Cretaceous Research 165 (2025) 105981

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

The impact of microbial mats in promoting record of Maastrichtian crocodylomorph tracks from Yacoraite Formation, Argentina

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A R T I C L E I N F O

Article history:
Received 4 May 2024
Received in revised form
26 July 2024
Accepted in revised form 9 August 2024
Available online 14 August 2024

Keywords:
Overtracks
Palaeoenvironment
Palaeoecology
Swimming behaviour
Late Cretaceous

A B S T R A C T

Here we report tetrapod tracks from a stratigraphic level of Maastrichtian age in the Yacoraite Formation (Maimará ichnosite, Jujuy Province, Argentina). The ichnological material consists of convex hyporeliefs whose formation was induced by growth of microbial mats in an upper subtidal-lower intertidal setting. Ichnological features that are recognized in tracks and traces allowed to include them into the categories of ‘punting tracks’ and ‘buoyancy tracks’. These categories suggest swim behaviours of the producers, which are tentatively interpreted as crocodylomorphs. Reconstruction of the filling process leading to tracks preservation and inclusion into the geological record enabled reconstructing at least two different phases of mats development, one dominated by chemical precipitation and the other by trapping and binding of coated grains and other particles. These two phases of mat growth are related to slightly changing energetic conditions of the palaeoenvironment and further support a marine origin for the unit. Finally, it is suggested that biologically induced, in-situ mineral precipitation promotes fast formation of overtracks through early lithification achieving preservation of tetrapod tracks well before their complete filling.

1. Introduction

The Maastrichtian-Danian Yacoraite Formation is a mainly carbonate, richly fossiliferous unit cropping out in Salta and Jujuy provinces (northwestern Argentina). In Jujuy province, the unit has been related to a mainly shallow marine, mixed carbonate and siliciclastic sedimentation within an epeiric sea (Marquillas et al., 2005). The Yacoraite Formation is worldwide known for its abundant and diverse vertebrate ichnological record, which is associated to a body-fossil record of ostracods, gastropods, bivalves, microfossils, microfloral remains, and vertebrates (e.g. Bonarelli, 1927; Gasparini and Buffetaut, 1980; Alonso, 1989; Arratia and Cione, 1996; Cónsole-Gonella et al., 2012, 2017). The ichnological record of the unit is mainly represented by footprints assigned to theropods, sauropods, ornithischians, birds, and mammals, plus a plethora of other, currently indeterminate vertebrate and invertebrate traces. One of the most striking exposures of shoreline carbonate deposits included in the Yacoraite Formation is at Maimará (Quebrada de Humahuaca, Jujuy province, Argentina). Here a diverse ichnofauna related to non-avian dinosaurs and birds, as well as invertebrate traces and associated suites, were recognized in two distinct tidal sub-environments (Díaz-Martínez et al., 2016; Cónsole-Gonella et al., 2017; De Valais and Cónsole-Gonella, 2019).

New ichnological material, recently found on loose slabs from this ichnosite and stratigraphically repositioned within the Maastrichtian portion of the unit (Martín, 2023; Martín et al., 2024), enriches this record and is here discussed.

Tracks and traces are preserved as convex hyporelief consisting of a stack of laminated overtracks whose formation is related to growth of microbial mats. Microbial mats are composed of diverse communities of microorganisms capable of trapping and binding particles and/or serving as sites for mineral precipitation, leading to mat lithification. Accreted and lithified microbial mats are referred to as microbialites (Eymard et al., 2020) and constitute an excellent example of organo-sedimentary structures in different marine and

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https://doi.org/10.1016/j.cretres.2024.105981

continental environments (e.g. Riding, 2008). The Yacoraite Formation exhibits a diverse record of microbialites (e.g. Marquillas et al., 2003, 2007; Cónsole-Gonella et al., 2009, 2017). Microbialitic deposits have been related to hydrocarbon reservoirs, their recently increased importance leading to greater attention of the scientific community (e.g. Muniz and Bosence, 2015), also in South America, after the discovery of important microbialitic hydrocarbon in the pre-salt Cretaceous series of the South Atlantic (see Villafañe et al., 2023 for discussion). At Maimará, different types of microbialitic deposits have been recognized and discussed, among them domic stromatolites (e.g. Cónsole-Gonella et al., 2012; Frías-Saba et al., 2021; Villafañe et al., 2021a) and mat-like stromatolites with a laminated and homogeneous internal structure (Cónsole-Gonella et al., 2017). These organo-sedimentary structures have been related to lagoon-shoreline facies within the subtidal-lower intertidal zone, in moderate to high energy conditions under wave and tide actions (Cónsole-Gonella et al., 2017).

Moreover, the role of microbial mats in stabilization of palaeosurfaces, and formation and preservation of tetrapod footprints has been long debated (e.g. Thulborn, 1990; Avanzini, 1998; Conti et al., 2005). In this contribution, we present an interesting example of the role of microbial mats in promoting fast formation of overtracks (e.g. Lockley, 1991; Marty et al., 2009). Recognition of different stages in the growth of microbial mats allowed us to define how the studied overtracks were formed, and under which conditions of the palaeoenvironment ichnofossils were rapidly preserved. The recovered material is included within the broad category of swim tracks and tentatively attributed to crocodylomorph producers. The proposed attribution to crocodylomorphs would constitute the first report of this kind of trackmaker from the Yacoraite Formation. Our reconstruction also contributes to current debate about the depositional environment of the Yacoraite Formation, suggesting a marine origin for this lithostratigraphic unit in the Tres Cruces sub-basin.

2. Geological and palaeontological setting

The Yacoraite Formation (Turner, 1959) includes mixed carbonate and siliciclastic deposits (Sánchez and Marquillas, 2010; Deschamps et al., 2020) sedimented within an intracontinental rift-type basin (Salfity and Marquillas, 1994; Viramonte et al., 1999). According to lithostratigraphical correlations, U–Pb datings and palynomorphs, the Yacoraite Formation is Maastrichtian-Danian (Moroni, 1984; Marquillas, 1985; Quattrocchio et al., 2000; Sial et al., 2001; Marquillas et al., 2011). The unit is included in the Upper Cretaceous-lower Paleocene Balbuena Subgroup. It represents the early post-rift unit of the Lower Cretaceous-Eocene Salta Group (Marquillas et al., 2005). The Salta Group is represented in seven sub-basins, namely Tres Cruces, Lomas de Olmedo, Metán, Alemanía (Reyes, 1972), El Rey (Salfity, 1980), Sey (Schwab, 1984) and Brealito (Sabino, 2002).

The depositional setting of the Yacoraite Formation has been long debated. The unit has been related to a lacustrine palaeoenvironment (e.g. Palma, 2000; Röemers-Oliveira et al., 2015; Mutti et al., 2023) as well as to a shallow epeiric restricted sea (e.g. Marquillas et al., 2007; Cónsole-Gonella, 2011; Cónsole-Gonella et al., 2012; Cónsole-Gonella and Marquillas, 2014; Coppa Vigliocco et al., 2022; Coppa Vigliocco, 2023). In the latter case, sedimentation was mainly controlled by marine transgressions related to the high global sea level (Hay et al., 1999). In the Central Andes, the unit has been correlated by Marquillas et al. (2011) with the El Molino Formation (Bolivia; Sempere et al., 1997), Vilquechico Formation (Peru; Jaillard et al., 1993), Estratos de Quebrada Blanca de Poquis (Chile; Salfity et al., 1985), and sedimentary deposits of Pirity basin in Paraguay (see Clebsch, 1991 for stratigraphic nomenclature), on chronological and lithostratigraphic bases.

