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Palaeoecology of Middle Triassic tetrapod ichnoassociations (middle Muschelkalk, NE Iberian Peninsula) and their implications for palaeobiogeography in the western Tethys region

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Abstract

Tetrapod ichnology is a powerful tool to reconstruct the faunal composition of Middle Triassic ecosystems. However, reconstructions based on a single palaeoenvironment provide an incomplete and impoverished picture of the actual palaeodiversity. In this paper, we analyse Middle Triassic tetrapod ichnoassociations from the detrital Muschelkalk facies of the Catalan Basin of northeast Spain, ranging from terrestrial to coastal settings. We identified two main tetrapod ichnoassociations, preserved in two different palaeoenvironments, comprising the following ichnogenera and morphotypes: *Procolophonichnium*, *Chelonipus*, *Rhynchosauroides*, *Rotodactylus*, *Chirotherium*, *Isochirotherium*, *Sphingopus*, and indeterminate chirotheriids. We also statistically analyse a database of all known Middle Triassic tetrapod footprint localities worldwide;

this database includes, for each track locality, the precise age, the palaeoenvironment and the presence/absence of ichnotaxa. Our results on the composition of ichnofauna within the palaeoenvironments of the Catalan Basin are integrated into this database. This approach allows us to revisit the palaeoenvironmental bias linked to the marine transgression that affected the Western Tethys region. Tetrapod ichnoassociations reveal the following palaeoenvironmental patterns: (1) in coastal settings, ichnoassociations are *Rhynchosauroides*-dominated and diversity is relatively low; (2) in terrestrial settings and those with less marine influences, ichnoassociations are non-*Rhynchosauroides*-dominated, usually characterised by more abundant chirotheriid tracks and, generally, a higher track diversity. The correlation between tetrapod ichnoassociations and sedimentary facies reveals how palaeoenvironmental constraints influenced faunal assemblages, especially those of the Middle Triassic of the Western Tethys region. Ichnoassociations allow the ecological response of tetrapod faunas to the environmental changes to be inferred for this critical time interval. Marine transgressions strongly influenced tetrapod ecosystems: environmental conditions were key for the faunal recovery in the aftermath of the end-Permian extinction, with the settlement of the so-called modern faunas and the rise of the dinosaur lineage.

Keywords

tetrapod footprints; palaeoenvironments; coastal settings; Anisian; Ladinian; equatorial Pangaea

1. Introduction

The Triassic period is characterised by recovery in the aftermath of the most severe biotic crisis of Earth history, the end-Permian mass extinction, which led to the origin of so-called modern ecosystems (Benton, 2016). However, the complete faunal recovery was delayed until the Middle Triassic due to the harsh environmental conditions (Irmis and Whiteside, 2012), especially in equatorial Pangaea (Sun et al., 2012; Benton and Newell, 2014; Benton, 2018). While in the marine realm the severity of the biotic crisis and subsequent recovery are relatively well understood, the magnitude of the event is still uncertain for the continental ecosystems, especially considering vertebrates (Lucas, 2017, 2018). The Middle Triassic continental vertebrate faunas globally present a relatively high diversity, with the radiation of newly successful diapsid groups (Ezcurra, 2010), the lineages of which most probably appeared during the late Palaeozoic (Simões et al., 2018; Bernardi et al., 2019). On the one hand, the Lower–Middle Triassic tetrapod record from middle-high palaeolatitudes is particularly well-known, based on the great sampling efforts performed in South Africa and Russia, which reveal that these ecosystems were characterised by abundant temnospondyl amphibians, as well as therapsids, being neodiapsid reptiles present, but less abundant (Lucas, 2010; Romano et al., 2020, and references therein). On the other hand, Middle Triassic continental vertebrate faunas from equatorial Pangaea include temnospondyl amphibians (e.g., capitosaurids and plagiosaurids) and a high diversity of reptiles ranging from terrestrial to semi-aquatic and aquatic habitats (Sues and Fraser, 2010). Dominant diapsid reptiles (particularly archosauromorphs) coexisted with procolophonid parareptiles, stem-turtles, lepidosauromorphs and a few cynodonts (Schoch and Milner, 2000; Damiani et al., 2009; Ezcurra, 2010; Schoch and Sues, 2015, 2018; Schoch et al., 2018; Simões et al., 2018). Environmental changes through time, including a greater marine influence, are reflected by coastal and marine vertebrate faunas, such as tanystropheids (e.g., *Macrocnemus* and *Tanystropheus*), stem turtles, ichthyosauriforms, thalattosaurians, sauropterygians (e.g., pachypleurosaurs, nothosaurians and placodonts), saurosphargids, as well as fish faunas (actinopterygians and sarcopterygians) (Rieppel and Hagdorn, 1998; Rieppel, 2000; Ezcurra, 2010; Xing et al., 2020). Terrestrial ecosystems and the role of their faunas are far from being fully understood because of the small number of sites, although some exceptional *Fossil-Lagerstätten* localities exist (Schoch and Seegis, 2016). In fact, the number of terrestrial taxa from Middle Triassic low-latitude localities is generally sparse (Lucas, 2010; Fortuny et al., 2011a).

The skeletal information of Middle Triassic terrestrial faunas is complemented by a notably richer tetrapod ichnological record. Continental Middle Triassic vertebrate footprints are globally recorded (Fig. 1) in many palaeoenvironments ranging from inland fluvial and lacustrine settings to coastal (shores, lagoons, tidal flats) and shallow marine settings (Table S1). Therefore, ichnofaunal diversity may broadly reflect the habitat preferences of vertebrates, as well as environmental changes through space and time, as it is observed in other time intervals (Mujal et al., 2016a, 2017a, 2017b; Bernardi et al., 2018; Marchetti et al., 2019a). In fact, tetrapod footprints are useful tools in palaeoenvironmental analyses (Melchor and Sarjeant, 2004; Hunt and Lucas, 2007a, 2007b; Diedrich, 2008; Melchor, 2015; Marchetti et al., 2017, 2019b; Mujal et al., 2018a; Schneider et al., 2020). Noteworthy, biases in the ichnofaunal record also exist, as is the case for the Triassic amphibian temnospondyl record, with abundant bones and scarce footprints (Klein and Lucas, 2010a; Marsicano et al., 2014; Mujal and Schoch, 2020; Farman and Bell, 2020; Schneider et al., 2020).

Important changes took place during the Middle Triassic in the western peri-Tethys region: most of the earliest Triassic terrestrial ecosystems of the central-eastern part of Pangaea (nowadays Europe and northern Africa) evolved to coastal-marine environments (Bourquin et al., 2011). This was due to the marine transgression that affected most of the European and North-African basins (Escudero-Mozo et al., 2015; Franz et al., 2015) (Fig. 1). This transgression was not coeval in all these basins as revealed by the diachronic nature of the facies (López-Gómez et al., 2002; Franz et al., 2013, 2015; Ortí et al., 2017, 2018; Maron et al., 2019), resulting in diachronous faunal changes. The record of Middle Triassic vertebrate footprints from the Western peri-Tethys basins is significantly abundant (Fig. 1; Table S1), with localities known from Spain (Demathieu et al., 1978; Pérez-López, 1993; Gand et al., 2010; Fortuny et al., 2011a; Díaz-Martínez et al., 2015; Mujal et al., 2015, 2018a; Reolid and Reolid, 2017; Berrocal-Casero et al., 2018a, 2018b; Reolid et al., 2020), Morocco (Klein et al., 2011), Algeria (Kotański et al., 2004), Tunisia (Niedźwiedzki et al., 2017), France (Demathieu and Demathieu, 2004; Gand et al., 2007, and references therein), Italy (Avanzini and Mietto, 2008; Avanzini et al., 2011; Citton et al. 2020; Mietto et al., 2020, and references therein), Switzerland (Klein et al., 2016; Cavin and Piuz, 2020, and references therein), the Netherlands (Demathieu and Oosterink, 1983, 1988; Diedrich, 2002, 2008; Marchetti et al., 2019c) and Germany (e.g., Haubold, 1971a, 1971b, 1984; Haubold and Klein, 2002; Diedrich, 2008, 2012; Klein et al., 2015; Klein and Lucas, 2018; Marchetti et al., 2020; Mujal and Schoch, 2020).

In order to understand the relationship of Middle Triassic vertebrate faunas, in particular those from the Western Tethys, with the palaeoenvironment, we provide a detailed analysis of the ichnological record from the middle Muschelkalk unit of the Catalan Basin (NE Iberian Peninsula). Such unit corresponds to a coastal and distal alluvial succession embedded within the two (lower and upper) Muschelkalk marine carbonate units (Calvet and Marzo, 1994; see section 2 below). So far, Muschelkalk terrestrial ichnoassemblages from the Iberian Peninsula are scanty (Fortuny et al., 2011a), only known from two middle Muschelkalk sites from the Catalan Basin (Mujal et al., 2015, 2018a), and two additional Muschelkalk sites from the Iberian Ranges (Demathieu et al., 1987; Berrocal-Casero et al., 2018a, 2018b). This work significantly enlarges the knowledge of the Middle Triassic vertebrate ichnofaunas from the Iberian Peninsula by describing three new ichnosites.

As a whole, we pursue to understand tetrapod palaeoecology on the basis of the ichnological record, i.e., how palaeoenvironments constrain the distribution of ichnotaxa, either prompting an abundant presence or the complete absence of specific ichnotaxa (e.g., Diedrich, 2008; Melchor, 2015; Mujal et al., 2018a). Additionally, because sea level fluctuations caused strong changes on these ecosystems, the present work sheds light on the vertebrate footprint palaeoecology according to: (1) the newly discovered tetrapod ichnoassemblages, in relation to their stratigraphic and sedimentological setting, from the Catalan Basin (Texts S1 and S2); (2) the Western Tethys tetrapod ichnological record. The integrated review of Middle Triassic tetrapod tracks and corresponding palaeoenvironments sheds light on the evolution of a key time interval for the tetrapod evolution in an area, the equatorial Pangaea, in which the skeletal record is scanty.

2. Geological setting

During the Middle Triassic, the Iberian plate was situated in the western peri-Tethys, eastern part of Pangaea, equatorial latitudes (Fig. 1). The Catalan Coastal Ranges (CCR, NE Iberian Peninsula; Fig. 2) were a depressed, tectonically controlled zone (a rift system) known as the Catalan Basin, corresponding to the north-eastern region of the Iberian plate (Marzo, 1980). The CCR evolved as a NE-SW oriented rift with conjugate NW-SE fault systems (Galán-Abellán et al., 2013). During this time interval, all western peri-Tethys basins were intersected by marine transgressions (occurring at different times as indicated by the diachronic facies at European scale) that resulted in the formation of shallow epicontinental sea areas (Escudero-Mozo et al., 2015; Ortí et al., 2017).

As regards the Iberian plate, the Early to early Middle Triassic terrestrial ecosystems are represented by the siliciclastic Buntsandstein red-beds facies mostly corresponding to alluvial and fluvial deposits (e.g., Dinarès-Turell et al., 2005; Bourquin et al., 2011; Fortuny et al., 2011b; Galán-Abellán et al., 2013; Mujal et al., 2016b, 2017a, 2017b). These facies were gradually replaced by shallow marine environments from East to West, represented by the carbonate and evaporitic Muschelkalk facies (Escudero-Mozo et al., 2015). During the Anisian–Ladinian transition, a short regression episode took place in eastern Iberian plate, leading the marine areas of the Catalan Basin to evolve to coastal environments, such as tidal mud flats, sabkhas and distal floodplains (Calvet and Marzo, 1994; Ortí et al., 2017, 2018). Later, a new transgression took place, affecting most parts of Iberia during the Ladinian (Escudero-Mozo et al., 2015) (Fig. 1). In the sedimentary record, the palaeoenvironments of the regression interval are represented by detrital deposits composed of mudstone and sandstone red-beds with gypsum and limestone/dolostone intervals between the two carbonate units of the Muschelkalk facies (Calvet and Marzo, 1994; Morad et al., 1995; Mujal et al., 2015, 2018a; Ortí et al., 2018). Thus, in the Catalan Basin, three Muschelkalk (informal) units are well-differentiated: lower, middle and upper Muschelkalk facies.

The thickness of the Triassic (Buntsandstein, Muschelkalk and Keuper) successions of the Catalan Basin ranges from 500 to 800 m (Calvet et al., 1990). The Middle Triassic Muschelkalk successions are arranged in three different domains, from SW to NE: Priorat-Baix Ebre, Prades and Gaià-Monsteny (Marzo, 1980). The newly herein reported tetrapod footprint localities, as well as those studied by Mujal et al. (2015, 2018a) are all found in the Gaià-Montseny domain. The middle Muschelkalk facies successions, which in several areas are highly affected by alpine tectonics deformations, present an average thickness of about 100 m (Calvet and Marzo, 1994) (Fig. 2). These facies are dated as late Anisian–middle Ladinian based on palynomorph and conodont biostratigraphy (Solé de Porta et al., 1987; Márquez-Aliaga et al., 2000). The middle Muschelkalk facies consist of a mixed succession of siliciclastic, carbonate and evaporitic lithologies. According to Ortí et al. (2018), the succession can be divided in three main basin-scale units: Lower (Paüls Gypsum), Middle (Arbolí Gypsum/Guanta Sandstone) and Upper (Camposines Gypsum). For the detailed descriptions of each unit, especially regarding the evaporitic content, see Morad et al. (1995) and Ortí et al. (2018). The stratigraphic and sedimentological framework for the published (Mujal et al., 2015, 2018a) and new track-bearing successions are described and discussed in sections 4.1 and 5.1 below and Texts S1 and S3. All the tetrapod footprint localities correspond to the Middle Unit of the middle Muschelkalk, specifically to the Arbolí Gypsum and/or the Guanta Sandstone, within the Gaià-Montseny domain. In this domain, according to Ortí et al. (2018):

1) The Arbolí Gypsum, mainly corresponding to the lowermost part of the Middle Unit, is a succession of massive, laminated and/or nodular gypsum alternated with

red mudstones and discrete greyish dolostone intervals. It is interpreted as "an extensive, evaporitic, red mudflat lodging a mosaic of shallow salinas and sabkhas fed by marine water. This evaporitic mudflat was sensitive to record depositional cyclicity of high-frequency" (Ortí et al., 2018:167).

