha (2015) described some sauropterygian remains in this area. Berrocal-Casero *et al.* (2018a) described plants (*Scolopendrites* sp.), brachiopods (*Lingula tenuissima*), bivalves (*Lyriomyophoria* cf. *sublaevis*, *Pleuromya* sp., *Costatoria killiani*), and vertebrate bone remains, including Sauropterygia (Nothosauroida, Placodontia) and possible archosaurs (Rauisuchia), with an exceptional mode of preservation, and vertebrate swimming tracks (see Berrocal-Casero *et al.* 2018a) in the upper part of the Muschelkalk section, in the Royuela Formation. In the upper part of the section, in the Tordelrribano locality, an exceptional Middle Triassic rauisuchian archosaur tracksite was also discovered, containing the impressions of abundant isolated tracks and several trackways of quadrupeds (Meléndez & Moratalla 2014; Berrocal-Casero *et al.* 2018b).

Regarding the age of the materials of Riba Anticline, Sopena (1979) described some pollen assemblage characteristic of the Ladinian in the Cuesta del Castillo Formation, and pollen assemblages that were common in the Carnian, at the top of the Royuela Formation, being considered between the Ladinian-Carnian by García-Gil (1990, 1991). Nevertheless, more recent works about these types of Triassic pollen assemblages of the Tethyan realm (Hochuli *et al.* 2015) revealed that some of these palynomorphs classically attributed to Carnian were present in the Ladinian too. The mentioned bivalves of the section that appear in some levels above and below the track surface (Fig. 1D) are characteristic of the Ladinian (see Berrocal-Casero *et al.* 2018a). Goy & Martínez (1996) assigned the nautiloid *Picardiceras sopegnai* to the Upper Ladinian, being a species confirmed as

Upper Ladinian in a revision realized by Pérez-Valera *et al.* (2017: p. 187, fig. 13). The precise stratigraphical position in which appear the main part of vertebrate remains from the Riba anticline (mainly nothosaur and placodont remains) were also assigned to the Upper Ladinian (see Berrocal-Casero *et al.* 2018a). The Valdelcubo tracksite here studied is located at the lower part Cuesta del Castillo Formation, below these levels rich in sauropterygians remains; although in some levels below the track surface, nothosaur and placodont isolated bone remains can be also found. The faunal assemblage of this section allows attribution of the tracksite to the Ladinian.

The Riba Anticline is an exceptional place, with numerous palaeontological sites, very relevant to understanding the Middle Triassic environments and faunal assemblages, where the discoveries of new sites occur due to erosion that exposes new palaeontological treasures.

The Valdelcubo reptile tracksite

The Valdelcubo tracksite is located at the Riba Anticline (see Geological context above and Fig. 1) and the reptile tracks are preserved at the top of a single carbonate bedding plane. The surface that contains the tracks shows a total of two square metres that were recorded and photographed (Fig. 2). It is very bioturbated, with numerous marks on its surface, among which ichnogenus *Rhizocorallium* can be easily recognized.

Tracks and trackway description

On this surface, one trackway has been recognized, comprising four paddle-swimming impressions clearly visible and another three, although in worse conditions of preservation (Fig. 2). Characteristically, only the left side of the trackway shows well preserved tracks. The trackway shows considerable variation in the distance between successive impressions (which is characteristic of trackways left by swimming vertebrates) of the same side of the trackway, ranging from 40 to 60 cm. The trackway shows a stride length of 42 cm from track A to track B, of 56 cm from track B to Track C, of 38 cm between track C and track D, 52 cm between track D and track E, and 80 cm between track F and G (Fig. 2). The trackway width, measured between the tracks B and F (made by the left and right frontlimb of the same trackmaker) is 50 cm.

Each impression is broad, elliptical in plan view, with lateral extensions (mainly paired), with values of track width up to 10 cm and showing variable values of track length, but they are generally much wider than long. These extensions seem to correspond to

digits. In some tracks, the claw marks are also evident. A mound of sediment behind the tracks, sometimes with an anterior sweep at the medial edge, can be differentiated in all of them. Individual imprints are transverse to the direction of travel. The tracks are positioned symmetrically and they are inwardly rotated in relation to the trackway midline.