The Yacoraite Formation has a rich palaeontological record consisting of invertebrate and vertebrate body- and ichnofossils (e.g. Bonarelli, 1927; Raskovsky, 1968; Benedetto and Sánchez, 1971, 1972; Gasparini and Buffetaut, 1980; Alonso, 1989; Arratia and Cione, 1996; Marquillas et al., 2003). The ichnological record from the unit stands out for the quite high diversity of dinosaur (mainly of theropod and sauropod affinity) and avian tracks, which led to the establishment of different ichnotaxa after the first discoveries, like *Hadrosaurichnus australis* Alonso, 1980, *Salfitichnus mentoor* Alonso and Marquillas, 1986, *Taponichnus donottoi* Alonso and Marquillas, 1986, *Telosichnus saltensis* Alonso and Marquillas, 1986, *Yacoraitichnus avis* Alonso and Marquillas, 1986, and *Acheralichnus leonardii* Sánchez Rioja, 2004. This record can be compared with that described from other uppermost Cretaceous deposits in Bolivia (e.g. Leonardi, 1981, 1984; Meyer et al., 2001, 2018, 2020; Lockley et al., 2002) and Peru (Trottereau, 1964; Jaillard et al., 1993).

Sedimentary strata at the Maimará stratigraphic section are exposed along the southeastern side of the Quebrada de Humahuaca (23°37′30.92″ S, 65°23′56.07″ W) in Jujuy province (Argentina; Fig. 1A) with a sub-vertical attitude (Fig. 1B). This area is part of the austral sector of the Tres Cruces sub-basin and displays geological features typical of basin edge due to proximity of the Salta-Jujuy ridge. Differently from other localities (Sánchez and Marquillas, 2010), the Pirgua Subgroup is missing at Maimará and deposits included in the overlying Balbuena Subgroup unconformably lay above the Mesón Group of Cambrian age. The Lecho Formation (i.e. the basal lithostratigraphic unit included in the Balbuena Subgroup) is here represented by few metres of poorly sorted conglomerates, deposited by debris flows within an alluvial fan environment and intercalated with coarse- to fine-grained sandstones (Cónsole-Gonella et al., 2017). Above, the Yacoraite Formation is represented by about 42 m of tabular, well-stratified, fossiliferous limestones alternating with calcareous sandstones. The succession is also characterized by laminated mudstones, intercalated with the former deposits (Cónsole-Gonella et al., 2017), and by several stratigraphic levels bearing three-dimensionally preserved stromatolites (Villafañe et al., 2021a; Fig. 1C). On the whole, these deposits were related to a lagoon palaeoenvironment with tidal influence associated to ephemeral ponds in supratidal conditions (Cónsole-Gonella et al., 2017; see Fig. 1E for a detailed stratigraphic column).

The palaeontological content is represented by both Maastrichtian and Danian palynomorphs (Moroni, 1984; Quattrocchio et al., 2000), gastropods (Cónsole-Gonella et al., 2009), invertebrate traces (e.g. Cónsole-Gonella and Aceñolaza, 2009, 2010; Cónsole-Gonella and Marquillas, 2014), vertebrate footprints (e.g. Alonso and Marquillas, 1986; Cónsole-Gonella et al., 2017), plus ostracods and fish remains (see Cónsole-Gonella, 2011; Cónsole-Gonella et al., 2012). Díaz-Martínez et al. (2016) reported dinosaur footprint referred to *Hadrosauropodus* isp.; Cónsole-Gonella et al. (2017) described titanosaurian, ornithischian, and theropod tracks, while De Valais and Cónsole-Gonella (2019) proposed a review of avian tracks. In particular, Cónsole-Gonella et al. (2017) discussed mixed suites of vertebrate and invertebrate trace fossils related to the carbonate and clastic geological record of the Yacoraite Formation, following the approaches applied to marine palaeoshorelines by Kvale et al. (2001) and Pazos et al. (2012).

3. Materials and methods

Studied material consists of five track-bearing slabs found as loose material. Track-bearing slabs are temporarily stored at Museo Miguel Lillo de Ciencias Naturales (Tucumán, Argentina) with

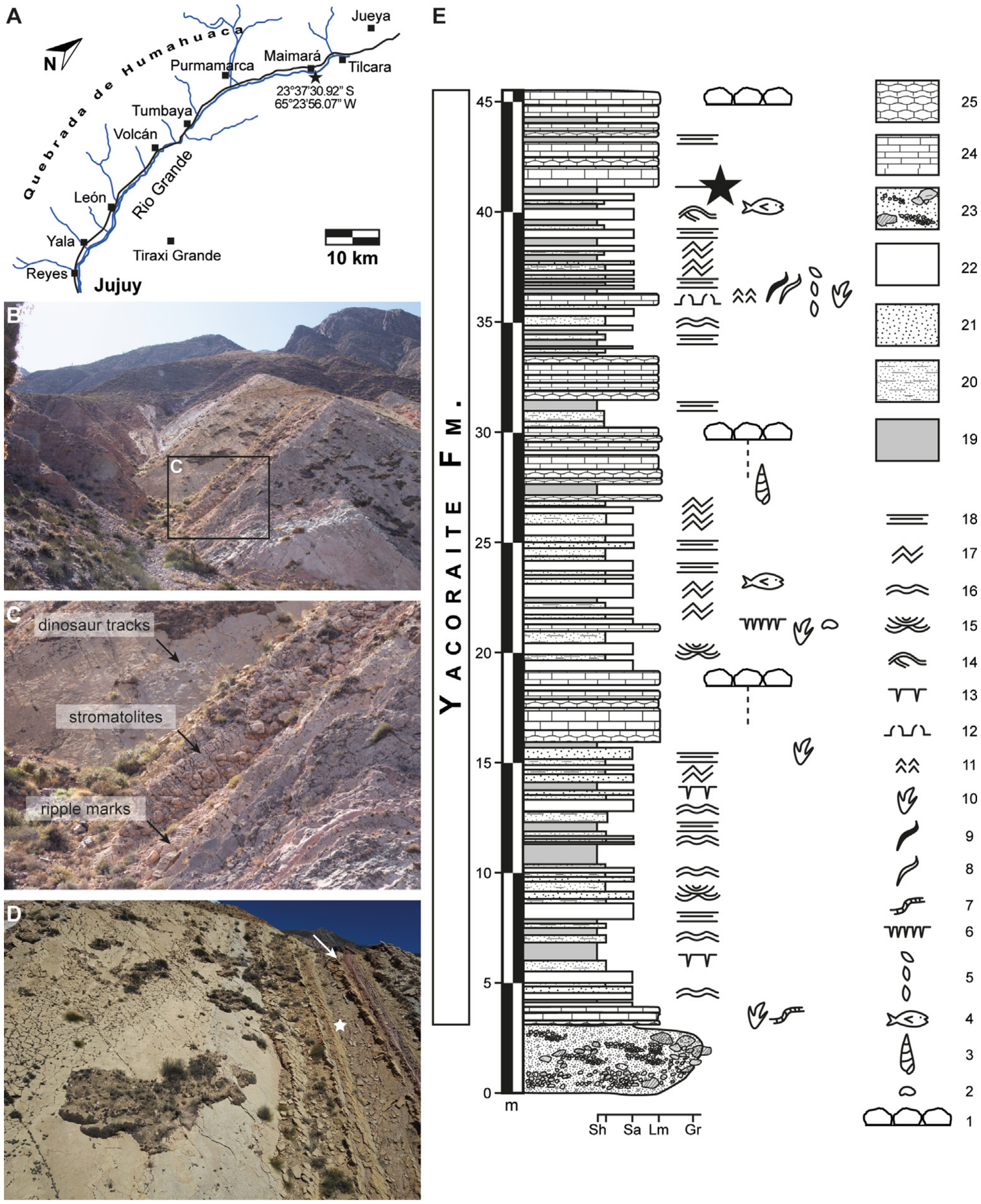

Fig. 1. Geographic location, views of the ichnosite and stratigraphy; A) Location map of the Maimará site in the Quebrada de Humahuaca (Jujuy province, Argentina); black star indicates the ichnosite (redrawn and modified from de Valais and Cónsole-Gonella, 2019); B) Inclined strata of the Yacoraite Formation as they are viewed from the path leading to the outcrop; C) Stromatolite level from the middle-upper portion of the measured stratigraphic section (approximately between 27 and 30 m from the base of the stratigraphic section); D) View of the huge exposed track-bearing surface with dinosaur footprints (the same indicated in C) and the upper portion of the stratigraphic section from which the studied tracks come. White star indicates position of finding loose slabs here described; white solid arrow indicates the most probable stratigraphic level of provenance; E) Stratigraphic column at Maimará site (redrawn and modified from Villafañe et al., 2021a). 1 – Stromatolites; 2 – Ostracods; 3 – Gastropods; 4 – Fish remains; 5 – *Lockeia*/?*Ptychoplasma*; 6 – *Skolithos linearis*; 7 – cf. *Taenidium*; 8 – *Palaeophycus tubularis*; 9 – *Planolites* cf. *montanus*; 10 – Tetrapod footprints; 11 – Gypsum; 12 – Petee structures; 13 – Mudcracks; 14 – Hummocky cross-stratification; 15 – Through cross-bedding; 16 – Wave ripple cross-lamination; 17 – Current ripple cross-lamination; 18 – Horizontal lamination; 19 – Shales; 20 – Siltstones; 21 – Sandstones; 22 – Sandy limestones; 23 – Polymictic conglomerates; 24 – Limestone (mudstones, wackestones and packstones); 25 – Oolitic grainstones.