2) The Guanta Sandstone, encompassing most of the Middle Unit, consists of a mainly cyclic red-bed siliciclastic succession of fine- to medium-grained sandstones alternated with mudstones. The sedimentary setting is interpreted as "midfan distributive channels and floodplains of ephemeral streams in sandy alluvial fans" (Ortí et al., 2018:172). As described and discussed (see sections 4.1 and 5.1 below and Texts S1 and S3), these deposits were also influenced by salty waters.

3. Material and methods

A total of five middle Muschelkalk tetrapod footprint localities from the Catalan Coastal Ranges (NE Iberian Peninsula) are here analysed, together with reference sections by Ortí et al. (2018) (Fig. 2). The track-bearing localities are named, from south to north and west to east (according to their position within the Catalan Basin), as follows: Penya Rubí – new locality (Vallirana, Baix Llobregat), Puigventós – new locality (Vacarisses, Vallès Occidental), Collcardús (Vacarisses, Vallès Occidental; from Mujal et al., 2015), Pedrera de Can Sallent (Castellar del Vallès, Vallès Occidental; from Mujal et al., 2018a), Montmany – historical finding and new locality (Figaró-Montmany, Vallès Oriental).

While carrying out the palaeontological prospections, stratigraphic sections have been measured by means of a Jacobs staff and a measuring tape (when possible, as some outcrops are highly tectonised, see below). Some X-ray diffractions were carried out to check dolomite content in dolostones from Penya Rubí. The stratigraphic position and the GPS coordinates of the footprint-bearing localities have also been recorded. The exact geographic and stratigraphic origin of the historical finding from the Montmany is unknown. However, this area has been recently prospected, and several layers bearing tetrapod footprints, as well as *ex situ* track-bearing slabs, have been discovered. The historic specimen of Montmany, a previously unpublished sandstone slab bearing several tetrapod ichnites in convex hyporelief, was located in the fossil collections of the University of Montpellier (France) in 2014 by one of the authors (EM). It has a label from the Museu Geològic del Seminari of Barcelona (MGSB) with catalogue number

26310; the label indicates that it was donated in 1975 to the Montpellier institution. In this regard, under the corresponding permits, it was returned to the MGSB in 2018.

The new trace fossils recovered from Penya Rubí, Puigventós and Montmany were consolidated for proper conservation with ethyl silicate when necessary, and are stored at the Institut Català de Paleontologia Miquel Crusafont (ICP, Sabadell, Catalonia, Spain). Descriptions and measurements follow the conventions of Haubold (1971a, 1971b) and Leonardi (1987). The specimens used for the ichnotaxonomic assignments are those with a higher degree of morphological preservation (see Marchetti et al., 2019b). Skin impressions preserved in some of the herein analysed footprints are also described in detail and compared to those reported in the literature. Selected ichnites were digitised to obtain 3D models using photogrammetry technique. Photographs were obtained using a digital reflex camera Nikon D3200, with an objective AF-S Nikkor 15-55 mm 1:3.5-5.6 GII and following the procedures of Falkingham (2012) and Mallison and Wings (2014). 3D models were processed with different softwares, following the procedures of Mujal et al. (2016a, 2020): Agisoft Photoscan (standard v.1.1.4) to generate the dense point cloud and the mesh, MeshLab (v.2016.12 and v.2020.07) to edit the mesh (cleaning, scale and orientation) and ParaView (v.4.1.0) to generate colour depth maps and contours.

A database of the worldwide known Middle Triassic tetrapod tracksites has also been built (Table S1), including for each region/locality: age, inferred palaeoenvironment and ichnotaxa present. Descriptive statistics have been performed based on relative abundance (Tables S2, S3), counting presence (1) and absence (0) of each ichnotaxon in the different palaeoenvironments. We calculated the percentages of occurrence of each ichnotaxon, without considering the absolute number of footprints from the analysed regions/localities. In this sense, the representativity of each ichnotaxon in a certain setting is calculated by dividing its occurrences within that palaeoenvironment by all the occurrences reported from this type of palaeoenvironment (Table S2). Also, the percentage of occurrence of a specific ichnotaxon in a determinate palaeoenvironment is calculated as its occurrences in a certain palaeoenvironment by the number of localities assigned to this palaeoenvironment (Table S3).

Tetrapod ichnogenera are taken as the basic counting unit, because they are the best defined ichnotaxonomic level, though some exceptions are also considered. Less precisely identified trace fossils are also counted, because some tetrapod trace morphotypes may bear relevant information regarding the distribution of the potential tracemakers. They include: Dinosauromorpha tracks and tridactyl tracks (the latter may correspond to poorly preserved chirotheriids or dinosauromorphs as well); and indeterminate chirotheriid tracks, because in some localities these are not identified at ichnogeneric level, but such ichnorecord indicates the presence of relatively large archosaurs. Similarly, tetrapod swimming traces, even if they encompass different producers (and include different ichnogenera; e.g., Xing et al., 2020), are also counted as their presence is indicative of a peculiar locomotion gait, and thus provide information on the palaeoenvironmental setting, and on the taphonomy of track bearing localities.

Palaeoenvironmental settings of each locality/region are classified into four major groups, from proximal to distal: 1) alluvial/inland (including fluvial and lacustrine deposits), 2) distal alluvial/supratidal (including playa lake and coarse-grained sabkha deposits), 3) coastal/tidal flats (including fine-grained sabkha or sabkha-like deposits), and 4) shallow marine. The criteria to classify these settings follow the palaeoenvironmental analyses of each work (see references in Table S1), including specific palaeoenvironmental definitions and, especially in the absence of precise information, the sedimentary characteristics of the facies preserving tetrapod traces. In addition, in the case of palaeoenvironments defined as continental-marine transition without further specification, we consider those composed of fine- to very fine-grained and carbonate facies in the coastal group, whereas those composed of coarser facies are put in the distal alluvial group. Regarding sabkha or sabkha-like settings, we follow a similar rule: those with finer facies are in the coastal group, and those with coarser facies are in the distal alluvial group. This responds to the fact that the coarser deposits are considered as more proximal than the finer deposits. Notwithstanding, we might expect further palaeoenvironmental interpretations of the track-bearing localities in future works in order to refine these analyses.

3.1. Institutional abbreviations

IPS, Institut Català de Paleontologia Miquel Crusafont (formerly, Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain.

MGSB, Museu Geològic del Seminari de Barcelona, Barcelona, Catalonia, Spain.

4. Results

4.1. Stratigraphy and sedimentology

The newly discovered tetrapod footprint localities of Penya Rubí, Puigventós and Montmany, all from the middle Muschelkalk facies, are briefly described here. For extended description and interpretation of each outcrop, see Text S1. Furthermore, our results on the stratigraphy and sedimentology of those facies are compared with those from Ortí et al. (2018) and references therein, along with those derived from the tracksites described in Mujal et al. (2015, 2018a). Figure 2 summarizes the stratigraphic position of the tracksites within the middle Muschelkalk succession.

The Penya Rubí outcrop (Fig. 3) includes a stratigraphic succession up to ~27 m thick and encompasses the Lower Unit (Paüls Gypsum) and part of the Middle Unit (Arbolí Gypsum and Guanta Sandstone). The succession presents a terrestrialization trend (Fig. 3A). The lowermost part consists of whitish gypsum deposits overlying the lower Muschelkalk carbonates. They correspond to the Paüls Gypsum. The overlying deposits consist of alternating and finely laminated reddish mudstones and very fine- to fine-grained sandstones. In between this reddish succession there is a distinct interval (~50 cm thick) of finely laminated greyish mudstones and dolostones (Fig. 3A, B), which laterally become coarsier and display cross lamination (Fig. 3C). The red layers commonly display cross lamination (including unidirectional, wave and climbing ripples) (Fig. 3D). Some intervals preserve abundant load and water escape structures (Fig. 3E). All in all, these red deposits mostly show bidirectional water currents and periods of rapid sedimentation. The surfaces of the greyish interval occasionally display wrinkle structures (elephant skin-like textures; Fig. 3F), may indicating periods of low energy environmental conditions. This part of the succession was mostly deposited under subaqueous conditions and/or the substrate was mostly water saturated (high moisture), though sporadic dryer episodes or seasons might also took place. We interpret these deposits as most probably representing intertidal and sabkha-like areas, where finely laminated microbial mats (Fig. 3B, G) were developed (greyish deposits and dolostones), and correspond to the Arbolí Gypsum. Most of the tetrapod footprints from Penya Rubí (i.e., those of relatively small size) are preserved on the surfaces of the grey carbonate (dolostone) microbial mat deposits (lower arrow in Fig. 3A, and Fig. 3G, H); yet the first reddish sandstones and mudstones also preserve sparse small-sized tetrapod footprints, as well as a xiphosuran traceway (De Jaime-Soguero et al., 2020). Notably, the large archosaur footprints are preserved at the basal surface of the mud-cracked, medium-grained sandstone (upper arrow in Fig. 3A), representing the onset of the Guanta Sandstone (see Text S1 and S3). Our interpretations match those by Calvet and Marzo (1994), Mujal et al. (2018a) and Ortí et al. (2018), suggesting that during the marine regression the Catalan Basin was a vast tidal flat, with a low relief that included a mosaic of environments ranging from subtidal to supratidal areas (Ortí et al., 2017) (see Text S1 for further details). The topmost part of the succession is built up of tabular reddish medium-grained sandstones with cross stratification and red laminated mudstones and fine-grained sandstones (Fig. 3A). This succession denotes a marked palaeoenvironmental change towards a more terrestrial setting that represents the onset of the Guanta Sandstone. Noteworthy, the succession of Pedrera de Can Sallent (see Mujal et al., 2018a) can be generally compared to that of Penya Rubí, especially in terms of granulometry, sedimentary structures, and strata arrangement: strata are finely laminated, wave (bidirectional) ripples are common, and wrinkle structures most probably induced by microbial activity are also present. Otherwise, the Pedrera de Can Sallent succession differs with that of Penya Rubí in the main lithological composition: the former is more siliciclastic than the latter. This difference may be explained by the palaeogeographic position of the localities within the Catalan Basin (see Ortí et al., 2018; Texts S1 and S3).

The tectonization of the Puigventós outcrop (Fig. 4A) prevents the measuring of a complete stratigraphic succession with confidence (though a composite section is fairly possible; Fig. 2). The main lithological and sedimentological features reveal closer similarities to the medium-grained sandstone at the top of the succession of Penya Rubí (Guanta Sandstone; upper half in Fig. 3A) rather than to the underlying fine-grained intervals (Arbolí Gypsum; lower half in Fig. 3A). The Puigventós succession mostly consists of reddish fine- to medium-grained sandstones usually with cross stratification and lamination that are interbedded with red mudstones. Wave ripples are common, and occasional mud-cracked surfaces and moulds of hopper crystals also occur. Bioturbation produced by invertebrates (consisting in both vertical and horizontal burrows) is especially abundant in some sandstone layers. In general terms, the succession is similar to that of Collcardús, previously reported by Mujal et al. (2015), and located just 5 km eastwards. The Collcardús outcrops are composed of red bed deposits corresponding to mudstones alternated with fine- to medium-grained sandstones, often with cross stratification, ripples and, occasionally, desiccation cracks (Mujal et al., 2015). Based on these features (see Text S1 for further details), we interpret the palaeoenvironmental setting of Puigventós (and Collcardús) as a distal alluvial area with frequent desiccation periods and with highly salty waters, but also with flooding (at least periodical) events, which is consistent with the presence of tetrapod swimming traces. The studied outcrop might correspond to the Guanta Sandstone, although a short interval in the lowermost part could correspond to the Arbolí Gypsum. In general terms, the Puigventós succession is here interpreted as a proximal sabkha plain or a tidal mixed-flat (with notable terrestrial or terrigenous influence, as denoted by a major presence of siliciclastic deposits), except for the basalmost part, which it was probably more similar to the tidal flats of Penya Rubí.

The succession of Montmany (Fig. 4B–J) is similar to that of Puigventós and Collcardús as well. The main components of the succession are decimetre-thick reddish fine- to medium-grained sandstones, with cross stratification and lamination, interbedded with red mudstones deposits ~0.5 to 1 m thick (Fig. 4B). Within sandstone layers, wave ripples are common structures, but climbing and unidirectional flow ripples are also present (Fig. 4C). Most of the tetrapod footprints are found on the basal surfaces of the sandstone layers (Fig. 4D), tetrapod swimming traces (though not very abundant) are also preserved. As in Puigventós, some sandstone layers are highly bioturbated (Fig. 4E), with both vertical and horizontal sinuous burrows commonly with meniscate infill. Other more occasional structures are wrinkled surfaces probably of microbial mats (Fig. 4E), mud-cracks (Fig. 4G), moulds of large gypsum nodules (Fig. 4H) and of hopper crystals, all these being indicative of desiccation periods. Otherwise, water escape and load structures (Fig. 4I) are also present, suggesting rapid flooding and increase of the sedimentation rate and higher energy of the system. Of note, potential xiphosuran traces have been identified in Montmany (IPS120436 and IPS120437), further pointing to connections to the palaeocoast, though Triassic xiphosurid ichnofossils are known from far inland settings in the nearby Pyrenean Basin (Mujal et al., 2018b). These traces will be studied in future works and compared with the xiphosuran traceway already described at the Penya Rubí locality (De Jaime-Soguero et al., 2020). A distinct 25 cm thick massive carbonate layer (probably a dolostone) bears *Rhynchosauroides tirolicus* Abel, 1926 footprints in concave epirelief, being different to the rest of the succession (left *in situ*; arrow in Fig. 4J). According to all the mentioned features, this succession may be equivalent to those of Puigventós and Collcardús, mostly corresponding to the Guanta Sandstone. In this case, the facies correspond to a distal alluvial setting, being a proximal sabkha plain, with salty waters and with frequent desiccation periods, but also periods of flooding and a relatively strong terrigenous inpunt. Nonetheless, as indicated by Ortí et al. (2018), some intervals (such as the carbonate layer) may correspond to interdigitated parts of the Arbolí Gypsum (Fig. 2C).