Track A reveals an elliptical-elongated shape with some lateral extensions which seem to correspond to digit impressions. The width of this track is 9.5 cm, and its length is 2 cm (Figs 2, 3A).

Track B reveals a rounded-elliptical to horizontal V shaped. This impression is deeper in its posterior part. Two lateral extensions of different dimension can be observed, providing 10 cm of width in total, while the track length is about 3 cm. In track B, the mound of sediment is differentiated behind the whole track, and behind the more anterior and shorter extension (Figs 2, 3B).

Track C is rounded, and a sigmoid extension can be differentiated in the print, being the double sigmoid curve less well differentiated comparing to track B. It is 7 cm along its longest axis (track width) and 3 cm along its perpendicular axis (track length). As occur in track A, the deepest part is located posteriorly. This track shows certain crescent shape. The mound of sediment can be differentiated behind the track (Figs 2, 3C).

Track D is very elliptical and elongated, measuring 5 cm along its longest axis (track width), where a little extension can be differentiated behind the print, and 1.5 cm along the shorter axis (track length). The mound of sediment seems to be bigger than that observed in prints A and B, and three-four scratches corresponding to swim tracks seems to be also associated, as well as claw marks (Figs 2, 3D).

Tracks E, F and G show a poorly differentiated morphology. The track E is small, being its track width of 4 cm and its track length difficult to determine because of the track condition. Two or three lateral extensions are present. One of them could be well differentiated, but the other are poorly inferred. The deeper part of the track is located posteriorly. The print F shows 6 cm along its longest axis and 4 cm along the perpendicular axis, being the depth of the print well pronounced and vertical posteriorly, decreasing anteriorly. Track G is poorly defined, being differentiated by an oval depression of around 5 cm (Fig. 2).

Discussion

Swim tracks of reptiles have been described under the ichnogenus *Characichnos* from numerous localities, including the Riba Anticline (see Berrocal-Casero

et al. 2018b, fig. 9). This ichnogenus mostly consists of three or more parallel scratches of the claws, left when the trackmakers touched the ground with their hind legs while swimming. However, *Characichnos* is represented only by scratch marks without heel impression. Moreover, this ichnogenus does not represent a trackmaker that consistently registered a symmetrical trackway, with elliptical prints with lateral extensions, as those reported here.

The shape of these Valdelcubo tracks resembles the ichnogenus *Accordiichnus* (Manni et al. 1999) from the Jurassic of Italy, especially in the 'pear shape' morphology of some tracks. However, this ichnogenus is characterized by the impressions of the forelimbs and with the hindlimbs traces alternating regularly. Moreover, the pear shape (the thinner area of the impression) of the manus print is oriented inwards, while the tracks studied here show the pear-shape rotated outwards.

These tracks described here only present similarities with the ichnotaxa *Dikoposichnus luopingensis* Zhang et al. (2014), from the Middle Triassic of China. These authors described this new ichnogenus and ichnoespecies in the Ladinian of Luoping, Yunnan Province. The same ichnotaxa was later identified by Xing et al. (2020) in the Anisian-Ladinian of Qingyuant, Guizhou Province. This ichnotaxa corresponds, according to Zhang et al. (2014) and Xing et al. (2020), to nothosaur tracks, being, to date, unknown out of the Triassic of China. Indeed, tracks of any kind that might have been produced by any of the Mesozoic marine reptiles are very rare. The double row of tracks, narrow, V-shaped, slot-like depression, with a mound of sediment behind, elliptical in plain view, sometimes with an anterior sweep at the medial edge, are diagnostic of the ichnogenus *Dikoposichnus* Zhang et al. (2014). Some tracks assigned to this ichnotaxa by Xing et al. (2020) show laterally directed sharp digit traces. Moreover, some of these Chinese tracks comprise sometimes a single trackway (made only by the same left or right forelimb). However, the Valdelcubo tracks present some differences related to the tracks described by Zhang et al. (2014), being tentatively classified as aff. *Dikoposichnus*.