provisional labels AAM1 to AAM5. The material was tentatively repositioned in the stratigraphic succession and the most probable sedimentary level of provenance is indicated by the white arrow in Fig. 1D, which was the only one sharing the same sedimentary features observed in track-bearing slabs. On this sedimentary level, search for *in situ* convex hyporeliefs was conducted but with no positive result.

Track-bearing slabs are intensely printed. Tracks that will be discussed were numbered with Arabic numerals; letters ‘p’ and ‘m’ indicate pes print and manus print, respectively. Basic terminology and mode of track preservation (e.g. concave epirelief, convex hyporelief, true track, elite track, underprint, undertrack, natural cast, overtrack, internal overtrack) follow Leonardi (1987), Allen (1989, 1997), Lockley (1991), Fornós et al. (2002), and Marty et al. (2009, 2016). Rock classification follows Dunham (1962) and Embry and Klovan (1971).

Close-range, high resolution digital photogrammetry was undertaken to achieve three-dimensional models of the track-bearing surfaces and objective representations of footprint morphologies, following the proposal by Falkingham et al. (2018). The technique enables reconstructing full metric, three-dimensional textured meshes of any object in space from bi-dimensional object projections taken from different points of view. The software package Agisoft Metashape Professional was adopted for semi-automatic processing of images, automatic camera calibrations, and three-dimensional model reconstruction. Photogrammetric survey was conducted to collect raw photographic data maintaining a high overlay redundancy index (i.e. averaged number of pictures in which surveyed surface points are present). Camera images were acquired using a 24 megapixel reflex digital camera with 5.34×5.34 μm pixel size mounted on a tripod and equipped with a 50 mm f/1.4 fixed focal length. A variable number between 44 and 96 images were acquired for modelling the ichnological material at a distance between 43 and 45 cm. In each case, a mean ground sampling resolution of 0.03 mm/pix was obtained. After scaling, a sub millimetric error was achieved for each model. Three-dimensional meshes were converted to contour maps using the open-source software Paraview.

Thin sections were obtained at the Thin Section Laboratory of the Instituto Superior de Correlación Geológica (INSUGEO, CONICET-Universidad Nacional de Tucumán, Tucumán, Argentina) by cutting two convex hyporeliefs perpendicular to the bedding plane, and subsequently observed and photographed by using a petrographic microscope equipped with a digital camera at the Instituto de Investigación en Paleobiología y Geología (IIPG, CONICET-Universidad Nacional de Río Negro, General Roca, Argentina).

4. Results

4.1. Ichnology

Two footprint morphologies were recognized on track-bearing slab AAM1. The first morphology is represented by four footprints interpreted as pes prints (labelled as 1p to 4p in Fig. 2A-B). Footprint 1p is only represented by distal digit traces displaying subparallel pointed tips. Footprints 2p to 4p appear as semi plantigrade, roughly triangular in outline, tridactyl (tracks 1p and 3p) to tetradactyl (track 2p and 4p) and longer than wide. Morphology of footprint 2p is obscured by overprinting that is indicated by other digit traces with rounded tips and pointing in a different direction. Footprints 3p and 4p have a total length of 11.4 cm and 12.2 cm, respectively. Digit traces are characterized by a total divarication of 32° (track 3p) and 19° (track 4p). Digital bases

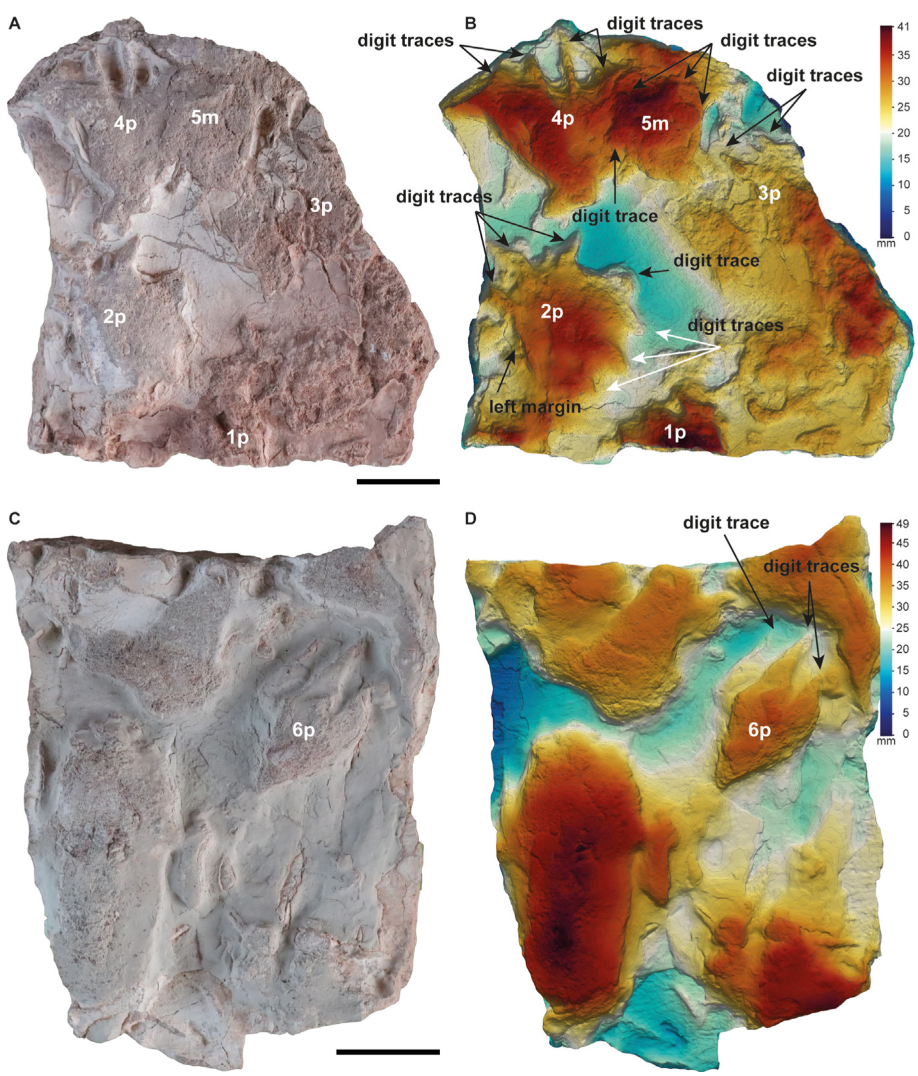

Fig. 2. A, B) Track-bearing slab AAM1 and related digital elevation model; C, D) Track-bearing slab AAM2 and related digital elevation model. Arabic numerals indicate tracks described in the text. Letters 'p' and 'm' refer to pes and manus prints, respectively. Warmer colours in digital elevation models indicate portions of the slabs topographically higher. Slabs are upside down. Scale bars equal 5 cm.

are not clearly recognizable, so digit lengths were not measured. Nevertheless, if distal tip of digit traces is taken into account, central digits are the most forwardly projecting ones and are roughly subparallel to the footprint main axis. In footprints 2p to 4p, digit traces are slightly more shallowly imprinted than the proximal portion (Fig. 2B). The second footprint morphology is indicated by a footprint interpreted as a manus print and labelled 5m (Fig. 2A-B). This footprint appears as digitigrade to semi plantigrade, tetradactyl, and wider than long. It is 5.3 cm wide and 4.4 cm long. The proximal margin of the track is roughly rectilinear. As in the previous case, digital bases are not clearly recognizable and digit lengths were not measured. Central digit traces are the longest and are slightly divaricated (divarication equals to 3°), while lateral digit traces, shorter and sub-equal in total length, are adducted and abducted, determining a total divarication of about 145°. All digit traces display rounded termination. Footprint depth is uniform proximo-distally (Fig. 2B).