4.2. The middle Muschelkalk track record of the Catalan Basin

Numerous tetrapod tracks have been recovered from the Penya Rubí, Puigventós and Montmany outcrops. They are assigned to at least 10 different ichnotaxa. Specimens of the same ichnotaxon but from different localities may display distinct features, though in some cases differences appear to be related to substrate composition, as discussed below and in Text S3. In this section we briefly describe each tetrapod ichnotaxon of the middle Muschelkalk ichnoassemblage from the Catalan Basin, mainly from the three newly reportedlocalities (Penya Rubí, Puigventós and Montmany), but also including remarks from the previously described localities of Collcardús (Mujal et al., 2015) and Pedrera de Can Sallent (Mujal et al., 2018a). The detailed systematics of each ichnotaxon, as well as additional figures are provided in the supplementary information (Text S2, Figs. S1–S10).

Tracks of *Procolophonichnium haarmuehlensis* (Holst et al., 1970) have been identified in the Penya Rubí locality by relatively small, pentadactyl and semiplantigrade impressions (Figs. 5A, S1). The digit proportions and relative position make their imprints wider than long. The digit imprints shape is moderately robust and straight to distally curved outwards. The length of digit impressions increases from I to III, with digit IV imprint slightly shorter than digit III. The imprint of digit I is the shortest. The imprint of digit V is separated from the others and more proximally positioned, and its length is subequal to digit II (Klein et al., 2015). Claw impressions are preserved in all digits, being deeply impressed and markedly curved outwards. Awaiting further analyses, including the study of relative depth patterns (e.g., Mujal et al., 2020), procolophonid parareptiles and therapsid synapsids are considered the most probable producers of *P. haarmuehlensis* (Klein et al., 2015; Marchetti et al., 2019c).

Three small-sized ichnites from Montmany have been referred to *Procolophonichnium* isp. (Figs. 5B, S2). They are pentadactyl and plantigrade, with robust and straight to slightly bent outwards digits imprints displaying relatively large clawed tips. The lateral portion of the footprints is relatively deeply impressed, suggesting a different trackmaker to those of *P. haarmuehlensis*.

Several footprints assigned to an indeterminate ichnospecies of *Chelonipus* Rühle von Lilienstern, 1939 have been recovered from Puigventós and Montmany localities (Figs. 5C, S2A, D, S3). As observed in the studied specimens, this ichnogenus is characterised by a relatively wide trackway, with a low pace angulation (Haubold, 1971a; Lovelace and Lovelace, 2012; see Lichtig et al., 2018 for a review of the ichnogenus). The footprints outlines are represented by roundish proximally concave arches, with imprints of the digit tips usually displaying a dragging trail traces anteriorly directed. The imprints are digitigrade to semiplantigrade and wider than long. The digit impressions are short and with round tips. Pes tracks display three to five digits impressions, while manus tracks show up to four digit impressions. A characteristic feature is the impression of the interdigital area between digits II, III and IV. The potential trackmaker of *Chelonipus* is traditionally referred to turtles (Lichtig et al., 2018). Nevertheless, other potential producers, such as temnospondyl amphibians (e.g., Mujal and Schoch, 2020) or other unknown producers cannot be discarded.

The most abundant morphotype of the middle Muschelkalk is *Rhynchosauroides* Maidwell, 1911 (Figs. 3G, H, 5D, E, F, S4, S5). This ichnotaxon is featured by relatively small, lacertoid-like and markedly ectaxonic tracks, with slender digit impressions. In both manus and pes tracks, the imprints of digits I to IV increase in length and are curved inwards, while digit V imprint (similar to digit I in length) is separated, more proximally positioned and rotated outwards. The manus impressions tend to be semiplantigrade (occasionally digitigrade to semidigitigrade), with digit imprints relatively shorter and wider than those of pes impressions. Pes tracks are mainly digitigrade to semidigitigrade; most commonly only composed by the impression of digits II, III and IV. Pes tracks anterolaterally or laterally overstep manus tracks. All the footprints from Penya Rubí and Pedrera de Can Sallent (Mujal et al., 2018), most of those from Puigventós, and those from the carbonate layer of Montmany (see Text S2 for details on the specimen numbers) fall into the range morphology of *R. tirolicus*, which is well known from Middle Triassic coastal fine-grained and carbonate deposits of the Italian Southern Alps (e.g., Avanzini and Renesto, 2002; Valdiserri and Avanzini, 2007; Mietto et al., 2020), and possibly from Germany (e.g., Diedrich, 2002, 2008). Otherwise, the relatively poor preservation of other specimens from Montmany and Puigventós (e.g., Figs. 5F, S5), as well as Collcardús (Mujal et al., 2015), precludes an ichnospecific identification. The large chronological and palaeobiogeographical occurrence of *Rhynchosauroides* may suggest that different taxa could have produced these characteristic lacertoid-like tracks, most likely being small neodiapsids, including lepidosauromorphs and/or archosauromorphs (e.g., Avanzini and Renesto, 2002; Diedrich, 2002, 2008; Valentini et al., 2007; Mujal et al., 2018).

Tracks of *Rotodactylus* Peabody, 1948 have been recovered from Penya Rubí and Puigventós localities (Figs. 5G, 6C, S6, S8). These footprints are digitigrade, longer than wide, pentadactyl and relatively small. The digit length increases from I to IV. Imprints of digits I to IV are straight, subparallel, with the tips markedly bent inwards. Imprint of digit V is only represented with a round impression in a far proximal position from the rest of the imprint, being a characteristic feature of this ichnogenus (Peabody, 1948; Haubold, 1971a; Klein and Lucas, 2010a; Niedźwiedzki et al., 2013). Dinosauromorphs are considered the potential trackmakers of *Rotodactylus* (e.g., Peabody, 1948; Haubold, 1967, 1999; Haubold and Klein, 2002; Brusatte et al., 2011; Niedźwiedzki et al., 2013); non-dinosauromorph archosauromorphs have also been proposed as producers (Padian, 2013), although a thorough track-trackmaker correlation for this alternative attribution is not available so far.

The largest tetrapod ichnites recovered from the middle Muschelkalk of the Catalan Basin belong to the ichnofamily Chirotheriidae. Two ichnospecies of *Chirotherium* Kaup, 1835 have been recovered. Both morphotypes are characterised by pes tracks with tightly grouped imprints of digits II, III, IV, being digit III the longest, and with digit I imprint slightly separated and more proximally. Imprints of digits I to IV are straight and distally tapering, with relatively large triangular claw impressions. Digit V imprint is separated from the others, more proximally positioned and rotated outwards. These are diagnostic features of *Chirotherium*, a very common morphotype from Lower and Middle Triassic terrestrial deposits and with a global distribution (Haubold, 1971a, 1984; Klein and Haubold, 2007; Klein and Lucas, 2010b; Díaz-Martínez and Pérez-García, 2012; Lagnaoui et al., 2019; Xing and Klein, 2019).

From Montmany, two manus-pes sets of relatively small tracks with slender (elongated) shape are conferred to *Chirotherium sickleri* Kaup, 1835 (Figs. 6A, S2A, D). Pes tracks are semiplantigrade and manus tracks are semidigitigrade. In pes tracks, digit II imprint is notably shorter than digit IV imprint. Manus tracks are smaller than pes tracks, but with similar digit proportions and more anteriorly positioned. Pes tracks are slightly outward rotated in comparison with the manus impressions, a feature characteristic of this ichnospecies, and opposite to *C. barthii* (e.g., Klein and Lucas, 2010a; Klein et al., 2016). “Rauisuchian” (pseudosuchian) archosauriforms are possible trackmakers of this ichnospecies (Klein and Lucas, 2010a).

The second ichnospecies recovered is *Chirotherium barthii* Kaup, 1835, found in Puigventós and in the medium-grained sandstone stratum of Penya Rubí (upper arrow in Fig. 3A, Figs. 6B, S7). Pes tracks are semiplantigrade and relatively large. The diagnostic features of this ichnospecies (e.g., Haubold, 1971b, 2006; Klein and Lucas, 2010a) observed in the Catalan specimens are: the longest digit III impression, followed by digit II and a clearly shorter digit IV imprint; the triangular, large claw impressions of the pedal digits; the pedal digit V imprint outlining a large, deeply impressed oval-shaped proximal pad, and thinning distally. Pseudosuchian archosaurs or stem archosaurs are the potential trackmakers of this ichnospecies (Haubold, 2006; Haubold and Klein, 2000, 2002; Klein and Haubold, 2003; Klein et al., 2011).

A single left pes track from Puigventós is referred to *Isochirotherium* Haubold, 1971a (Figs. 6C, S8). It is semiplantigrade and pentadactyl imprints, with robust digits with rounded claw impressions. Imprints of digits I to IV are straight and subparallel, wider on the middle-distal portion, being somewhat oval-shaped. The digit III imprint is the longest, with the digit II imprint subequal in length. Imprint of digit IV is much shorter, but longer than the impression of digit I imprint. These four digit imprints form a compact group. The impression of digit V is separated from the others, proximally positioned slightly curved outwards and a laterally orientated. Among *Isochirotherium* ichnospecies, *I. coureli* (Demathieu, 1970) is the most similar to that from Puigventós (e.g., Gand et al., 2007; Klein and Lucas, 2018). Despite the fact that the absence of the typical large pad in the imprint of digit V (due to breakage of the slab) and the lack of manus impressions make the ichnospecies identification uncertain, the *Isochirotherium* tracks of Puigventós display the same features as that of Collcardús (see Mujal et al., 2015). In addition, one of the tracks recovered in Collcardús preserves a large pad impression of the digit V, also characteristic of *I. coureli*. Thus, we assign all *Isochirotherium* tracks of the middle Muschelkalk from the Catalan Basin to *I.* cf. *coureli*. The potential trackmakers of *Isochirotherium* were archosaurs, as in *Chirotherium*, though no skeletal counterparts are so far correlated to this ichnogenus (Klein and Lucas, 2010a).

Several tracks recovered from Montmany and a single partial track from Puigventós are attributed to *Sphingopus ferox* Demathieu, 1966 (Figs. 4C, D, 6D, S9). The pes tracks are semiplantigrade with a characteristic functionally tridactyl trend, with the predominating imprints of II, III and IV. The manus of this ichnogenus is located in an inner position regarding the pes tracks. The diagnostic features of this ichnospecies (e.g., Demathieu, 1966, 1985; Haubold and Klein, 2002; Gand et al., 2007; Klein and Lucas, 2018) observed in the Catalan specimens are: the longest digit III imprint, followed by a notably shorter digit II imprint, which is longer than digit IV imprint; the relatively low angle of digits II and IV (27º–38º, mean of 31º); the impression of digit I more proximally positioned respect to digits II–IV, located behind digit II imprint and rotated outwards; the digit V imprint, being curved and rotated outwards, and more proximally positioned than and clearly separated from the other digit imprints; the smaller manus tracks positioned at the height of pedal digit III imprint and on the inner side of pes tracks. This ichnotaxon has been related to dinosauromorph trackmakers (Haubold and Klein, 2000; Haubold and Klein, 2002; Brusatte et al., 2011).

Moreover, several tracks from Puigventós and Montmany localities display features characteristic of chirotheriid ichnotaxa (e.g., Demathieu and Demathieu, 2004; Haubold and Klein, 2002) (Fig. S10). However, due to their poor and incomplete preservation, and/or because they are isolated manus tracks (Fig. S10A), these ichnites cannot be assigned to any ichnogenus. Of interest, some of these tracks were probably impressed under swimming locomotion (Figs. S2D, S10B), a behaviour already known from the Triassic archosaur ichnological record (e.g., Thomson and Droser, 2015; Mujal et al., 2017a).

4.3. Distribution of the Middle Triassic track record: descriptive statistics

Table S1 consists in a database of the global Middle Triassic tetrapod track occurrences, including up to 75 regions/areas/localities. On its basis, a counting study of the presence/absence of the tetrapod ichnorecord in each region reveals a total of 329 tetrapod trace occurrences classified in 29 different morphotypes (mostly ichnogenera but also other specific cases, see methods in section 3 above). Following the palaeoenvironmental classification used in this work, 33% of the localities correspond to inland settings, 32% to distal alluvial, 28% to coastal, and 7% to shallow marine (Fig. S11). Noteworthy, a very few track occurrences are classified in the shallow marine setting; therefore, the obtained results may suffer changes with future field data from such settings. Despite the similar proportions of the three most represented palaeoenvironments, the inland and distal alluvial settings accumulate, respectively, the 36.78% (121) and 34.35% (113) of all ichnological occurrences. The coastal settings record the 25.84% (85) of the total occurrences, and shallow marine environments only account for the 3.04% (10) of the total occurrences (Table S2). Also, the tetrapod ichnodiversity recorded in distal alluvial (26 morphotypes) and inland (23 morphotypes) settings is clearly higher than in those of the coastal (16 morphotypes) and shallow marine (6 morphotypes) settings (Table S2). It should be noted that shallow marine settings mainly yield swimming traces, which are not distinguished at a detailed ichnotaxonomic level, though clearly different ichnogenera and ichnospecies are included within swimming traces (for thorough descriptions of tetrapod swimming ichnotaxa, see Xing et al., 2020, and references therein; see also Table S1).