The tracks described by Zhang et al. (2014) do not show claw marks, while some tracks from Valdelcubo site seem to show differentiated claw marks associated to swim tracks (Figs 2, 3, track D). Comparing to the morphotypes described by Zhang et al. (2014), the prints B and C from Valdelcubo are very similar to those tracks from the trackways A and L, showing the same shape with lateral extensions (Fig. 4A, B) (see also Zhang et al. 2014, Figs 2, 4). Referring to the other morphologies described by Zhang et al.

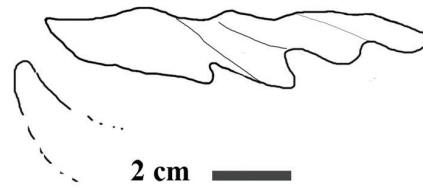
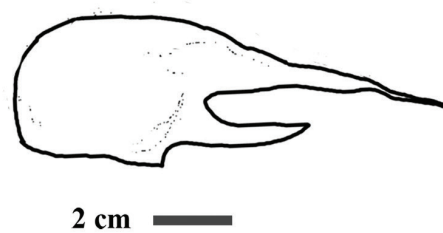
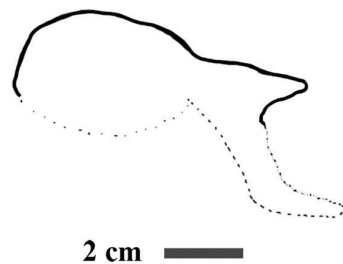
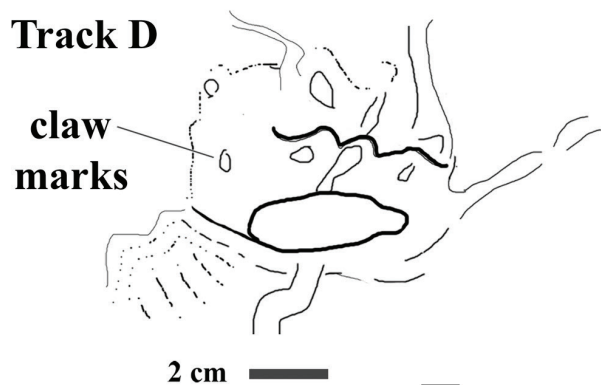
**Track A****Track B****Track C****Track D**

Fig. 3. Detail of the best-preserved tracks aff. *Dikoposichnus*. A, elliptical track with digits impressions. B, C, track with lateral extensions. D, elliptical track with associated swim tracks and claw marks. Arrow indicates the direction of movement.