Footprint labelled 6p is interpreted as a pes print and is preserved on track-bearing slab AAM2 (Fig. 2C-D). This footprint displays a clearer morphology with respect to that observed in tracks 1p to 4p. It is semi plantigrade, tridactyl, triangular in outline and longer than wide. Length is 12 cm, width is 7.4 cm. Total digit divarication is 18°. Digital bases are not clearly recognizable, so digit lengths were not measured. Based on the previous reasoning, the central digit is the most advanced one and subparallel to the footprint main axis. A depth pattern similar to that observed previously characterizes footprint 6p (Fig. 2D).

Track-bearing slab AAM3 preserves two clear tracks, the footprint labelled as 7m, interpreted as a manus print, and track 8, as undetermined (Fig. 3A-B). Footprint 7m is digitigrade to semi

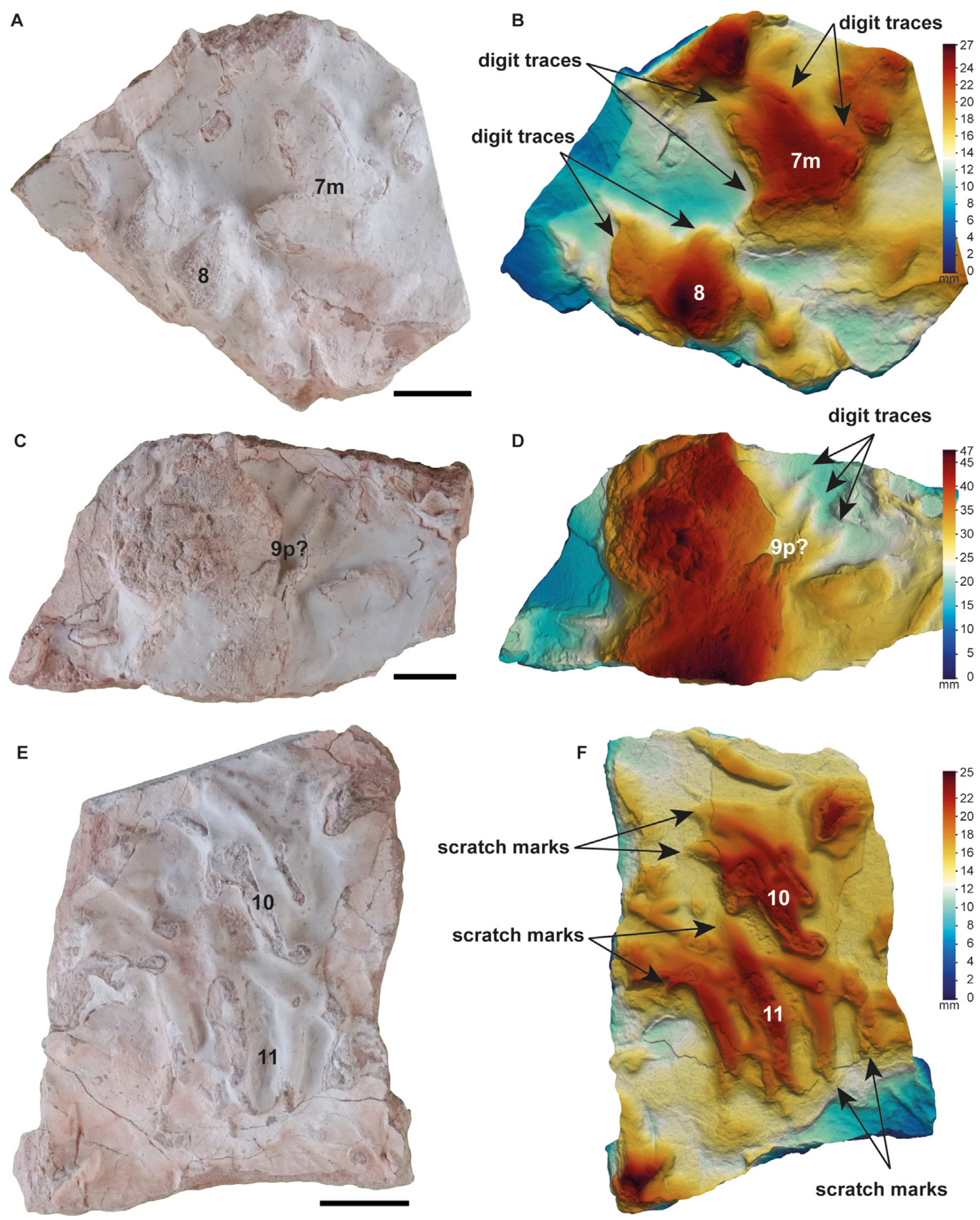

Fig. 3. A, B) Track-bearing slab AAM3, line drawing and related digital elevation model; C, D) Track-bearing slab AAM4 and related digital elevation model; E, F) Track-bearing slab AAM5 and related digital elevation model. Arabic numerals indicate tracks described in the text. Letters 'p' and 'm' refer to pes and manus prints, respectively. Warmer colours in digital elevation models indicate portions of the slabs topographically higher. Slabs are upside down. Scale bars equal 5 cm.

plantigrade, tetradactyl, and wider than long. It measures 8.3 cm in total width and 7.3 cm in total length. Its morphology is similar to that characterizing footprint 5m on track-bearing slab AAM1. Central digit traces are subparallel, while lateral digit traces account for the total divarication of 172°. The proximal margin of the footprint is slightly curved. All digit traces display rounded termination. Footprint depth is uniform (Fig. 2B). Track 8 is identified by at least three partial digit traces, seemingly subparallel, characterized by a roughly ovoidal morphology with pointed tips.

Footprint labelled as 9p? is tentatively interpreted as a pes print and is preserved on track-bearing slab AAM4 (Fig. 3C-D). This footprint is deemed similar to track 1p. It only consists of the impression of the median and distal portion of three digit traces, with subparallel pointed tips. Also in this case, no measures were taken.

Track-bearing slab AAM5 preserves two distinct groups of traces, labelled as 10 and 11 (Fig. 3E-F). Group 11 is represented by four subparallel, slightly curved traces with apparently tapered tips. This group of traces interferes with group number 10, which consists of three traces similar to those constituting group 11 but shorter and more arched.

4.2. Track filling process

As above mentioned, material under study consists of convex hyporelief, i.e. tracks and traces preserved on the slabs represent the filling of concave epireliefs that were printed on a palaeosurface. Convex hyporelief originates on the bottom surface of one or more layers, the deepest one covering the track bottom (sensu Brown, 1999), sedimented subsequently to trampling until complete filling of track. Thus, convex hyporeliefs under study provide information about dynamics of filling process of the original concave epireliefs.