Figure S12 shows that, among all the tetrapod trace occurrences analysed, the dominant ichnogenera are: *Rhynchosauroides* (16.11%), *Chirotherium* (13.68%), *Isochirotherium* (10.33%), *Procolophonichnium* (7.90%), *Rotodactylus* (7.29%), and *Synaptichnium* (6.38%). Also, swimming traces morphotypes (4.56%) and Chirotheriidae indet. tracks (4.26%) tend to be frequent in Middle Triassic outcrops. The occurrence of the remaining tetrapod ichnogenera and morphotypes is relatively low (each one representing <4% of the total occurrences) (represented within “Others” in Fig. S12). Of note, the relative proportions of each ichnotaxon in each palaeoenvironment (Fig. 7A) show the palaeoenvironmental distribution of each tetrapod trace morphotype without considering the total number of footprints in each region (i.e., counting only presence/absence of each morphotype in each region). Therefore, these data reflect the tetrapod ichnodiversity, but not the relative abundance of each ichnotaxa/morphotypes.

Figure 7B shows the total number of occurrences of each tetrapod ichnotaxon/morphotype (see also Tables S2 and S3), *Rhynchosauroides* occurrences are higher in coastal settings than in distal alluvial and alluvial settings. *Procolophonichnium* shows the same trend with a proportionally higher presence in coastal palaeoenvironments than in the other ones. The occurrences of *Chirotherium* and *Isochirotherium* have a very similar trend to each other, being more abundant in distal alluvial and inland palaeoenvironments, the opposite trend to those of *Rhynchosauroides* and *Procolophonichnium*. The distribution of *Synaptichnium* occurrences should be taken with caution, as some tracks assigned to "*Brachychirotherium*" may correspond to the former ichnogenus (or to *Chirotherium* as well; see discussion in Klein and Lucas, 2010b, 2018). The number of Chirotheriidae indet. track occurrences is markedly higher in inland palaeoenvironments than in the other ones (i.e., following the trend of the identified chirotheriid ichnogenera). Lastly, occurrences referred to swimming traces show a relatively homogeneous distribution through all palaeoenvironments. Table S3 shows the percentage of occurrence of each morphotype in each palaeoenvironmental setting (taking into account the number of localities from this palaeoenvironment). *Rhynchosauroides* and *Procolophonichnium* have a markedly higher occurrence in coastal environments (90.5% and 57.1, respectively) than in distal alluvial (66.7% and 29.2%, respectively) and alluvial (64.0% and 24.0%, respectively) palaeoenvironments. This is, tracks of these two ichnogenera are more frequently found in deposits corresponding to coastal settings than those of distal alluvial and alluvial ones. As with the total number of occurrences, the percentages of chirotheriid track occurrences are inverse to *Rhynchosauroides* and *Procolophonichnium*, being higher in inland and distal alluvial palaeoenvironments than in the coastal ones. *Rotodactylus* occurrences show a slight increase towards inland settings, though it is not as marked as that of chirotheriid ichnotaxa. Therefore, Tables S2 and S3 generally show the same proportions in number of occurrences and percentage of occurrences for each ichnotaxon in each palaeoenvironments.

A comparison of the proportions of the different tetrapod morphotypes in each palaeoenvironment (Fig. 7B) shows that *Rhynchosauroides* and *Procolophonichnium* are proportionally more abundant in coastal settings than in distal alluvial and inland palaeoenvironments. Such proportion decrease of these ichnogenera towards inland settings is reverse to the tetrapod ichnodiversity (Table S2), which increases from coastal to distal alluvial and inland settings (Fig. 8). Otherwise, the presence of chirotheriid ichnotaxa (including *Chirotherium*, *Isochirotherium* and Chirotheriidae indet.) and *Rotodactylus* increase in those palaeoenvironmental settings that have a higher diversity.

Summarising, we can observe how the palaeoenvironmental distribution and proportions of *Rhynchosauroides* and *Procolophonichnium* is generally inverse to that of chirotheriids and to the track diversity (Figs. 7B, 8). This is especially well-reflected by the tetrapod ichnoassociations of the Middle Triassic Western Tethys, which represent the bulk of data of the analysed localities (Table S1).

5. Discussion

5.1. Palaeoecology of the middle Muschelkalk tetrapod ichnoassociations

In the Catalan Basin, the onset of the detrital siliciclastic middle Muschelkalk deposits over the marine carbonate succession of the lower Muschelkalk mirrors a regression of the Tethys during the late Anisian–early Ladinian. Areas such as Puigventós and Montmany (Fig. 4) record a succession of changing/alternating environmental settings, ranging from relatively low energy conditions and evaporation periods (i.e., during the development of hopper crystals, gypsum nodules and desiccation cracks) to floodings and events of increased energy with water currents (medium- to coarse-grained thick bedded sandstones with cross stratification; as well as the presence of abundant vertical invertebrate burrows, and horizontal sinuous burrows as well). In the palaeoenvironments of the Puigventós and Montmany successions, relatively large archosaur tracks are found (*Chirotherium*, *Isochirotherium* and *Sphingopus* ichnogenera, as well as indeterminate chirotheriid tracks), even if extensive surfaces are not exposed. This most probably indicates that their trackmakers were common inhabitants of these environments. In contrast, the relatively low presence of *Rhynchosauroides* indicates that their trackmakers (generally small-sized diapsid reptiles) were much less abundant and/or that the preservation of their more gracile footprints was difficult. Even if taphonomic and sampling biases exist, they alone cannot explain the low proportion of *Rhynchosauroides* footprints in these settings (being much less abundant than the chirotheriid tracks; Figs. 7, 8, Text S2), especially if tracks of this ichnogenus dominate in nearby localities (i.e., Penya Rubí and Pedrera de Can Sallent). In this regard, the preservation of skin and claw impressions in the *Chirotherium barthii* specimen IPS85803 indicates that the substrate was able to record small and delicate details and structures, which could include small-sized tetrapod footprints. These observations support the hypothesis that environmental conditions constrained the spatial or areal distribution of tetrapods. Furthermore, *Rotodactylus* tracks (with sizes similar to those of *Rhynchosauroides*) are more abundant in Puigventós than in Penya Rubí, denoting a similar distribution to that of chirotheriid tracks. This is, even if *Rotodactylus* specimens are of small size, they are more abundant in deposits that appear not to favour their preservation. Therefore, the low presence of

Rhynchosauroides is probably not caused by a low potential of preservation of small-sized footprints, but by an actual low presence of their trackmakers. Moreover, some of the Puigventós slabs containing *Rhynchosauroides* (e.g., IPS110267 and IPS110269) display thin laminae, similar to the microbial mats of Penya Rubí (see below). In the same way, the tracks of *Rhynchosauroides tirolicus* from the Montmany locality are only found in a distinct carbonate layer (interbedded within a red bed succession of mudstones and sandstones; Fig. 4J), where no other ichnotaxa have been observed. This could also denote a palaeoecology-related distribution of this ichnogenus, since it is more common within certain lithologies of various settings that are different from those characterising the Puigventós and Montmany successions. In a qualitative approach, these observations on the presence/absence and relative abundance of ichnotaxa agree with the expected results applying the census methods of Marchetti et al. (2017): poorly exposed surfaces of the Puigventós and Montmany successions (Fig. 4A, B, D), as well as the sandstone layer from the upper portion of the Penya Rubí succession (upper arrow in Fig. 3A), (usually) only preserve relatively large (archosaur) footprints, whereas the carbonate layers of the lower portion of the Penya Rubí succession (lower arrow in Fig. 3A; see below) preserve only small-sized ichnotaxa (dominated by *Rhynchosauroides tirolicus*). These distinct distributions are also found in the previously described middle Muschelkalk localities from the Catalan Basin: the surface of Collcardús (Mujal et al., 2015) contains seven footprints of chirotheriids and one of *Rhynchosauroides*, whereas on the surfaces of Pedrera de Can Sallent (Mujal et al., 2018a) all footprints are of *Rhynchosauroides* (*R. tirolicus*, according to the reanalysis of the present work; see Text S2), except of a single and poorly preserved indeterminate footprint of a relatively large size.

In contrast to Puigventós, Montmany and Collcardús, the very fine-grained and carbonate finely-laminated deposits of the Penya Rubí locality presents extremely abundant *Rhynchosauroides tirolicus* footprints (Fig. 3G, H), whereas chirotheriid tracks are absent in the very same layers. *Procolophonichnium* and *Rotodactylus* are present, although these track morphotypes are much less abundant. The presence of microbial mats in the sedimentary succession of Penya Rubí might have prompted the high-quality preservation of the ichnites, including the preservation of scale prints, even if the trackmakers of *Rhynchosauroides* and *Procolophonichnium* were lightweight organisms. In fact, in present day intertidal areas with growing of microbial mats, Carmona et al. (2011) correlated the preservation of tiny details of footprints (in their case, skin of birds' feet) with the presence of thin microbial mats. Such good quality of preservation in microbial mats may depend on the specific environmental conditions, water content and mat overgrowth, affecting the rheological properties of the substrate (Marty et al., 2009; Marchetti et al., 2019b). We therefore suggest that the Penya Rubí fossil footprints underwent similar formation and preservation processes (microbial mats are also finely laminated), within a similar environment, as that reported by Carmona et al. (2011). A similar high-quality preservation of tetrapod tracks is found in the Anisian successions of Winterswijk, the Netherlands (Demathieu and Oosterink, 1983, 1988; Marchetti et al., 2019c) and Southern Alps, Italy (Avanzini, 2000; Mietto et al., 2020). Similar experimental analyses on the preservation of footprints on microbial mats carried out by Marty et al. (2009) could also explain the virtually absence of large ichnotaxa: their trackmakers would have moved with difficulties on such substrates, being too inconsistent to support the weight of large organisms.

From the *Rhynchosauroides*-dominated tracksite of Pedrera de Can Sallent, Mujal et al. (2018a) documented three different types of footprint preservation correlated to the substrate rheology and environmental variations. In this regard, most samples of the *Rhynchosauroides* from Penya Rubí would be a mix between preservation type 2 (high number of footprints) and preservation type 3 (high level definition in a small sampling) of Mujal et al. (2018a). The high quality of most footprints would be enhanced by the presence of microbial mats (e.g., Marty et al., 2009; Carmona et al., 2011; Marchetti et al., 2019b). The high abundance of footprints, moreover, may have resulted from a combination of: (1) increased activity of the trackmakers (i.e., environment favourable for their presence), implying that the trackmakers would be gregarious as suggested by Demathieu and Demathieu (2004) (see also Diedrich, 2008; Mujal et al., 2016b, 2018a); (2) high preservation potential because of the presence of microbial mats, implying a potential overrepresentation of trackmakers in cohesive substrates exposed during a relatively long period (i.e., time averaging of substrates, see Falkingham, 2014). An additional explanation for the abundance of *Rhynchosauroides* is that this ichnogenus was probably produced by several different small- to medium-sized "lacertoid-like" taxa (neodiapsids, including archosauromorphs and lepidosauromorphs), which would have been common inhabitants of the Middle Triassic coastal settings (cf. Ezcurra, 2016). In this sense, the high presence of *Rhynchosauroides* might be a reflection of an expansion of reptiles that printed similar ichnites and adapted to coastal areas and/or continental floodplains (Fig.

8). Even if coastal settings were more favourable to the presence of *Rhynchosauroides* trackmakers, they were also present in alluvial settings (Fig. 7, Table S1; see also discussion above). This indicates that trackmakers were adapted to a wide range of environments and/or that *Rhynchosauroides* encompass a wide range of trackmakers. The latter is also supported by the fact that the time span of this ichnogenus is very long, from the late Permian to the Late Jurassic (Valentini et al., 2007; Avanzini et al., 2010; Lucas, 2019; Marchetti et al., 2019d; Schneider et al., 2020). As noted in section 4.2 above and Text S2, the *Rhynchosauroides* tracks on IPS110265 from Puigventós are different from the other specimens from the same locality and from those of the nearby Penya Rubí and Pedrera de Can Sallent localities. This could be related to the presence of a different trackmaker, being the trackmakers of the imprints on IPS110265 from a more inland setting than the others.

Other tetrapod ichnotaxa, not as abundant as those previously discussed, also appear to be linked to specific palaeoenvironments (Table S1). *Procolophonichnium haarmuehlensis* tracks are only found, together with *Rhynchosauroides*, in the microbial mat layers of Penya Rubí. This ichnospecies is more commonly found in coastal or marine-influenced palaeoenvironments, although it is also present in terrestrial or more inland settings, such as those from Spain, Germany and Morocco (see Klein et al., 2015). In addition, the *Chelonipus* specimens from the Puigventós locality represent the first Middle Triassic record of the ichnogenus outside Germany, where it is present within coastal settings (Lichtig et al., 2018). *Chelonipus* is also known from older terrestrial Triassic localities from the USA (Lovelace and Lovelace, 2012), as well as from coastal ichnosites of the Upper Triassic of Spain (Reolid et al., 2018) and Germany (Lichtig et al., 2018). *Rotodactylus*, although present in both fully terrestrial and coastal-influenced palaeoenvironments, is more abundant in the terrestrial ones (see further discussion in section 5.2 below).

An interesting occurrence is that of potential dinosauriforms (*Sphingopus ferox*) in the Montmany and Puigventós successions. These footprints further support former studies and inferences that this group was already present during the Middle Triassic, as also suggest the occurrences of *Sphingopus* from France (see Gand et al., 2007), Germany (Haubold and Klein, 2000, 2002; Klein and Lucas, 2018) and Poland (Brusatte et al. (2011). Further material may help to elucidate the palaeoenvironmental distribution and general evolution of the group, as well as the nature of the potential trackmakers.

To sum up, the different middle Muschelkalk localities here surveyed and reviewed suggest that the *Rhynchosauroides*-dominated ichnoassociations were generally linked to low energy environments with more marine influence, such as intertidal flats, as well as distal sabkha plains (see also Mujal et al., 2018a). As already suggested (Diedrich, 2002, 2008; Mujal et al., 2018a), a separate ichnocoenosis for *Rhynchosauroides* may characterise the Middle Triassic coastal settings. On the contrary, the Chirotheriidae-bearing ichnoassociations likely correspond to more terrestrial environments (although still with marine influence), such as alluvial plains and inland sabkha settings (Fig. 13). Of note, the two ichnoassociations of Penya Rubí (lower and upper) mirror the change from the Arbolí Gypsum to the Guanta Sandstone, representing the onset of a more terrestrial environment (see Text S3 for further discussion and details) and thus prompting the appearance of chirotheriid tracks.