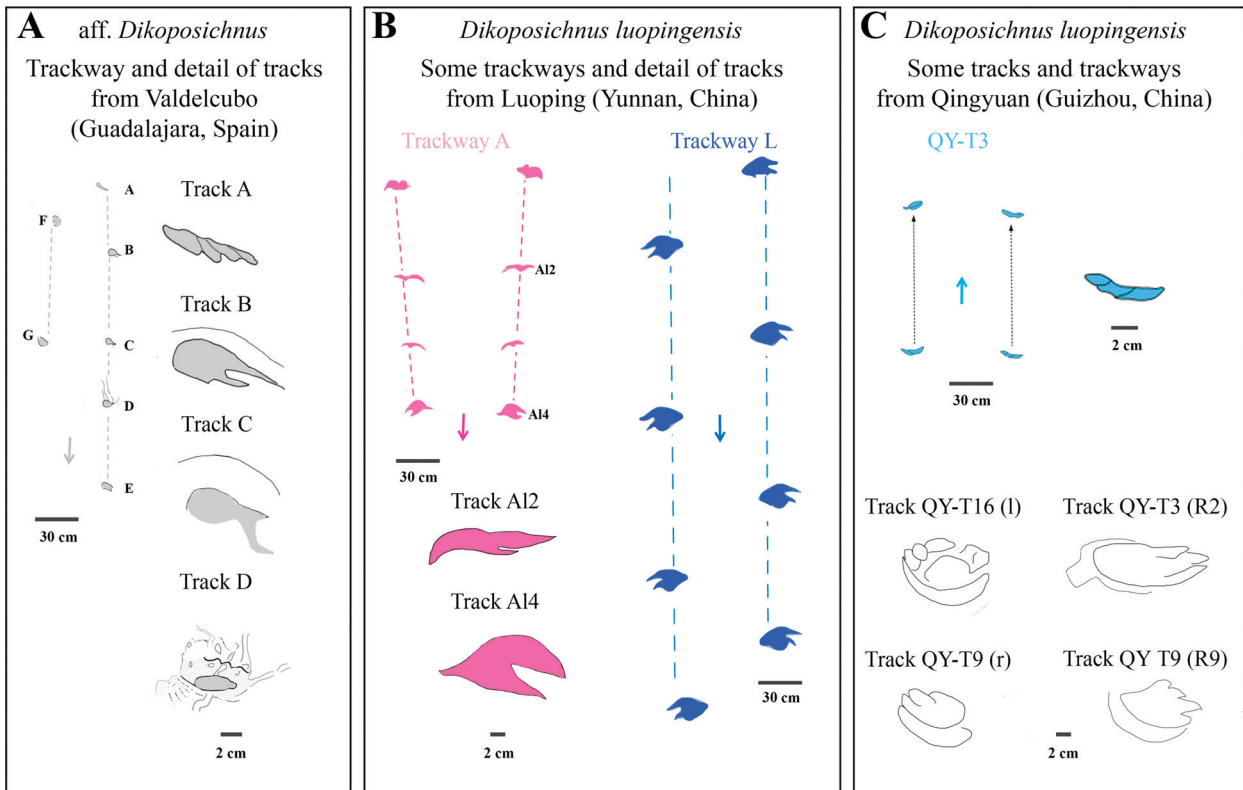


Fig. 4. Comparison of the tracks and trackways of the nothosaur tracksites described in the world, until today. A, aff *Dikoposichnus*. Trackway and detail of the tracks from Valdelcubo (Guadalajara, Spain). B, trackways and tracks from the ichnogenus *Dikoposichnus luopingensis* taken and modified from Zhang *et al.* (2014, fig. 2), trackways A and L, and detail of tracks AI2 and AI4 from Zhang *et al.* (2014, fig. 4). C, section of the trackway and some tracks from the ichnogenus *Dikoposichnus luopingensis* taken and modified from Xing *et al.* (2020, fig. 5E), detail of the track (in blue) and tracks Track QY-T16 (l) from fig. 3a, Track QY-T3 (R2) from fig. 5C, Track QY-T9 (r) from fig. 3G, and Track QY-T9 (R9) from fig. 5C. Trackway scale bars: 30 cm. Scale bars of tracks: 2 cm.

2014, the tracks here studied from Valdelcubo are less sigmoid in shape and are more rounded-elliptical. Moreover, they are much deeper inwardly, being the elliptical shape very marked, while the lateral extensions are longer, less marked and shallower (Figs 2, 3).

The tracks described here are also morphologically close to those figured by Xing *et al.* (2020, figs 3A,F,G, 5) which are assigned to *D. luopingensis*, especially the track A from the Valdelcubo site, that is very similar to the tracks figured by these authors in figure 5d-e (trackway QY-T3), especially in the digit print, although the track from Valdelcubo show less developed half-moon or crescent shape (Fig. 4A, C).

The tracks from Valdelcubo differ from *Anshunpes aquacursor* Xing *et al.* 2020, from the Middle Triassic of Qingyuan, China, recognized as placodont tracks, because *A. aquacursor* is characterized by the presence of fully impressed autopodium with digits and sole traces, with plantigrade to semi-plantigrade tetradactyl robust imprints, outwardly curved (Xing *et al.* 2020, fig. 6).