Macroscopic observation suggests the same filling process for the five track-bearing slabs and allows identification of a complex sedimentation that led to complete filling of tracks and traces and their inclusion into the geological record. Products of these sedimentation events are indicated in Fig. 4, which provides observation from the bottom surface of track-bearing slabs. The track-bearing slabs are interpreted as bindstone, following the classification of Embry and Klovan (1971). The filling process is initially expressed by two millimetre thick, micritic/microsparitic laminae. In stratigraphic order, the first lamina (i.e. appearing the uppermost one when overturning the slab and indicated by solid black stars in Fig. 4A-B) consists of a whitish micrite/microsparite with an almost smooth bottom surface, locally characterized by jointed micro-fractures with no or very limited displacement, which give a mosaic appearance to the lamina itself (solid black arrows in Fig. 4A). This lamina is undulated only when covering tracks and traces (dashed black arrows in Fig. 4A). Above it, there is a second, pinkish lamina (indicated by contoured black stars in Fig. 4A-B). From a sedimentological standpoint, this second lamina is identical to the underlying one, also sharing the occurrence of very shallow and subparallel, slightly curved and in cases coalescing, relatively continuous crests separated by flat areas (solid white arrows in Fig. 4A-B). Above the laminae, the filling is represented by the

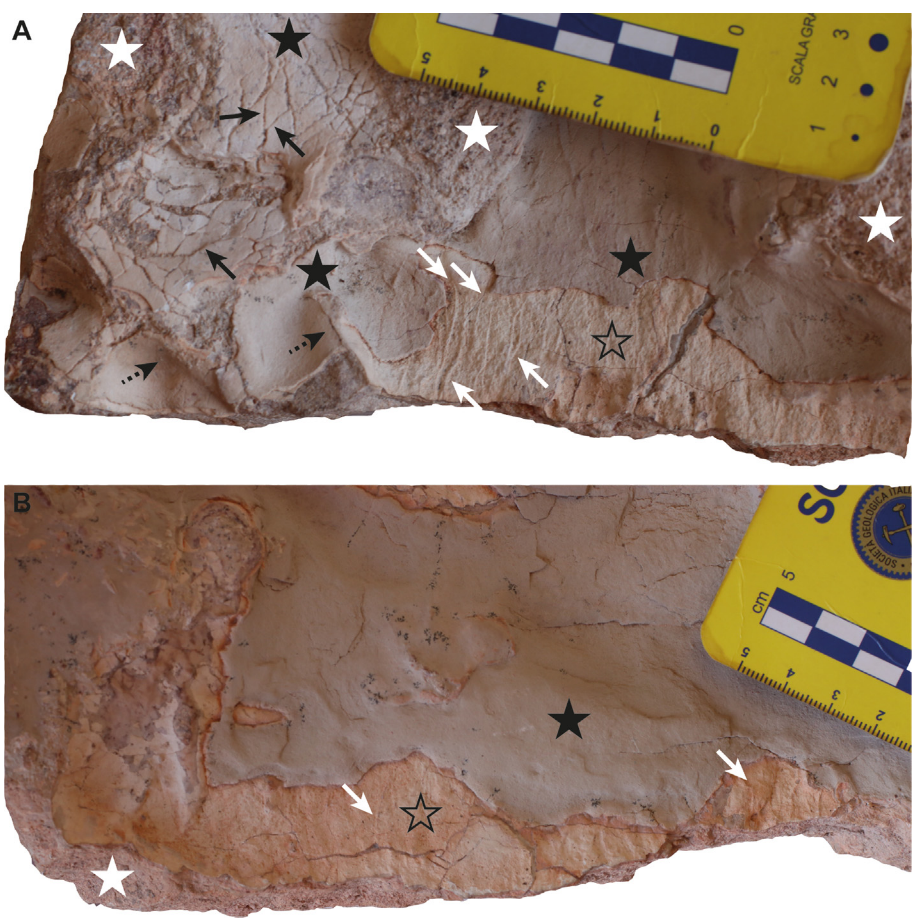

Fig. 4. Bottom view of track-bearing slabs AAM1 (A) and AAM5 (B). In both photographs, the laminae at the top (indicated by black stars) represent the most basal ones draping original concave epireliefs. See main text for symbols. Scale in cm.

sedimentary deposit indicated by solid white stars in Fig. 4A-B. Sediments are coarser than those forming underlying laminae, and mainly composed of ooids, skeletal fragments and a very small percentage of dark coloured lithoclasts immersed in a micritic matrix. This lithotype blanketed the original concave epireliefs, accomplishing complete filling.

Sedimentation process and related products leading to complete filling of concave epireliefs can be observed through slab cross-sections in Fig. 5. The previous described products are observable in stratigraphic order in Fig. 5A, where the same symbols that were used in Fig. 4A-B are repeated. In cross-section, laminae representing the first and second filling event (respectively the solid and contoured black stars in Fig. 5A) appear completely welded. When the upper coarser portion of track-bearing slabs that finalized filling of concave epireliefs is observed in cross-section, further packed laminae made up of finer sediments and characterized by a wavy pattern, analogous to the previous described ones, can be observed (solid white and black arrows in Fig. 5B and C, respectively). These packed laminae display different degrees of lateral continuity, being in some cases truncated. Morphology and development of these continuous and sinuous laminae appear related to the pre-existing “micro-topography” triggered by trampling, which deformed the original surface generating depressed and elevated areas.

Further information is provided by observation of thin sections (Fig. 6). As already mentioned, two track-bearing slabs were cutted perpendicular to the bedding plane in order to obtain thin sections passing through digit traces, with the aim of observing the succession of filling events at a microscopic scale. The boundary between sets of laminae and the overlying coarser portion with ooids and ostracods is undulate where a portion of digit traces is cross-cut (dashed white line in Fig. 6A). In other cases the boundary appears irregular. Micro-fractures affecting finer sediments (dashed white line in Fig. 6B-C) were subsequently filled by coarser sediments. Within coarser sediments (Fig. 6D-E), laterally discontinuous micritic laminae can be observed, locally determining pseudo-columnar morphology (solid white arrows in Fig. 6F). Finally, both finer and coarser lithologies are characterized by non-selective factory porosity of vug type and subordinate fenestral porosity.

5. Discussion

5.1. Interpretation of behaviour, putative producers and ichnotaxonomic remarks

The fragmentary nature of track-bearing slabs hinders assessment of ichnological parameters related to the record of putative manus-pes sets and trackways, as well as the interpretation of whether footprints and traces on the different track-bearing slabs are related or not. As aforementioned, track-bearing slab AAM1 preserves at least four tridactyl to tetradactyl pes prints and a fifth tetradactyl manus print. Pes prints are roughly oriented in the same direction of advancement, as indicated by digit tip traces; the manus print displays a similar orientation to pes print 4p, which lies beside it, but we discard the possibility that the two tracks constitute a manus-pes set on the basis of their relative position. We tentatively relate manus print 5m to pes print 3p and interpret these five tracks as pertaining to the same trackway. On these bases,

Fig. 5. Cross sections of track-bearing slabs AAM2 (A), AAM3 (B) and AAM5 (5). See main text for symbols. Scale bars are 3 cm (A, C) and 1 cm (B).