5.2. Middle Triassic tetrapod palaeoecology and palaeobiogeography of the Western Tethys

The palaeoenvironmental distribution of tetrapod ichnotaxa within the middle Muschelkalk of the Catalan Basin mirrors the palaeobiogeographic distribution at Western Tethys scale. As shown below, the detailed analysis of the occurrence and absence of tetrapod ichnotaxa (Figs. 7, S11, S12, Tables S2, S3) demonstrates that tetrapod ichnofacies can be a useful tool contributing to the understanding of past ecosystems and their evolution (Hunt and Lucas, 2007a, 2007b).

Our database of the Middle Triassic tetrapod ichnotaxa and localities all over the world, including the specific time interval and palaeoenvironmental settings (Table S1), shows that the distribution of ichnotaxa appears to be linked to the environmental changes derived from different marine transgressions (Fig. 7) (as reflected in the middle Muschelkalk from the Catalan Basin), being especially notable in the Western Tethys domain (cf. Diedrich, 2002, 2008, 2015; Mujal et al., 2018a). It is important to remark that most of the Middle Triassic tetrapod footprint localities so far known are dated as Anisian, and only a few of them correspond to the Ladinian (Fig. 1; see Table S1 for references). This could be related to the fact that during most part of the Ladinian most of these Triassic basins were under marine settings (e.g., Escudero-Mozo et al., 2015; Franz et al., 2015; Manzanares et al., 2020; and references therein) (Fig. 1). In this sense, successions ranging from the Anisian to the Ladinian, as those from the middle

Muschelkalk, give clues to the understanding of the (ichno-) faunal evolution during the Middle Triassic.

During the latest Early Triassic (Olenekian) and the early steps of the Middle Triassic (Anisian), the Western Tethys basins were characterised by the presence of archosauromorphs (Mujal et al., 2016b, 2017a). Chirotheriid tracks (and especially *Chirotherium barthii*) and *Rhynchosauroides* are abundant in Spain, France, Morocco, Italy, Switzerland, Germany, Poland, United Kingdom and the USA (see Table S1 for references). Other ichnotaxa are also recorded but not as widely present and abundant as the previous ones (e.g., *Procolophonichnium*, *Chelonipus*, *Isochirotherium*, *Synaptichnium*, and *Rotodactylus*, though the latter may be occasionally abundant). Interestingly, *Chirotherium barthii* and *Rhynchosauroides* are present in further Middle Triassic localities from China (Xing et al., 2013; Xing and Klein, 2019). *C. barthii* is also known from Argentina (Lagnaoui et al., 2019), indicating a virtual global distribution of the corresponding trackmakers.

Large-sized tracks referred to chirotheriids are also recorded in some southwestern-southern Gondwanan regions (e.g., Argentina: Marsicano et al., 2004; Melchor and de Valais, 2006; Lagnaoui et al., 2019; Brazil: Leonardi, 1980), including *Chirotherium* and *Isochirotheirum*. Therefore, the group of relatively large chirotheriid-trackmakers had already a cosmopolitan distribution during the early stages of the Triassic, as recently shown in the review of the Early Triassic tetrapod fauna by Romano et al. (2020). This is also indicated by the widespread presence across central Pangaea of *Protochirotherium* tracks in the Lower Triassic (Fichter and Kunz, 2004; Klein and Niedźwiedzki, 2012; Klein et al., 2013), which possibly extends back to the upper Permian (Bernardi et al., 2015; Marchetti et al., 2019d). *Rotodactylus* tracks are slightly more abundant in terrestrial palaeoenvironments than in coastal ones (Fig. 7B), which possibly reflect a similar distribution to that of chirotheriid tracks. In fact, chirotheriid and *Rotodactylus* ichnotaxa are commonly found associated (Table S1).

Palaeoenvironmental and/or taphonomic biases exist as demonstrated by the poor (or null) ichnological record of non-amniote tetrapods (temnospondyls sensu lato) in the Western Tethys during the Anisian. Only dubious records from few localities of France and Germany are known (Haubold, 1971a; Demathieu and Durand, 1991; Gand et al. 2007). Out from the Western Tethys, potential amphibian tracks are known only from the Moenkopi Formation, USA (Klein and Lucas, 2010a), and New South Wales, Australia (Farman and Bell, 2020) (Table S1). This is in contrast with the important osteological record of Anisian temnospondyls from the Western Tethys (e.g., Spain, Fortuny et al. 2011b; France, Germany and Poland, Schoch and Milner 2000). More recently, Mujal and Schoch (2020) reported temnospondyl tracks from the Ladinian (Lower Keuper) of southern Germany. These authors hypothesised that the lack of record is most probably related to the ecological preferences of temnospondyls, which usually roamed subaquatic settings performing a buoyant/swimming locomotion, hence reducing the preservation potential of footprints.

Even if transgressions resulted in different environments across the Western Tethys, basins remained connected during the Middle Triassic as demonstrated by the relatively homogeneous tetrapod ichnoassemblages throughout this domain. With the development of coastal areas, the trackmakers of *Rhynchosauroides* took advantage as reflected by the dominance of this ichnogenus in the Western Tethys coastal palaeoenvironments (Diedrich, 2008; Mujal et al., 2018a). Interestingly, *Procolophonichnium* tracks have a similar palaeoenvironmental distribution to that of *Rhynchosauroides* (Fig. 7), confirming the previous observations of Diedrich (2002) for the Central European Basin. Noteworthy, *Rhynchosauroides* is already abundant in the marginal marine setting of the Arenaria de Val Gardena Formation, from the Lopingian of Italy (Valentini et al., 2007; Marchetti et al., 2019d). This could be indicative of a similar palaeoecology of this older *Rhynchosauroides* morphotype to those of the Middle Triassic; hence further investigations should focus on the comparison of the whole record of this ichnogenus.

Rhynchosauroides already had a global distribution by the Early and earliest Middle Triassic, being recorded in western and central Europe (Haubold, 1971a, 1971b; Demathieu, 1985; Diedrich, 2002, 2008; Demathieu and Demathieu, 2004; Klein and Niedźwiedzki, 2012; Mujal et al., 2016b, 2017a), western USA (Klein and Lucas, 2010a; Lovelace and Lovelace, 2012), Argentina (Melchor and de Valais, 2006) and China (Xing and Klein, 2019). This ichnogenus encompasses a high number of ichnospecies, many of them possibly described from specimens with extramorphological variations (cf. Klein and Niedźwiedzki, 2012); similarly, in several cases *Rhynchosauroides* tracks are usually not identified at the ichnospecies level (Table S1). As a result, this ichnogenus is in need of a comprehensive revision in order to determine its ichnospecific diversity. In any case, certain *Rhynchosauroides* morphotypes are characteristic of specific time intervals and palaeoenvironmental settings: *R. schochardti,* known from the Lower and lowermost Middle Triassic terrestrial settings, and *R. tirolicus* and *R. peabodyi*, known from the Middle Triassic coastal settings of the Western Tethys (Table S1). Therefore, the global distribution of *Rhynchosauroides* during the Early Triassic could be explained by the presence of trackmakers mostly adapted to terrestrial environments. Several of these palaeoenvironments would have evolved to coastal settings during the Middle Triassic, possibly prompting a turnover within the trackmakers of *Rhynchosauroides*. The new trackmakers might have diversified and became dominant due to the expansion of coastal settings. Therefore, there could have been a turnover of faunas from the Early to the Middle Triassic, especially in the Western Tethys, due to the expansion of coastal settings and in detriment of most large archosaurians (see below). Nonetheless, a research bias, with the coastal settings from the Lower Triassic less studied than those of the Middle Triassic, cannot be ruled out.

Additionally, tetrapod swimming trace fossils, even if not abundant, are present in all the palaeoenvironments of the Middle Triassic (Fig. 7, Table S1). This could point to a potential taphonomic bias towards the preservation of footprints in environments with a relatively recurrent presence of water. Therefore, such bias could also be applied at a greater scale; this is, there could be a preferential preservation of coastal deposits against more inland ones, and thus the likelihood of finding tetrapod footprints is greater in coastal settings. However, as shown in section 4.3 above, tetrapod track localities of coastal settings are approximately the same as those of alluvial palaeoenvironments (Fig. S11). Regarding the shallow marine settings, a potential research bias is observed, as track localities under this palaeoenvironment are markedly less represented than the other ones (Fig. S11).

The potential faunal turnover within the trackmakers of *Rhynchosauroides* can be further explored by analysing the osteological record. Ezcurra and Butler (2015, 2018) and Foth et al. (2016) already documented an increase of the morphological disparity of archosauromorphs during the late Early and early Middle Triassic, although the low sampling of Lower Triassic deposits should also be considered (see also Butler et al., 2011; Romano et al., 2020). Ezcurra and Butler (2018), as well as Irmis and Whiteside (2012), suggested that the low rates of diversification within archosauromorphs, but also generally within tetrapods, could be linked to perturbations of the global carbon cycle in the aftermath of the end-Permian mass extinction (for alternative interpretations on the magnitude of the extinction, see Lucas, 2017). The stabilization of the carbon cycle, together with the expansion of coastal settings, would have allowed the diversification of certain tetrapod groups. Interestingly, MacDougall et al. (2019) also documented a turnover within parareptiles during the early steps of the Triassic (see Ruta et al., 2011), showing also a sharp decline during the Middle Triassic; these changes could be linked to the radiation of archosauromorphs. In this sense, the Lower and Middle Triassic tetrapod localities are commonly dominated by archosauromorph faunas (e.g., Pinheiro et al., 2016) and lepidosauromorphs, though the latter being less abundant (e.g., Schoch and Sues, 2018; Simões et al., 2018; Cavvichini et al., 2020; Sobral et al., 2020). Interestingly, the tetrapod tracks apparently mirror such changes, with a high increase and dominance of footprints produced by archosauromorphs (e.g., Mujal et al., 2017a).

As observed between the middle Muschelkalk localities of the Catalan Basin, while in Penya Rubí and Pedrera de Can Sallent small-sized footprints are extremely abundant and large ichnotaxa (i.e., chirotheriids) are completely absent, in Puigventós, Montmany and Collcardús chirotheriids are proportionally much more abundant than small-sized taxa (e.g., *Rhynchosauroides*). Interestingly, Penya Rubí and Pedrera de Can Sallent correspond to tidal flat settings, mostly composed of carbonate and very fine- to fine-grained siliciclastic deposits, whereas Puigventós, Montmany and Collcardús correspond to distal alluvial and proximal sabkha settings, mostly composed of fine- to medium-grained siliciclastic deposits. In addition, small ichnotaxa (i.e., *Rhynchosauroides* among others) are much less abundant than in the tidal (coastal deposits), even if present in these distal alluvial settings (Figs. 7B, 8). The main difference between Penya Rubí and Puigventós and Montmany is the palaeoenvironmental setting, with more terrestrial influence in Puigventós and Montmany than in Penya Rubí (Texts S1 and S3). These considerations can be discussed at Western Tethys (and possibly Pangaean) level: as recently discussed for the Upper Triassic boreal successions (Klausen et al., 2020), the proliferation of coastal areas, with more marine influence due to the Tethys transgression, may led to the loss of habitats of large archosaur faunas (mostly represented by chirotheriids in the ichnological record). As reflected in the Western Tethys (Table S1), large archosaur ichnofaunas in palaeoenvironments with relatively strong marine influence are persistent and diverse (Fig. 7), though in absolute numbers (e.g., Diedrich, 2008, 2015; Mujal et al., 2018a; Marchetti et al., 2020; Mietto et al., 2020) they are notably less abundant than in terrestrial (alluvial) settings (Figs. 7, 8, Tables S2, S3). This may be further indicative of environmental constraints for large-sized archosaurs as discussed in section 5.1 above. Nonetheless, further quantitative analyses are necessary to untangle the distribution of chirotheriid ichnotaxa.

The distribution of Middle Triassic tetrapod ichnotaxa also shows that the distal alluvial and inland settings present a higher (ichno-) diversity than the coastal settings (Figs. 7B, 8, Tables S2, S3). This could respond to the harsher conditions on coastal settings respect to more terrestrial ones. As a result, this could have favoured the proliferation of more generalist taxa (like the potential producers of *Rhynchosauroides*; e.g., Demathieu and Demathieu, 2004; Petti et al., 2013; Mujal et al., 2016b) that better adapted to these environments. In this regard, even without counting the absolute number of footprints of each locality, a reduced tetrapod ichnodiversity is observed in coastal settings, where *Rhynchosauroides* and *Procolophonichnium* tracks dominate (Diedrich, 2008; Mujal et al., 2018a; Marchetti et al., 2020; Mietto et al., 2020). In the same way, as suggested by Marchetti et al. (2020), the proportionally higher number of relatively large archosaur tracks in alluvial settings is probably linked to a different palaeoecology of the trackmakers.