Possible trackmaker

The continuous trackway pattern with imprints positioned symmetrically suggests a trackway of a tetrapod while swimming and touching the bottom with their forelimbs: i.e., punting (*sensu* Lee *et al.* 2019; Mustoe 2019; Xing *et al.* 2020) (Fig. 5). The crescent-shaped imprints, the laterally pointing digits and the posterior sediment mound support this interpretation (Figs 2 and 3). The morphology of each individual track and its position along the trackway suggest that they were formed by a limbed animal moving in a steady manner over the seabed. Individual tracks suggest a mode of formation in which the forelimb touched the bottom, entered the sediment to a depth of several centimeters, pushed backwards raising a sediment mound, and exited from the sediment (propelling itself), as described by Zhang *et al.* (2020, fig. 7). The stride lengths are variable. This is because animals floating may have different values for the stride lengths depending on their speed of movement over the seabed.

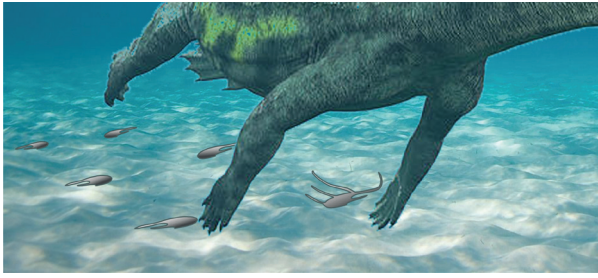


Fig. 5. Reconstruction of a tetrapod while swimming and touching the bottom with their forelimbs, and tracks created as a consequence of the propulsion of the animal along the seabed. The reconstruction scene is based on the tracks.

Regarding the trackmaker, the obvious culprits are marine reptiles. The size and morphology of the tracks and the way they are arranged along the trackway rule out arthropods or fishes. It is likely that the imprints were made only by the front limbs, for the following reasons: all imprints are similar in shape, so this is probably because they represent the manus or the pes only, and there is no case of a print of a putative hindlimb or foot overprinting a front limb print, and Mesozoic marine reptiles generally used their forelimbs much more actively than their hindlimbs in locomotion (Robinson 1975; Carpenter *et al.* 2010; Zhang *et al.* 2014). Torso width can be estimated by measuring the inner width of the trackway (spacing between medial edges of paired imprints) and adding an additional distance on each side to the length of the humerus. In this case, for a trackway of 50 cm in width, the torso of the animal would be around 35–40 cm.

The marine reptiles known from the study area include placodonts, pachypleosaurs and nothosaurs (Berrocal-Casero *et al.* 2018a). According to Xing *et al.* (2020), while searching for food such as the shells of marine invertebrates, buoyant or swimming placodonts might have touched the bottom mostly with their forelimbs, with the centre of mass being shifted anteriorly. During swimming or ‘punting’ placodonts may have held their hindlimbs in a horizontal position aligned to the body. However, placodonts generally have short hands with well differentiated fingers. The only known tracks attributed to placodonts are very different to those attributed to nothosaurs, being characterized by the presence of a fully impressed autopodium with digits and sole traces, similar to the tracks of terrestrially walking tetrapods (see Xing *et al.* 2020). Pachypleosaurs were too small (ranging in size from 20 cm to about a metre in length; e.g. Rieppel & Kebab 1995; Rieppel 2000) to have left this type of trackways here described.