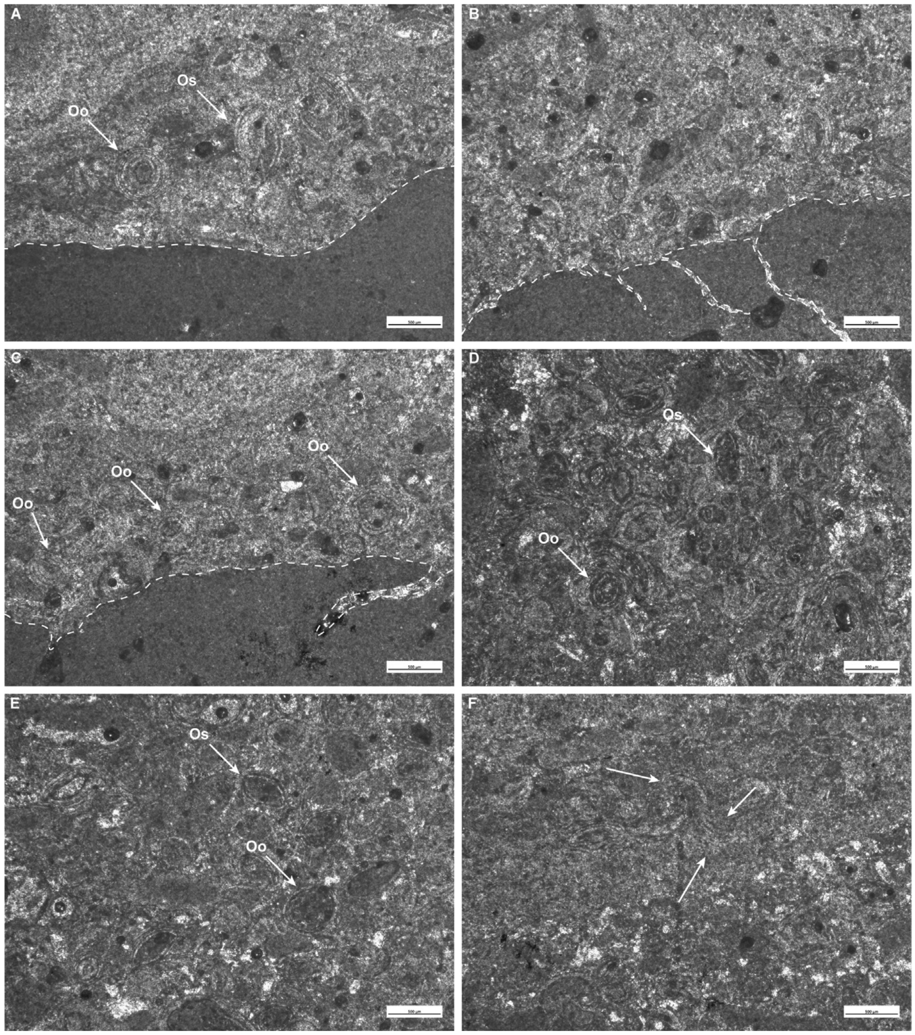

Fig. 6. Thin sections obtained from track-bearing slabs AAM1 and AAM2. A) Undulated boundary between biolaminites and interval with ooids (Oo) and ostracods (Os); B, C) Articulated boundaries between biolaminites and interval with ooids (Oo) and ostracods (Os). Dashed white lines indicate the boundary and highlight micro fractures filled by sediments from coarser interval. D, E) Coarser interval with ooids (Oo) and ostracods (Os), blanketing tetrapod tracks. F) Pseudo-microcolumnar micrite-binding microbialite (boundaries are indicated by solid white arrows) within the upper portion of bindstone with ooids and ostracods.

manus print 5m would be outwardly rotated and pes print 3p inwardly rotated. Footprint 2p, as above mentioned, is affected by overprinting. This is inferred on the basis of three slightly curved digit traces, pointing in a different direction (i.e. roughly towards footprint 1p). Interpreting morphology of this track, as well as of whether it is a manus print or a completely different trace is difficult and we suspend interpretation.

The whole ichnological material on the five track-bearing slabs can be distinguished into two separated groups based on the occurrence of clear digit traces and the amount of autopodial impression (i.e. digitigrade, semi plantigrade and plantigrade footprints). The first group includes footprints on track-bearing slab AAM1 and AAM2 (Figs. 2, 7A-B), footprint 7m on track-bearing slab AAM3 (Fig. 3A-B, 7C). For these footprints, morphology of digit traces can be observed and ichnological grady can be defined. The second group includes track 8 on track-bearing slab AAM3 (Fig. 3A-B, 7C), track 9p? on track-bearing slab AAM4 (Fig. 3C-D, 7D) and traces 10 and 11 on track-bearing slab AAM5 (Fig. 3E-F, 7E). For these tracks, the same features as above cannot be observed.

Before proceeding with the discussion about possible behavioural interpretation, it is important to underline that the overall palaeoenvironmental context exhibited by the Yacoraite Formation at Maimará site (following facies reconstruction provided by Cónsole-Gonella et al., 2017, fig. 13) and the sedimentological data here described suggest that studied material was formed underwater, most likely in an upper subtidal-lower intertidal setting. Obviously, not having been able to directly observe the originally trampled surface, we cannot establish with confidence the conditions under which concave epireliefs 1p to 4p, 5m, 5p, 7m and 9p? were produced.

Track 8 on track-bearing slab AAM3 (Fig. 3A-B) and tracks 10 and 11 on track-bearing slab AAM5 (Fig. 3E-F) suggest that producers, while printing them, were not fully contacting the substrate with their own autopods. This evidence supports the hypothesis that the producers were totally or partially floating in the water column and, in turn, these tracks would fall into the category of swim traces. An internal differentiation within this group can also be proposed, considering track 8 the result of digits sub-vertically or vertically oriented during displacement and group of traces 10 and 11 as the result of autopods scratching the substrate. These tracks (i.e. tracks 8 and traces 10 and 11) strongly resemble material published from different Cretaceous ichnosites of U.S.A. and Europe (e.g. Kukihara et al., 2010; Vila et al., 2015; Lockley et al., 2018, 2021) associated with swimming behaviour.

Fig. 7. Interpretative line drawings of described tracks. A) Track-bearing slab AAM1; B) Track-bearing slab AAM2; C) Track-bearing slab AAM3; D) Track-bearing slab AAM4; E) Track-bearing slab AAM5. Arabic numerals indicate tracks. Letters 'p' and 'm' refer to pes and manus prints, respectively. Scale bars equal 5 cm.

Taking into account the position of a tetrapod within a water column, and type and amount of contact of the autopods on the compliant substrate, two main categories of swim tracks and traces have been distinguished: buoyancy tracks and punting tracks (see Navarro-Lorbés et al., 2023 and references therein). Buoyancy tracks are interpreted to be formed by a producer that, while partially floating in the water column, touches a compliant substrate and displaces itself by pushing with its digits or the tips of digits (e.g. Romilio et al., 2013; Milner and Lockley, 2016). This type of tracks has been plentifully described in literature and related to different types of Mesozoic producers, among which sauropods (e.g. Farlow et al., 2020), ankylosaurs (e.g. Riguetti et al., 2021), theropods (e.g. Whyte and Romano, 2001), small (e.g. Lockley and Foster, 2006) and large (e.g. Fujita et al., 2012) ornithopods, crocodylomorphs (e.g. Castanera et al., 2022), turtles (e.g. Avanzini et al., 2005), pterosaurs (e.g. Lockley and Wright, 2003), and archosauriforms (e.g. Thomson and Lovelace, 2014) are the most mentioned. In our opinion, tracks and traces included in the second group fall within the category of buoyancy tracks.

Footprints included in the first informal group, i.e. pes and manus prints on track-bearing slabs AAM1 and AAM2 (Fig. 2), manus print 7m on track-bearing slab AAM3 (Fig. 3A-B), and track 9p? on track-bearing slab AAM4 (Fig. 3C-D), differ from the above mentioned buoyancy tracks and traces and suggest that the producer contacted the substrate with its own autopods not necessarily while floating, partially or totally, in the water column (e.g. McAllister, 1989). For these footprints, a second category of swim tracks can be invoked. Punting tracks include those impressions formed during bottom walking and imply a greater amount of contact between autopods and substrate while pushing is exerted. Tracks related to bottom walking can be affected by a huge range of variability in terms of morphological features, as well as by failure or success in recording anatomical elements (e.g. digit traces). They have been described and related to different tetrapods, such as turtles (e.g. Gaillard et al., 2003), placodonts (Xing et al., 2020), crocodilians (e.g. Kumagai and Farlow, 2010; Grigg and Kirshner, 2015; Farlow et al., 2018a, 2018b; Lee et al., 2019), theropods (Navarro-Lorbés et al., 2023) and hippopotami (Bennett et al., 2014). In particular, the paper of Bennett et al. (2014) claimed bottom walking tracks characterized by ichnological features that are not only related to digits, suggesting that punting tracks can form more completely than expected (see also Navarro-Lorbés et al., 2023).