We observe that, in fairly age equivalent localities, differences in ichnofaunal composition exist (Fig. 7, Tables S1, S2, S3). Therefore, at the Middle Triassic scale, the presence of certain ichnotaxa is generally more linked to the environmental setting than to the specific age of the deposits. Thus, the temporal evolution of palaeoenvironments may show an (ichno-) faunal replacement, as observed in the Upper Triassic (Stubbs et al., 2013; Bernardi et al., 2018). Further, such environmental constraint would eventually trigger the proliferation of faunas more adapted to the new environments, such as the dinosaur ascendants, which may be poorly represented in the track record before the Ladinian in the Western Tethys (Table S1). In this regard, thorough revisions of ichnotaxa attributed to dinosauromorphs, such as *Rotodactylus* and *Sphingopus* (see Peabody, 1948; Haubold, 1999; Haubold and Klein, 2000, 2002; Brusatte et al., 2011; and Padian, 2013 for alternative interpretations), together with the (so far poor) osteological record, are necessary to provide a wider picture of the temporal rage and spatial distribution of the dinosaur lineage. The decline of non-dinosauromorph archosaurs, leading to the dominance of the dinosaur lineage has been recently discussed for the Upper Triassic tetrapod record on the basis of (1) morphological and biomechanical disparity (Stubbs et al., 2013) and (2) the archosaur to dinosaur footprint turnover linked to the Carnian Pluvial Event (Bernardi et al., 2018). During the Middle Triassic, dinosauromorphs were still marginal components of tetrapod ecosystems, becoming significantly more abundant by the end of the Middle Triassic and especially during the Late Triassic. All these observations highlight the necessity of carrying out facies analyses together with ichnological (and generally palaeontological) studies. This is necessary to explore the role that the Middle Triassic environmental changes (linked to marine transgressions) played on the shape of tetrapod ecosystems, including also the radiation of the dinosaur lineage. The expansion of coastal and/or marine influenced environments possibly prompted a regression/decrease of large archosaur faunas (potential producers of chirotheriids), which later evolved to new faunas that took advantage of the new environmental settings (e.g., as represented by the evolutionary novelties present in dinosauromorphs and descendants). It is important to note that, in any case, small-sized neodiapsid faunas (mostly represented by *Rhynchosauroides*) persisted (and expanded) in these coastal/marine influenced environments (Diedrich, 2008; Mujal et al., 2018a, and references therein), though they almost disappeared in the Late Triassic.

In summary, we here suggest a link between the Middle Triassic environmental changes and the presence and relative abundance of certain (ichno-) faunas (Fig. 13). In this way, our data permit to distinguish between palaeo(bio)geographic domains of the Western Tethys: marine influenced ichnoassociations (*Rhynchosauroides*-dominated) and terrestrial ones (non-*Rhynchosauroides*-dominated). Moreover, in a reverse analysis, (i) the identification of palaeoenvironments (especially those yielding *Rhynchosauroides* and Chirotheriidae tracks) and (ii) the age of the successions (i.e., Lower or Middle Triassic) might allow to differentiate the potential producers of these ichnotaxa.

6. Conclusions

The Middle Triassic terrestrial record represents an excellent case to study the tetrapod palaeoecology. This is especially the case of the tetrapod ichnological record, particularly abundant from this time interval, as ichnites are preserved in the actual habitats of the corresponding trackmakers. Among the different track localities globally known (Table S1), those from the middle Muschelkalk successions of the Catalan Basin are of particular interest. The tracks herein reported, together with those previously known, reveal a relatively rich ichnodiversity, including: *Procolophonichnium haarmuehlensis*, *Procolophonichnium* isp., *Chelonipus* isp., *Rhynchosauroides tirolicus*, *Rhynchosauroides* isp., *Rotodactylus* isp., *Chirotherium* cf. *sickleri*, *Chirotherium barthii*, *Isochirotherium* cf. *coureli*, *Sphingopus ferox*, and Chirotheriidae indet. Such ichnotaxa are widely known among the Western Tethys basins and some (*Rhynchosauroides* and *C. barthii*) even have a global distribution.

The correlation of each ichnotaxon to its palaeoenvironmental setting, together with the comparison with further localities, shows that environmental changes (linked to the Middle Triassic marine transgressions) constrained the distribution of tetrapod faunas. In the Catalan Basin, the aforementioned ichnotaxa are settled in well-differentiated ichnoassociations, which are linked to different palaeoenvironments. This is, tetrapod ichnotaxa are probably controlled by the presence of specific facies.

The most representative ichnotaxon reflecting such constraints is *Rhynchosauroides*: in coastal palaeoenvironments it is commonly the dominant ichnotaxon (suggestive of a distinct ichnocoenosis: Diedrich, 2008; Mujal et al., 2018a), whereas in more inland settings its presence is reduced. Similarly, *Procolophonichnium* tracks are also more abundant in coastal settings than in alluvial ones. Chirotheriid footprints show the opposite trend: they are scarce in coastal settings, especially those built up of fine-grained facies, and commonly dominate in more terrestrial settings. Therefore, Middle Triassic ichnoassociations are generally either *Rhynchosauroides*-dominated (coastal settings, especially those with fine-grained facies) or non-*Rhynchosauroides*-dominated (alluvial settings, even with some marine influence, and with an increased presence of chirotheriid tracks). Furthermore, tetrapod track diversity in alluvial settings is notably higher than in coastal settings, suggesting that the trackmakers of *Rhynchosauroides*, possibly being generalist organisms, took advantage in coastal palaeoenvironments. This could possibly mirror faunal turnovers during the Early and Middle Triassic recovery of the ecosystems.

This work highlights the importance of facies analyses when studying tetrapod ichnofossils. This may result in a better understanding on the presence/absence of specific ichnotaxa. An integrated sedimentological and ichnological approach sheds light on the tetrapod palaeobiogeography at the given time interval. In this regard, the palaeoenvironmental constraints evidenced by the middle Muschelkalk of the Catalan Basin show the palaeobiogeographic variation of tetrapods of the whole Middle Triassic Western Tethys, and thus contribute to the understanding of the (ichno-) faunal responses to environmental change.

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Figure captions

Figure 1. Palaeogeographic maps depicting the global occurrences of Middle Triassic tetrapod tracksites (see Table S1 for references of the tracksites). **A.** Map of Pangaea at 240 Ma modified from Alroy (2013). **B–C.** Anisian and Ladinian maps of the Western Tethys, modified from Manzanares et al. (2020) (see also references therein).

Figure 2. Geographical and geological setting. **A.** Map of the Iberian Peninsula (modified from Escudero-Mozo et al., 2015 and Mujal et al., 2018a). **B.** Geological map of the Gaià-Montseny domain (modified from Ortí et al., 2018) with the location of the known tetrapod tracksites and other reference sections from the middle Muschelkalk facies. **C.** Synthetic stratigraphic sections of the middle Muschelkalk from the localities depicted in **B** with position of track levels.

Figure 3. The Penya Rubí locality. **A.** Stratigraphic interval including the bulk of the tetrapod footprints on: the dolostone interval of the Arbolí Gypsum (lower arrow), and the first sandstone stratum of the Guanta Sandstone (upper arrow). **B.** Finely laminated dolostone bearing footprints of the Arbolí Gypsum, note the cyclic change of thickness of the laminae. **C.** Lateral equivalent of the dolostone in **B**, displaying cross lamination and being coarsier (sandier). **D.** Ripples in red sandstones oriented in opposite directions, just above the track-bearing dolostone. **E.** Water escape and load structures within the red sandstones and mudstones just below the dolostone layers. **F.** Wrinkle structures resulting from desiccation of microbial mats (IPS106602). **G, H.** Footprints of *Rhynchosauroides tirolicus* preserved in finely laminated dolostones (IPS106601a; **G**), and relatively deeply impressed (IPS106617a; **H**).

Figure 4. The Puigventós (**A**) and Montmany (**B–J**) localities. **A.** Common aspect of the Puigventós strata, being partially covered and fragmented. **B.** Sandstones, with cross stratification and ripples on top of each stratum, interbedded in red mudstones. **C.** Lateral section of IPS120437 displaying parallel lamination at the lower part and climbing ripples at the upper part; the arrow points to the section of *Sphingopus ferox* digit imprints. **D.** Left pes track of *Sphingopus ferox* (IPS120433) with the common preservation state of tracks in Montmany. **E.** Densely bioturbated sandstone including vertical and horizontal cylindrical burrows. **F.** Potential wrinkle structures of a microbial mat on a fine- to very fine-grained sandstone. **G.** Desiccation cracks. **H.** Potential gypsum moulds (partially recrystallised with calcite). **I.** Mould of a hopper crystal. **J.** Distinct massive carbonate layer (arrow), probably a dolostone, bearing abundant *Rhynchosauroides tirolicus* footprints, and likely corresponding to a portion of the Arbolí Gypsum embedded within Guanta Sandstone siliciclastic red beds.

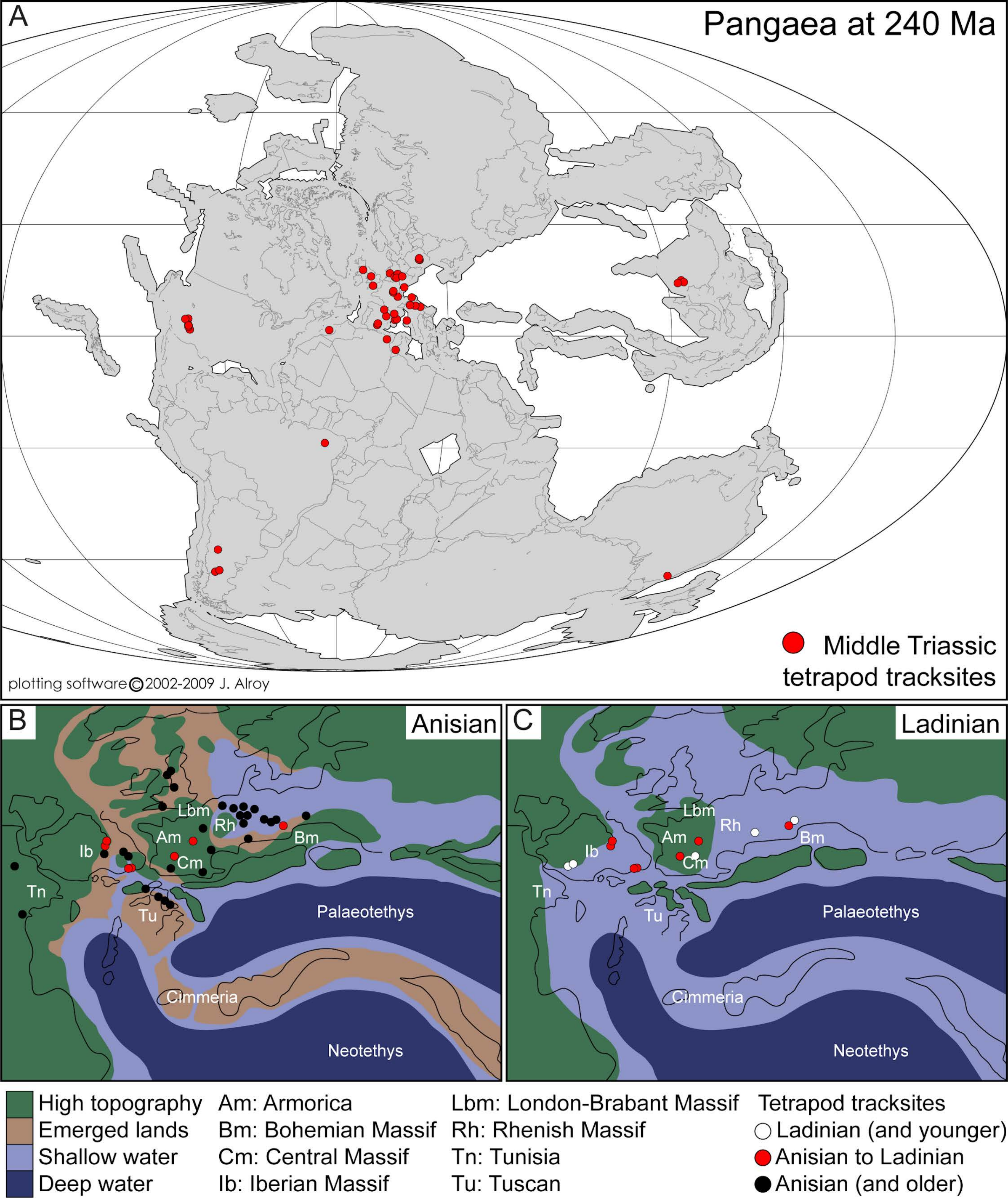
Figure 5. Middle Muschelkalk (Catalan Basin) tetrapod tracks I. **A.** Left track of *Procolophonichnium haarmuehlensis* with skin impressions in convex hyporelief (IPS106601b). **B.** Small right track of *P.* isp. in convex hyporelief (IPS120440). **C.** Trackway of *Chelonipus* isp. in convex hyporelief (IPS110268). **D.** Right manus track of *Rhynchosauroides tirolicus* with skin impressions in concave epirelief (IPS106605c). **E.** Right manus-pes set of *Rh. tirolicus* in convex hyporelief (IPS106617b). **F.** Tiny left manus-pes set of *Rh.* isp. in concave epirelief (IPS120439). **G.** Left track of *Rotodactylus* isp. in concave epirelief (IPS107033b).