The trackmaker of the ichnospecies *Dikoposichnus luopingensis* must correspond to a nothosaur (order Nothosauroidae), because these animals developed paddle-like extremities that might have left wide trackways with evidence of digits preserved as scratches of the distal parts only (Zhang *et al.* 2014; Xing *et al.* 2020). However, the tracks described and figured by Zhang *et al.* (2014) do not show evidence of claw marks, while the prints here studied show claw marks associated with swim tracks. These differences could be related to the type of Sauropterygia trackmaker (see Caldwell 1997, fig. 2; Caldwell 2002, fig. 4). The body shape of the different ‘nothosaur’ genera was rather similar, showing the same adaptations to aquatic life, mainly in the structure of the limbs and of the girdles (Carroll & Gaskill 1985), but the size and limb proportions were variable. Zhang *et al.* (2014) interpreted that *Lariosaurus* could be the trackmaker of *Dikoposichnus luopingensis*, but they do not exclude small *Nothosaurus* as possible trackmakers. However, is important to consider that *Lariosaurus* is characteristic among nothosaurs because its frontlimbs were adapted into paddles, while the hindlimbs remained five-toed (Rieppel 1998; Palmer 1999). For this reason, considering that in the trackway here described only the anterior limbs touch the seabed, it would be reasonable that *Lariosaurus* (and other nothosaurs with hyperphalangy in the anterior limbs, with their forelimbs adapted as paddles) tracks do not present digit impressions and claw drag marks, but probably other representatives of Nothosauroidae could register claw marks and scratches, because their anterior limbs have more differentiated digits, as occurs in *Nothosaurus* and *Simosaurus*. Nothosauroidae includes Nothosauria and Simosauridae, being Simosauridae remains also recorded in the Riba Anticline (Berrocal-Casero *et al.* 2018b). According to Rieppel (1998), *Simosaurus* has well-developed vertebrae and a dorsoventrally flattened trunk that would have inhibited side-to-side movement. Possibly, the forelimbs had a powerful downstroke and provided most of the thrust required for swimming, and maybe the upstroke of *Simosaurus* was weak. In the Middle Triassic of El Atance (Guadalajara, Spain), very close to the Riba Anticline, the marine Simosauridae *Paludidraco multidentatus* de Miguel Chaves *et al.* 2019, was defined. According to these authors, this reptile presents an extremely pachyostosis of the axial skeleton suggesting a highly specialized trophic adaptation like filter-feeding, which would have allowed him to swallow the food and the water from the bottom. Although the limbs morphology of this reptile is still unknown, the lifestyle of this reptile living close to the bottom could be compatible with the trackmaker

of the tracks here described. Possibly, the tracks described by Zhang *et al.* (2014) and Xing *et al.* (2020) were produced by representatives of Nothosauria (*Nothosaurus* or, much probably *Lariosaurus* as suggested by the former), while the tracks described here could be produced by Nothosauria, but also, by representatives of Simosauridae. The different nothosaur trackmaker, with different type of forefeet (with differenced digits instead of with the forelimb adapted to a paddle without differenced digits), and even other factors like possibly different behaviour, could explain some differences, as the presence of claw marks and associated swim traces in some tracks here studied.

Conclusions

The Ladinian (Middle Triassic) Valdelcubo track-site, in the Riba Anticline, Guadalajara, Spain, shows a trackway documenting subaqueous activities of bouyant animal touching the substrate while poling. There are seven impressions preserved that have been interpreted here as paddle prints made by nothosaurs, as it propelled itself across the seabed. At the newly described site in Riba area, aff. *Dikoposichnus* ichnotaxon suggests the occurrence of nothosaurian sauropterygians (excluding those with hyperphalangy in the anterior limbs as *Lariosaurus*) swimming in shallow marine habitats along the coast of the Western Tethys. Potential food of the sauropterygians were cephalopods, bivalves and other invertebrates as well as fish, all abundantly known from body fossils overlying Middle Triassic levels. This record appears to be the first ichnological documentation of the swimming and 'punting' movement of Triassic Sauropterygia outside China, supporting the supposed lifestyle of these animals swimming in shallow near coast habitats of the Tethys Ocean. This new discovery confirms some previous assumptions about the little-known modes of locomotion and feeding by these early sauropterygians. Moreover, this finding gives additional palaeobiological, palaeobiogeographical and palaeoenvironmental data, improving the global knowledge about this fauna.

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