With regard to prints on track-bearing slabs AAM1 and AAM3 (footprint 7m), occurrence and overall morphology of manus prints 5m and 7m allow excluding pterosaurs as putative producers, according to Lockley and Schumacher (2014). Tetradactyl pes prints and occurrence of manus prints allows excluding bipedal producers, such as theropods and other bipedal dinosaurs (e.g. Navarro-Lorbés et al., 2023). Overall morphology of both pes and manus prints allow excluding turtles, which commonly produce wider than long track and never with a triangular posterior edge (e.g. Kim and Lockley, 2016). Pes prints 1p to 4p on track-bearing slab AAM1, and manus prints 5m and 7m, respectively on track-bearing slabs AAM1 and AAM4 share different features with tracks that, in the literature, are commonly related to crocodylomorphs, including tetradactily and semiplantigrady of pes prints and overall morphology of manus print. The fossil ichnological record related to crocodylomorph producers, as well as the neoichnological record of crocodylians, displays a wide field of variability in terms of ichnological features, especially related to dactyly, both in terrestrial and underwater locomotion (e.g. Foster and Lockley, 1997; Fuentes Vidarte and Meijide Calvo, 2001; Avanzini et al., 2007, 2010; Lockley et al., 2010; Milán and Hedegaard, 2010; Abbassi et al., 2015; Farlow et al., 2018b; Kim et al., 2020; Lockley et al., 2020; Masrour et al., 2020; Castanera et al., 2021, 2022). Extant walking crocodylians commonly produce trackways with tail trace, pentadactyl manus prints with longer central digit traces (II, III, IV) than lateral ones (I and V), and three clawed inner digit traces; tetradactyl pes prints in which trace of digit III is the longest, traces of digit II and IV are shorter and subequal in total length, and trace of digit I is the shortest, with three clawed inner digit traces (Farlow et al., 2018b). During bottom walking, the common features characterizing crocodylians tracks are only claw traces but deeper tracks can be expected as function of producer overall size, for instance (see Farlow et al., 2018b). In the studied material, there are no clear claw traces, but the inherent process leading to track formation and preservation must be taken into account and can explain this missing feature. Except for footprints 2p and 4p, dactyly observed in the material under study do not fulfil typical features of tracks that can be impressed during terrestrial locomotion and has been related to swimming behaviour by Lockley et al. (2021). A crocodylomorph is considered the most plausible producer also for the ‘scratch traces’ impressed on track-bearing slab AAM5, as suggested by the two associated set of four- and three-grouped slightly curved traces. If we consider the osteological record from the Yacoraite Formation, crocodylomorphs are represented only by the taxon *Dolichochampsa minima* Gasparini and Buffetaut, 1980, originally considered an eusuchian but more recently redescribed as an undetermined longirostrine crocodyliform (Escobar et al., 2018).

From an ichnotaxonomical standpoint, pes and manus prints (assuming in the latter failure in impressing digit III in manus prints) on track-bearing slab AAM1 and footprint 7m on AAM3 can be compared with some not well-detailed material referred to cf. *Crocodylopodus* by Pascual Arribas et al. (2005) and Vila et al. (2015), to *Crocodylopodus* isp. by Lockley et al. (2020), as well as with some footprints discussed by Castanera et al. (2022) and referred to *Crocodylopodus meijidei* Fuentes Vidarte and Meijide Calvo, 2001. Interestingly, putative manus prints 4m (Fig. 2A-B) and 7m (Fig. 3A-B) are morphologically similar to that of *Novapes ulsanensis* Lee et al., 2020, an ichnotaxon tentatively referred to choristoderan producers but similar in all aspect to tracks attributed to crocodylomorphs (Lee et al., 2020, fig. 2). ‘Scratch traces’ on track-bearing slab AAM5 and track 8 on track-bearing slab AAM3 can be compared with *Albertasuchipes* McCrea et al., 2004 (specimen UALVP 134, fig. 5B in McCrea et al., 2004). However, in our opinion the material under study does not retain sufficient ichnological features to allow an ichnotaxonomical positioning, due to its fragmentary nature and the impossibility to observe clear trackways and manus-pes sets, and and we prefer to not assign it to any taxon with confidence.

As final remarks, we highlight that tracks characterized by the configuration related to punting tracks could be formed and preserved also on compliant substrates in subaerial conditions. Nevertheless, lacking sedimentological evidence suggesting subaerial conditions, and noting the association of putative punting tracks with buoyancy tracks, we propose that all the convex hyporelief most likely mirror a trampling that occurred underwater. Possible explanations about the coexistence of the interpreted different behaviours can be considered i) a change in the depth of the water column for the two trampling events (e.g. Romilio et al., 2013; Farlow et al., 2018b) or, assuming the same water depth, ii) different overall dimensions of the producers responsible of the two group of tracks. Preferring one explanation to the other is not possible, but it is nevertheless interesting to underline that the first explanation would require inferring a certain degree of time averaging affecting the original trampled surface.

5.2. Overtrack formation: clues about palaeoenvironmental conditions

Different modes of preservation of fossil tetrapod tracks have been described, as function of i) palaeosurfaces on which footprints are observed and ii) processes leading to their formation and inclusion in the geological record. Nomenclature regarding concave epireliefs encompasses different terms, such as palaeosurface (Marty et al., 2016), tracking surface (Fornós et al., 2002), true tracks (Gatesy, 2003), elite tracks (Lockley and Meyer, 2000), underprints (Avanzini et al., 2010; Falkingham and Gatesy, 2014), deep tracks (Gatesy et al., 1999), penetrative tracks (Gatesy and Falkingham, 2020), undertracks (Thulborn, 1990; Lockley, 1991; ‘transmitted relief’ in Thulborn, 2012). Also the nomenclature referred to convex hyporelief is complex. The lithified sediment filling a true track and generating a natural, convex replica is called natural track cast (Lockley, 1991). Besides potentially informing on producer anatomy and style of locomotion, natural track casts are valuable objects elucidating type and mode of footprint formation and filling. According to Lockley (1991) and following the track burial model of Marty et al. (2009), natural casts are formed by a rapid and important sedimentation event without an overtrack on top of the overall track. Natural casts are widely described in the palaeoichnological record and can be recognized when footprints are cross-cutted in order to observe a polished section (e.g. Sacchi et al., 2014). Differently, intermittent or biologically induced sedimentation (Marty et al., 2009) trigger the formation of a stack of overtracks, the deepest one covering the track bottom (sensu Brown, 1999).

The process described in section 4.2 suggests that convex hyporeliefs from Maimará fall within the category of ‘overtrack model’ described by Marty et al. (2009). Taking into account the sedimentological features associated to overtracks, the inherent process was triggered by the growth of microbial mats under different energetic conditions of the palaeoenvironment and type of mat development (Fig. 8).

Microbial mats originate from benthic microbial community mainly composed of cyanobacteria, photosynthetic bacteria, and eukaryotic microalgae, whose establishment and subsistence requires exposition to sunlight and steady conditions of moisture and contact with water (Krumbein et al., 2003). These conditions are fulfilled in a variety of environments in which water sheets and substrate moisture are persistent, e.g. lagoon, ponds, tidal flats subjected to daily flooding. As long as the microbial community is alive, development of mat is regulated by microbial communities by precipitation of sediments and/or trapping and binding sediment particles onto their mucilaginous EPS (Demicco and Hardie, 1994). Due to the inherent process leading to their development, and to their high potential of quickly lithify by calcium carbonate precipitation (e.g. Dupraz et al., 2004; Dupraz and Visscher, 2005), microbial mats have been considered to have played a pivotal role in forming and preserving fossil tetrapod footprints and traces by covering and stabilization (e.g. Thulborn, 1990; Lockley, 1991; Avanzini, 1998; Conti et al., 2005). However, the role of microbial mats in footprint formation should always be considered in light of other factors involving both the substrate and the producers. For instance, microbial mats can hamper footprint formation of light-weight trackmaker (Nicosia et al., 2007).