Figure 6. Middle Muschelkalk (Catalan Basin) tetrapod tracks II. **A.** Two left manus-pes sets of *Chirotherium* cf. *sickleri* (with corresponding 3D colour-depth model) in

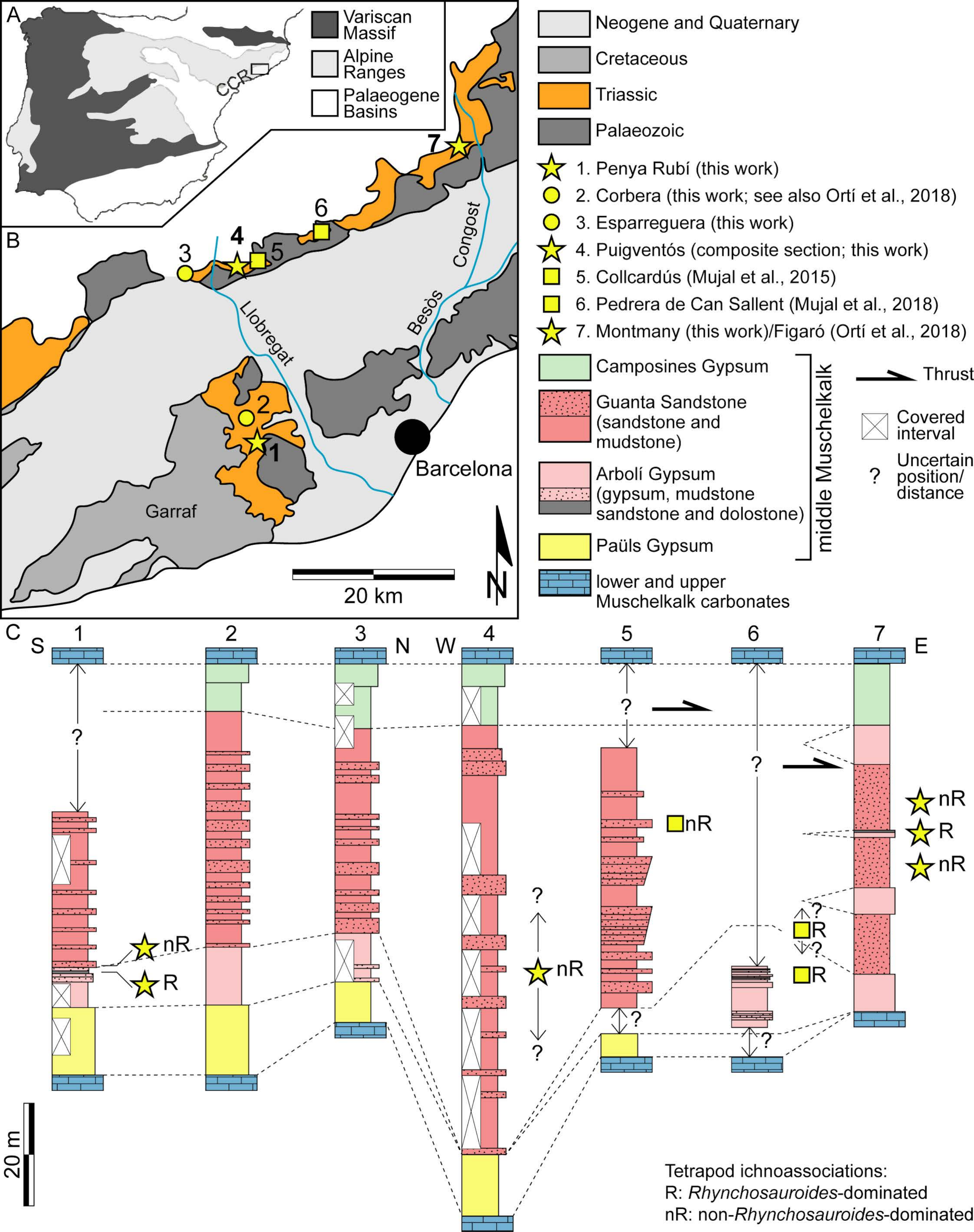
convex hyporelief (MGSB-26310). **B.** Left pes track of *C. barthii* with skin impressions in convex hyporelief (IPS85803), arrows point to hopper crystal moulds. **C.** Left pes track of *Isochirotherium* cf. *coureli*, with *Rotodactylus* isp. tracks (arrows) and *Rhynchosauroides tirolicus* above digit IV, in convex hyporelief (portion of IPS110269). **D.** Right manus-pes set of *Sphingopus ferox* (with corresponding 3D colour-depth model) in convex hyporelief (IPS120435). Roman numbers refer to digit imprints.

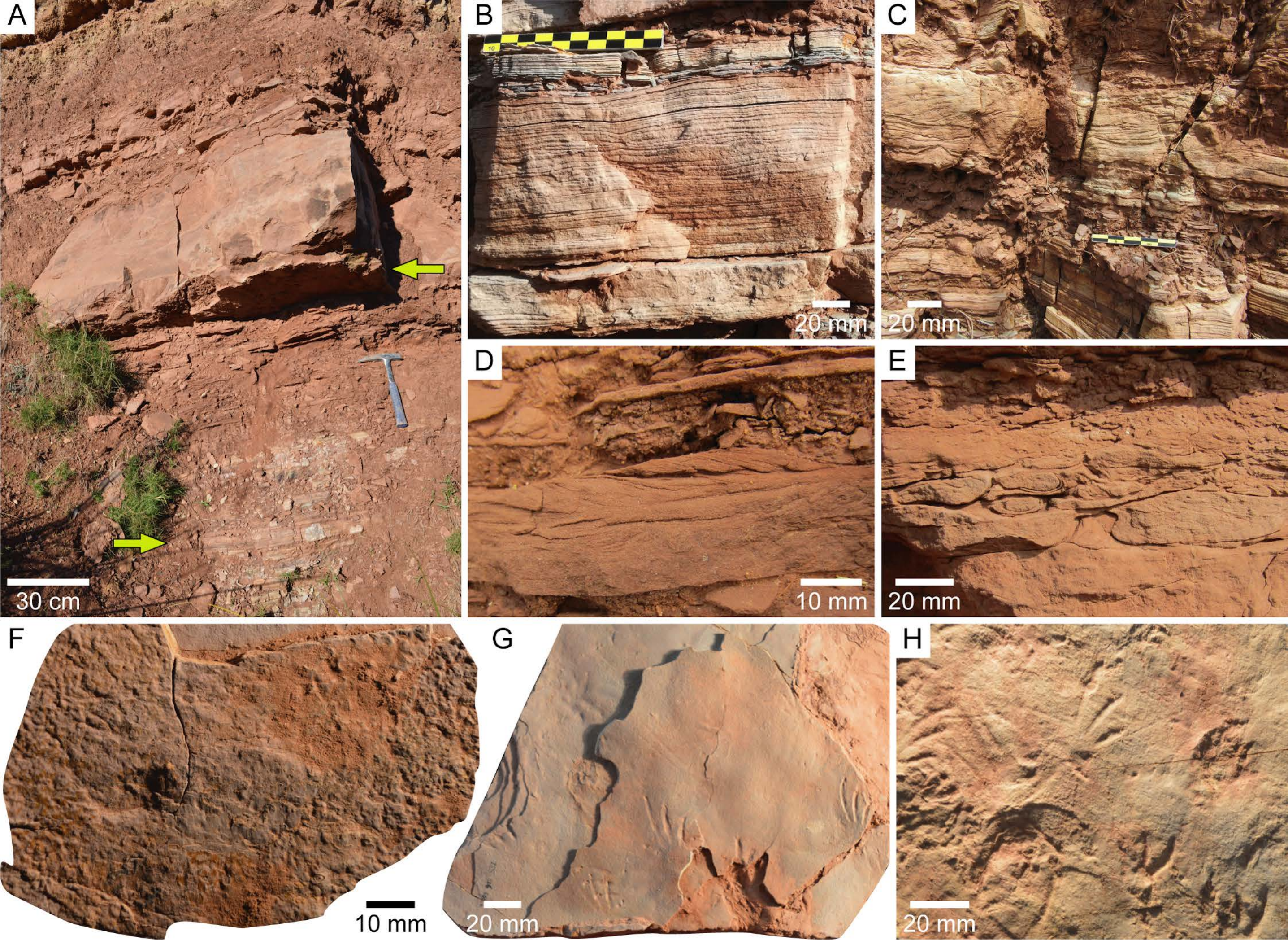
Figure 7. Occurrence of Middle Triassic tetrapod ichnotaxa and morphotypes based on Tables S1, S2 and S3. **A.** Percentage of occurrences of each ichnotaxon/morphotype within every defined palaeoenvironment; the number of total occurrences counted for each ichnotaxon/morphotype is above each bar; ichnotaxa and morphotype highlight in grey are those shown in **B**, whereas the rest are represented in “Others”. **B.** Ichnotaxon/morphotype relative proportions (percentages) in each palaeoenvironment; the graph shows the percentage that each ichnotaxon/morphotype represents in each setting; above each bar, the number of occurrences recorded in each setting is indicated. All ichnotaxa/morphotypes with less than 10 occurrences considering all regions/localities analysed (each being <4% of the total ichnodiversity) are included in “Others”. Data from both graphs correspond to presence/absence records of each ichnotaxon/morphotype without considering the absolute number of footprints from the analysed regions/localities.

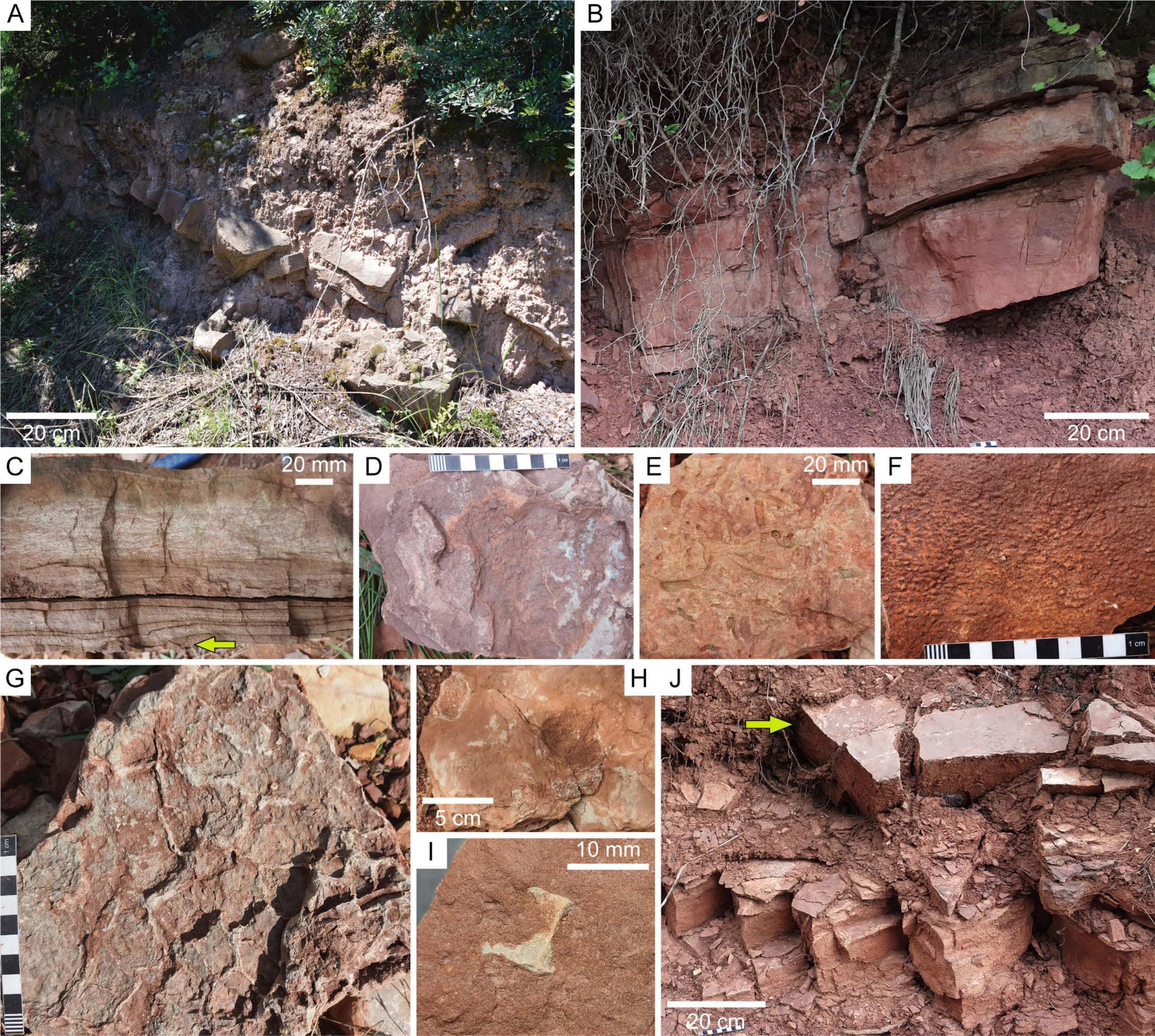
Figure 8. Idealised reconstruction of the Middle Triassic palaeoenvironmental settings showing the relative abundance of representative tetrapod (ichno-) taxa. Presence, distribution and relative abundance of tetrapod tracks is based on the references of Table S1, Fig. 7, and discussion in the text. Silhouettes are not to scale.



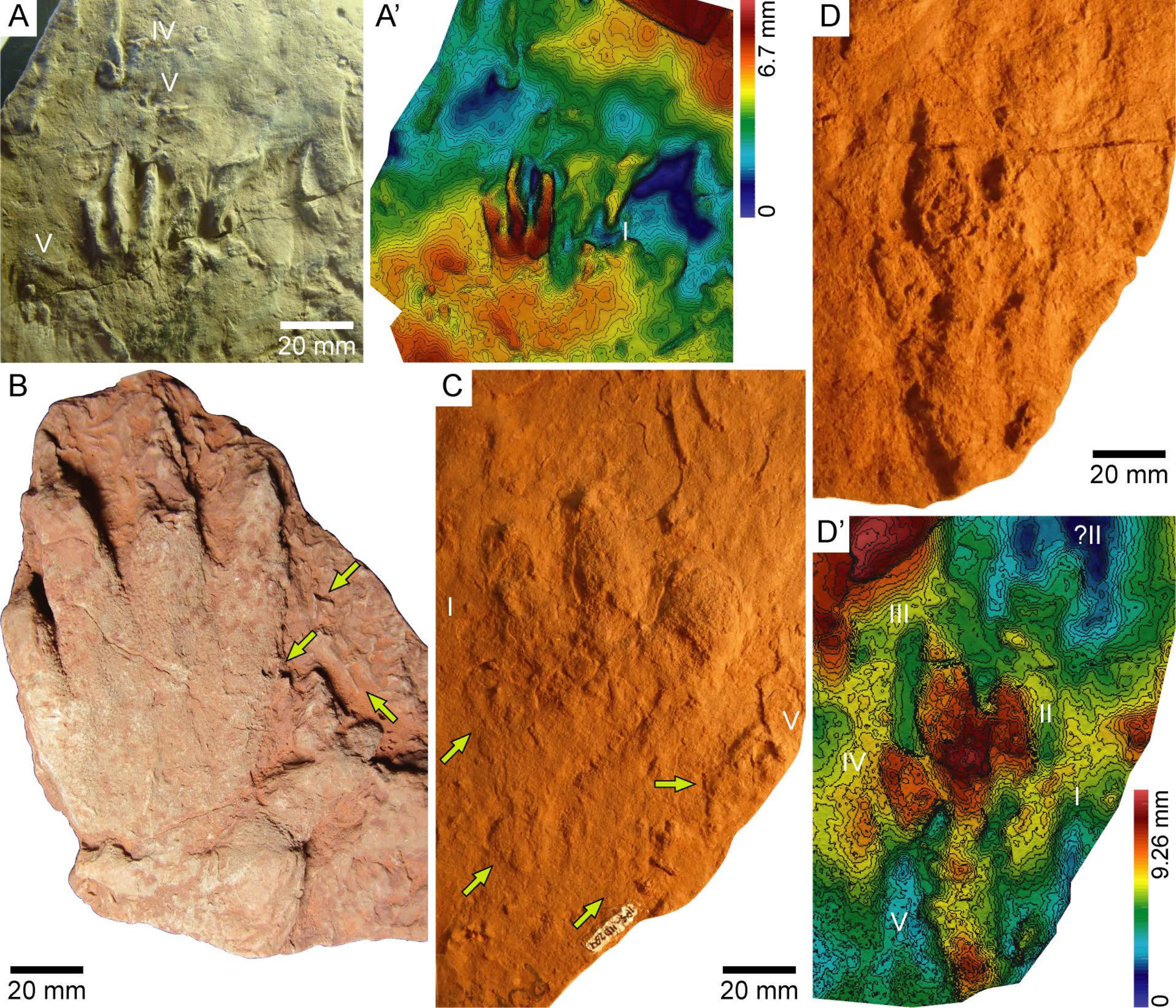
A
Pangaea at 240 Ma
● Middle Triassic tetrapod tracksites
plotting software © 2002-2009 J. Alroy
B
Anisian
C
Ladinian
Lbm
Rh
Am
Cm
Bm
Ib
Tn
Tu
Palaeotethys
Cimmeria
Neotethys
🟩 High topography
🟫 Emerged lands
🟦 Shallow water
🟦 Deep water
Am: Armorica
Bm: Bohemian Massif
Cm: Central Massif
Ib: Iberian Massif
Lbm: London-Brabant Massif
Rh: Rhenish Massif
Tn: Tunisia
Tu: Tuscan
Tetrapod tracksites
○ Ladinian (and younger)
● Anisian to Ladinian
● Anisian (and older)