In the present case, the process leading to the preservation of the ichnofossils was likely triggered by draping of concave epireliefs by growth of microbial mats through a biologically induced, in-situ mineral precipitation (Reid et al., 2000). Mineral precipitation in absence of coated carbonate granules and other components (i.e. skeletal fragments) would allow to infer low energetic conditions of the palaeoenvironment under chemical high $CaCO_3$ saturation state (Giuffre et al., 2013; Li and Jun, 2019). The related products are the first sets of packed laminae, which constitute internal overtracks (sensu Marty et al., 2009; see also Marty et al., 2016) (Fig. 8A). Rapid cementation of laminae may have favoured the stabilization of trampled surface and hampered the effect of the activity of grazer and burrower metazoans (Gebelein, 1976; Reid and Browne, 1991), promoting preservation of track morphologies. Reduced bioturbation has been considered as requisite for the preservation of tracks in subaqueous settings (Thomson and Droser, 2015). A following change in the energetic gradient of the palaeoenvironment led to an increase of the sedimentary input that

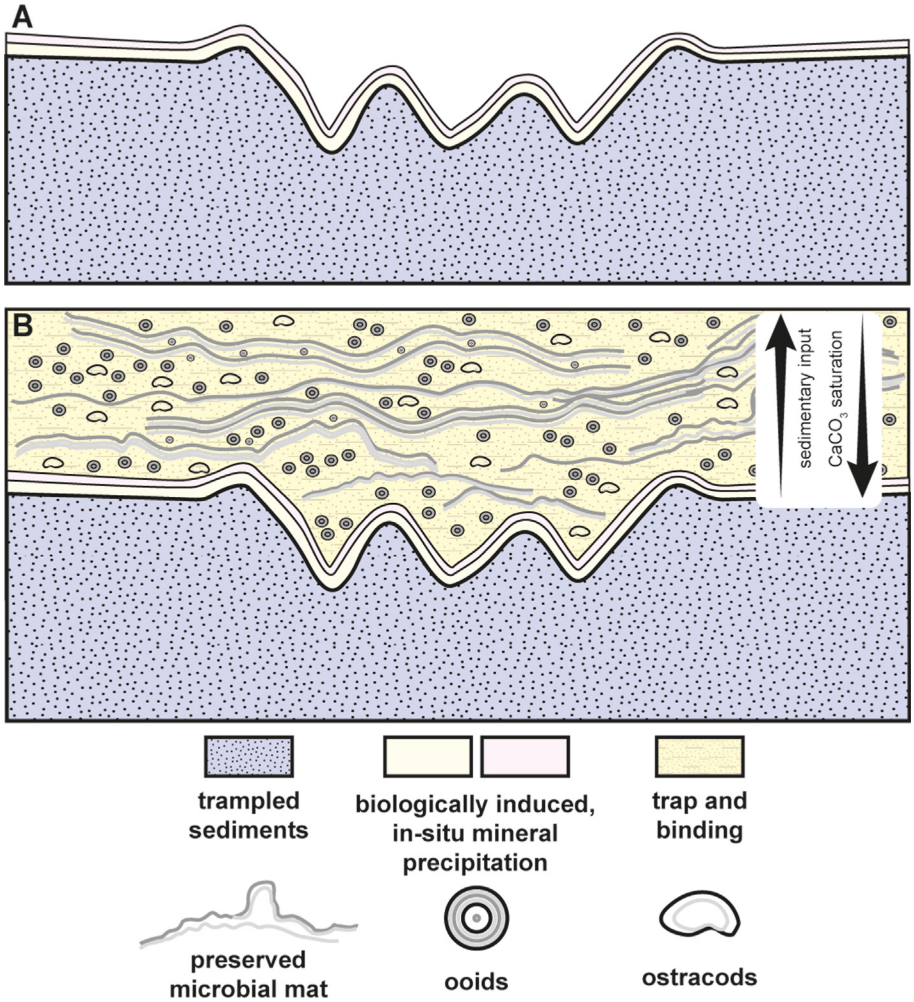

Fig. 8. Schematic drawing illustrating filling process of tracks and traces discussed in this contribution as the result of growth of microbial mats. A) First overtracks formed over the putative tracking surface, expressed by laminae that resulted from chemical precipitation during mat development, in a relatively low-energy environment; B) Microbial mats blanketing tracks and traces during a trapping and binding phase in mat development. Not in scale.

in turn shifted the mat development in a trapping and binding phase (Suárez-González et al., 2014), which completed blanketing of tracks and traces (Fig. 8B). Such development would be evidenced in the upper portion of the bindstone, in which the biolamination includes mainly ooids and other carbonate particles, and subordinate lithic fragments. The morphology of microbial mats resembles, in some cases, the pseudo-microcolumnar and banded fasciculate/fine grained agglutinant categories discussed by Villafañe et al. (2023, and references therein). Agglutinated microbial mats in the coarser portion of the bindstone would allow to infer sediment mobilization and a relatively lower $CaCO_3$ saturation state than previous condition, in order to provide softness of microbial mats (i.e. not calcified mucous EPS) able to trap and bind particles from the environment (Suárez-González et al., 2016). Considering that comparable fossil and present examples are restricted to tidal environments (Suárez-González et al., 2016), the fabric of the agglutinated mats in the coarser portion of the bindstone would confirm the marine, tidal and wave influenced origin of the Yacoraite Formation at Maimará.

As known, fresh traces have high possibilities of being distorted or deleted very quickly after their formation, unless they are stabilized and covered. Our reconstruction of overtracks formation suggests that biologically induced in-situ mineral precipitation played an essential role in molding original morphologies and preventing their distortion. Complete filling of tracks, achieved by the subsequent trapping and binding phase, lasted longer as suggested by data on growth rates of recent microbialites (e.g. Chivas et al., 1990; Webb and Jell, 2006; Brady et al., 2009; Power et al., 2011; Seard et al., 2011; Mackey et al., 2015; Villafañe et al., 2021b), and it was probably of lesser importance in preserving tetrapod tracks from post-formation modifications.

6. Conclusions

The ichnological record from the Yacoraite Formation is enriched by two additional track types, coming from a Maastrichtian level of the unit and found on loose slabs at Maimará site (Quebrada de Humahuaca, Jujuy province, Argentina). Studied tracks are tentatively related to crocodylomorphs and interpreted to derive from swim behaviour of the producers, implying both floating in the water column and bottom walking. Tracks attributable to crocodylomorph producers were never reported from the Yacoraite Formation up to date. Tracks here discussed are preserved as convex hyporelief, most likely originated in an upper subtidal-lower intertidal palaeoenvironment. Formation of convex hyporeliefs was controlled by growth of microbial mats under changing energetic conditions of the palaeoenvironment, and resulted in the stacking of internal overtracks. Differences in mat fabric allowed to distinguish two main phases of growth. Draping of original tracks was initially fulfilled by in-situ, biologically induced carbonate precipitation under low energy conditions of the palaeoenvironment and high $CaCO_3$ saturation state. Filling of tracks was finally accomplished under an increased sedimentary input and lower $CaCO_3$ saturation state that led microbial mats into a trapping and binding phase of development. The complete filling of tracks through this phase probably lasted longer after the establishment of different palaeoenvironmental conditions. Agglutinated mats would suggest a marine origin for the Yacoraite Formation, supporting previous interpretations.

"Microbially-induced" overtracks turn out to have a high potential in informing and constraining hydrodynamic and chemical conditions of ancient marine and transitional environments, besides interpretation about the behaviour of extinct producers. Our study further supports that early lithification by biologically induced, in-situ mineral precipitation promotes rapid formation of overtracks. Fast sealing provided by mat lithification inhibits modifications and distortions of three-dimensional morphology after track formation, appearing more efficient in preserving footprints than longer-term filling by allochthonous sedimentation. Finally, it adds significant information to pre-existing models, giving clues for interpreting similar cases in the palaeoichnological record.

CRediT authorship contribution statement

Alfredo Alejandro Martín: Writing – review & editing, Formal analysis, Data curation. **Silvina de Valais:** Writing – review & editing, Funding acquisition. **Ignacio Díaz-Martínez:** Writing – review & editing. **Patricio Guillermo Villafañe:** Writing – review & editing. **Gabriel Ricardo López Isla:** Writing – review & editing. **Paolo Citton:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We dedicate this contribution to our dear friend Carlos Cónsole-Gonella, who recognized the track-bearing slabs discussed in this paper during the field-trip to Maimará in 2018 with Silvina de Valais, Ignacio "Ina" Díaz-Martínez, Patricio "Pato" Villafañe and Paolo Citton. This work was supported by Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2018-01087 to Paolo Citton and PICT-2017-2057 to Silvina de Valais) and Paleontological Society International Research Program (Sepkoski Grants, 2017 call to Paolo Citton). Ignacio Díaz-Martínez is supported by a Ramón y Cajal fellowship (RYC-2022) and by the Ministry of Science. Patricio Guillermo Villafañe is supported by a CIAPOS fellowship (GVA-CIAPOS2022) of the Conselleria de Educación, Universidades y Empleo, Generalitat Valenciana. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The Editor in Chief, the Associate Editor, an anonymous reviewer and James Farlow are kindly acknowledged for their comments that contributed to improve the manuscript.

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