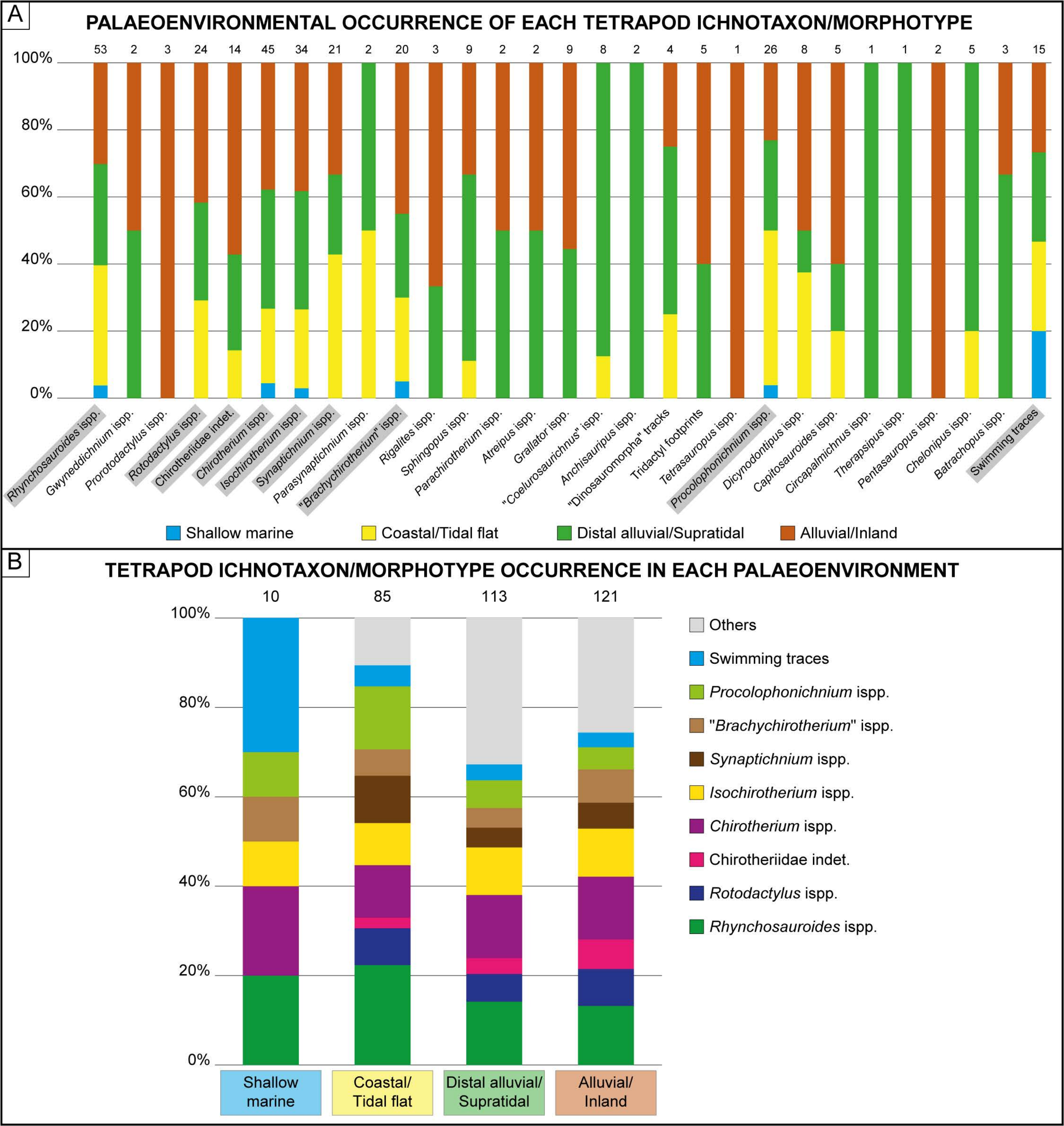

A
Variscan Massif
Alpine Ranges
Palaeogene Basins
CCR
B
1
2
3
4
5
6
7
Llobregat
Besòs
Congost
Barcelona
Garraf
20 km
N
Neogene and Quaternary
Cretaceous
Triassic
Palaeozoic
1. Penya Rubí (this work)
2. Corbera (this work; see also Ortí et al., 2018)
3. Esparreguera (this work)
4. Puigventós (composite section; this work)
5. Collcardús (Mujal et al., 2015)
6. Pedrera de Can Sallent (Mujal et al., 2018)
7. Montmany (this work)/Figaró (Ortí et al., 2018)
Camposines Gypsum
Guanta Sandstone (sandstone and mudstone)
Arbolí Gypsum (gypsum, mudstone sandstone and dolostone)
Paüls Gypsum
middle Muschelkalk
lower and upper Muschelkalk carbonates
Thrust
Covered interval
? Uncertain position/ distance
C
S
1
2
3
N
W
4
5
6
7
E
?
nR
R
20 m
Tetrapod ichnoassociations:
R: *Rhynchosauroides*-dominated
nR: non-*Rhynchosauroides*-dominated

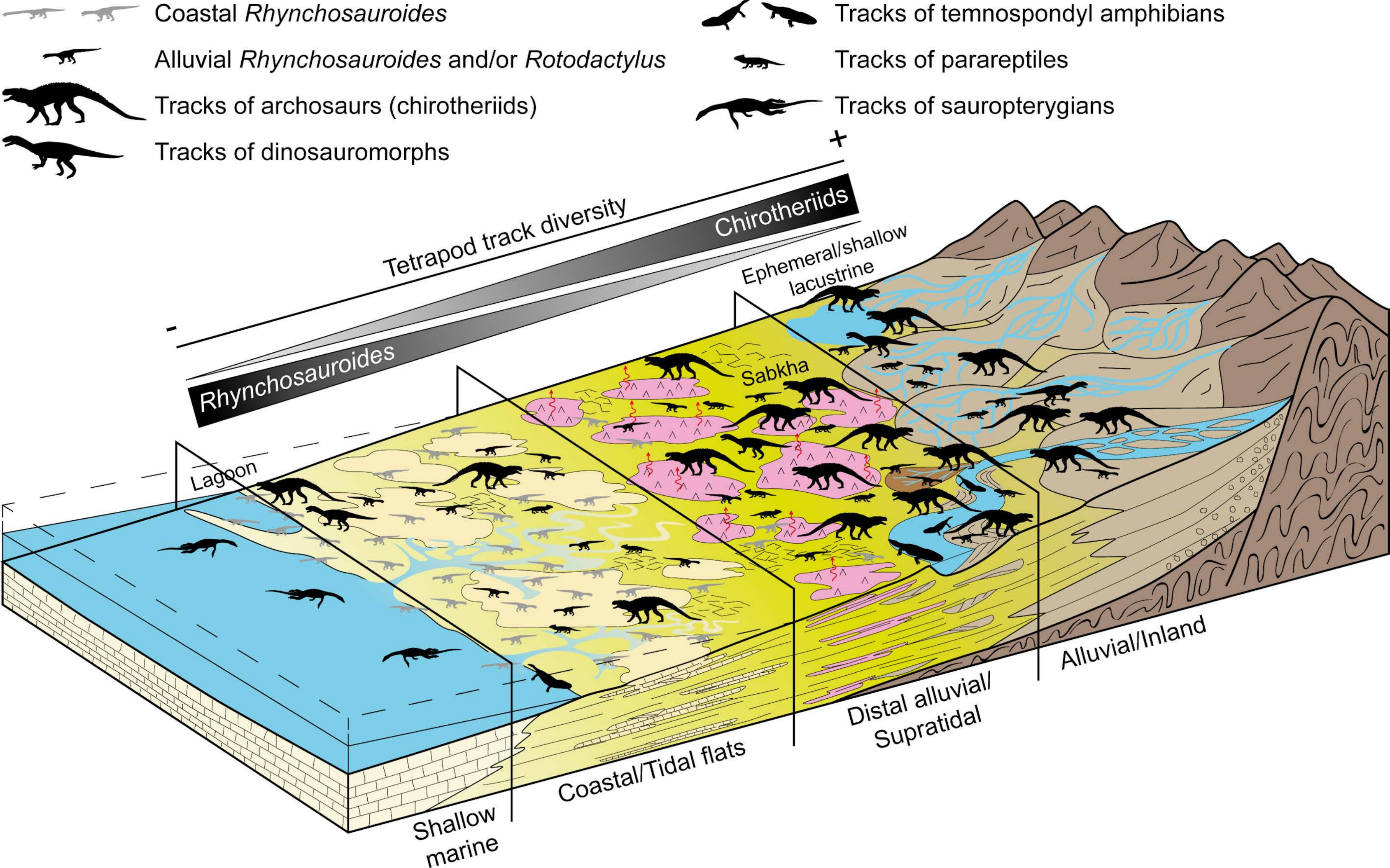

A
B
C
D
E
F
G
H
30 cm
20 mm
20 mm
10 mm
20 mm
10 mm
20 mm
20 mm


A
20 cm
B
20 cm
C
20 mm
D
1 cm
E
20 mm
F
1 cm
G
1 cm
H
5 cm
I
10 mm
J
20 cm


A
10 mm
B
5 mm
C
20 mm
D
10 mm
E
10 mm
F
5 mm
G
10 mm


A
IV
V
V
20 mm
A'
6.7 mm
0
I
D
20 mm
B
20 mm
C
I
V
20 mm
D'
?II
III
II
IV
I
V
9.26 mm
0


A
PALAEOENVIRONMENTAL OCCURRENCE OF EACH TETRAPOD ICHNOTAXON/MORPHOTYPE
53
2
3
24
14
45
34
21
2
20
3
9
2
2
9
8
2
4
5
1
26
8
5
1
1
2
5
3
15
100%
80%
60%
40%
20%
0%
Rhynchosauroides ispp.
Gwyneddichnium ispp.
Prorotodactylus ispp.
Rotodactylus ispp.
Chirotheriidae indet.
Chirotherium ispp.
Isochirotherium ispp.
Synaptichnium ispp.
Parasynaptichnium ispp.
"Brachychirotherium" ispp.
Rigalites ispp.
Sphingopus ispp.
Parachirotherium ispp.
Atreipus ispp.
Grallator ispp.
"Coelurosaurichnus" ispp.
Anchisauripus ispp.
"Dinosauromorpha" tracks
Tridactyl footprints
Tetrasauropus ispp.
Procolophonichnium ispp.
Dicynodontipus ispp.
Capitosauroides ispp.
Circapalmichnus ispp.
Therapsipus ispp.
Pentasauropus ispp.
Chelonipus ispp.
Batrachopus ispp.
Swimming traces
Shallow marine
Coastal/Tidal flat
Distal alluvial/Supratidal
Alluvial/Inland
B
TETRAPOD ICHNOTAXON/MORPHOTYPE OCCURRENCE IN EACH PALAEOENVIRONMENT
10
85
113
121
100%
80%
60%
40%
20%
0%
Shallow marine
Coastal/ Tidal flat
Distal alluvial/ Supratidal
Alluvial/ Inland
Others
Swimming traces
Procolophonichnium ispp.
"Brachychirotherium" ispp.
Synaptichnium ispp.
Isochirotherium ispp.
Chirotherium ispp.
Chirotheriidae indet.
Rotodactylus ispp.
Rhynchosauroides ispp.


Coastal *Rhynchosauroides*
Alluvial *Rhynchosauroides* and/or *Rotodactylus*
Tracks of archosaurs (chirotheriids)
Tracks of dinosauromorphs
Tracks of temnospondyl amphibians
Tracks of parareptiles
Tracks of sauropterygians
+
-
Tetrapod track diversity
Chirotheriids
Rhynchosauroides
Ephemeral/shallow lacustrine
Sabkha
Lagoon
Shallow marine
Coastal/Tidal flats
Distal alluvial/ Supratidal
Alluvial/Inland