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Registre sedimentari i icnològic del fini-Carbonífer, Permià i Triàsic continentals dels Pirineus Catalans

Evolució i crisis paleoambientals a l'equador de Pangea

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Tesi doctoral dirigida per:

Dr. Oriol Oms Llobet, Departament de Geologia, Universitat Autònoma de Barcelona

Dr. Josep Fortuny Terricabras, Institut Català de Paleontologia Miquel Crusafont

Dr. Oriol Oms Llobet

Dr. Josep Fortuny Terricabras

Eudald Mujal Grané

Capítol 7. *An archosauromorph dominated ichnoassemblage in fluvial settings from the late Early Triassic of the Catalan Pyrenees (NE Iberian Peninsula)*

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RESEARCH ARTICLE

An archosauromorph dominated ichnoassemblage in fluvial settings from the late Early Triassic of the Catalan Pyrenees (NE Iberian Peninsula)

Eudald Mujal^{1*}, Josep Fortuny^{2,3}, Arnau Bolet³, Oriol Oms¹, José Ángel López¹

1 Departament de Geologia, Universitat Autònoma de Barcelona, Bellaterra, Spain, **2** Centre de Recherches en Paléobiodiversité et Paléoenvironnements, Muséum National d'Histoire Naturelle, Bâtiment de Paléontologie, Paris, France, **3** Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP Building, Cerdanyola del Vallès, Spain

* eudald.mujal@gmail.com



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Abstract

The vertebrate recovery after the end-Permian mass extinction can be approached through the ichnological record, which is much more abundant than body fossils. The late Olenekian (Early Triassic) tetrapod ichnoassemblage of the Catalan Pyrenean Basin is the most complete and diverse of this age from Western Tethys. This extensional basin, composed of several depocenters, was formed in the latest phases of the Variscan orogeny (Pangea breakup) and was infilled by braided and meandering fluvial systems of the red-beds Buntsandstein facies. Abundant and diverse tetrapod ichnites are recorded in these facies, including *Prorotodactylus mesaxonichnus* isp. nov. (tracks possibly produced by euparkeriids), cf. *Rotodactylus*, at least two large chirotheriid morphotypes (archosauriform trackmakers), *Rhynchosauroides* cf. *schochardti*, two other undetermined *Rhynchosauroides* forms, an undetermined Morphotype A (archosauromorph trackmakers) and two types of *Characichnos* isp. (swimming traces, here associated to archosauromorph trackmakers). The Pyrenean ichnoassemblage suggests a relatively homogeneous ichnofaunal composition through the late Early Triassic of Central Pangea, characterized by the presence of *Prorotodactylus* and *Rotodactylus*. Small archosauromorph tracks dominate and present a wide distribution through the different fluvial facies of the Triassic Pyrenean Basin, with large archosaurian footprints being present in a lesser degree. Archosauromorphs radiated and diversified through the Triassic vertebrate recovery, which ultimately lead to the archosaur and dinosaur dominance of the Mesozoic.

Introduction

The earliest Mesozoic fossil record represents the life recovery and ecosystems turnover [1] after the loss of most species during the end-Permian mass extinction [2]. The environmental and climatic conditions hindered recovery of life on land, delaying the recovery until the

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Middle Triassic [3, 4]. Concerning the vertebrate non-marine fauna, several lineage pulses took place during the Early Triassic [4], but the role of the main tetrapod groups in the recovery, as well as their paleogeographic and environmental distribution, are still a matter of discussion.

The earliest Triassic non-marine tetrapod record (Induan to middle Olenekian) is only known from a few areas, such as the South-African Karoo Basin [5] and the Russian South Urals [1]. Most of the Early Triassic record is restricted to the late Olenekian, as occurs in the Western Tethys basins, mainly consisting of red-bed deposits of complex alluvial and aeolian continental systems [6–8]. The few Western Tethys vertebrate records, mostly footprints, are known from Morocco [9, 10], the Italian Southern Alps [11], southern Austria (the only known early Olenekian locality) [12], and the Catalan Pyrenees [8]. Further Lower Triassic records are found in the well-known archosaur-dominated tracksites from the Central European Germanic Basin [13–19], and in the Red Peak and Moenkopi formations of the USA [20–22].

In this contribution we present and discuss a diverse Triassic tetrapod ichnoassociation from the Catalan Pyrenees (NE Iberian Peninsula; Fig 1) framed in its stratigraphic and sedimentological setting. The reconstructed (ichno-) faunal assemblage and paleoenvironment (an archosauromorph-dominated fluvial setting) shed light on the paleobiogeography of the Early–Middle Triassic transition, as well as on the onset of continental vertebrate recovery after the end-Permian mass extinction.

Geological setting

The Catalan Pyrenees (NE Iberian Peninsula, S Europe) are a significant target to understand the late Paleozoic—early Mesozoic evolution in terms of paleontology and paleobiogeography, as long and continuous sedimentary successions ranging from the late Carboniferous to the Middle Triassic are recorded (Fig 1). The reference studies by Mey et al. [23] and Nagtegaal [24] defined the “post-hercynian” units containing the studied fossils. Séguret [25] and Zwart [26] performed the basic regional geology and mapping, while more recent works focused on tectonics and basin architecture and evolution [27–30]. Fortuny et al. [31] revised the vertebrate paleontological content, and Mujal et al. [8] revised and provided new data on the Permian-Triassic transition.

During the earliest Triassic, the continental Pyrenean Basin was arranged in several depocenters resulting from strike-slip (transtensional) tectonics developed in the latest phases of the Variscan cycle [27–30] related with the breakup of Pangea [32]. In this extensional regime, fluvial sediments covered the Variscan basement and the Carboniferous-Permian volcano-sedimentary sequences by means of an erosive angular unconformity (Figs 1 and 2). The resulting deposits are attributed to the syn-rift Buntsandstein facies, later overlaid by post-rift Muschelkalk and Keuper facies (Figs 2 and 3).

Material and methods

In order to provide a detailed geographical and geological framework, we mapped three fossil-bearing localities based on field tracking of strata and photointerpretation (Fig 1). We logged (by means of a Jacobs staff and a centimeter) and correlated bed-by-bed a total of nine stratigraphic sections (numbered I to IX from West to East; Fig 2). The sedimentary facies and architectural elements (Figs 3 and 4) were classified following nomenclature of Miall [33, 34] and further compared with those of Gretter et al. [30].

Tetrapod tracks and trackways (some represented in plastic films) were measured on both specimens and photographs (using ImageJ v.148, <http://rsbweb.nih.gov/ij/>) following Haubold

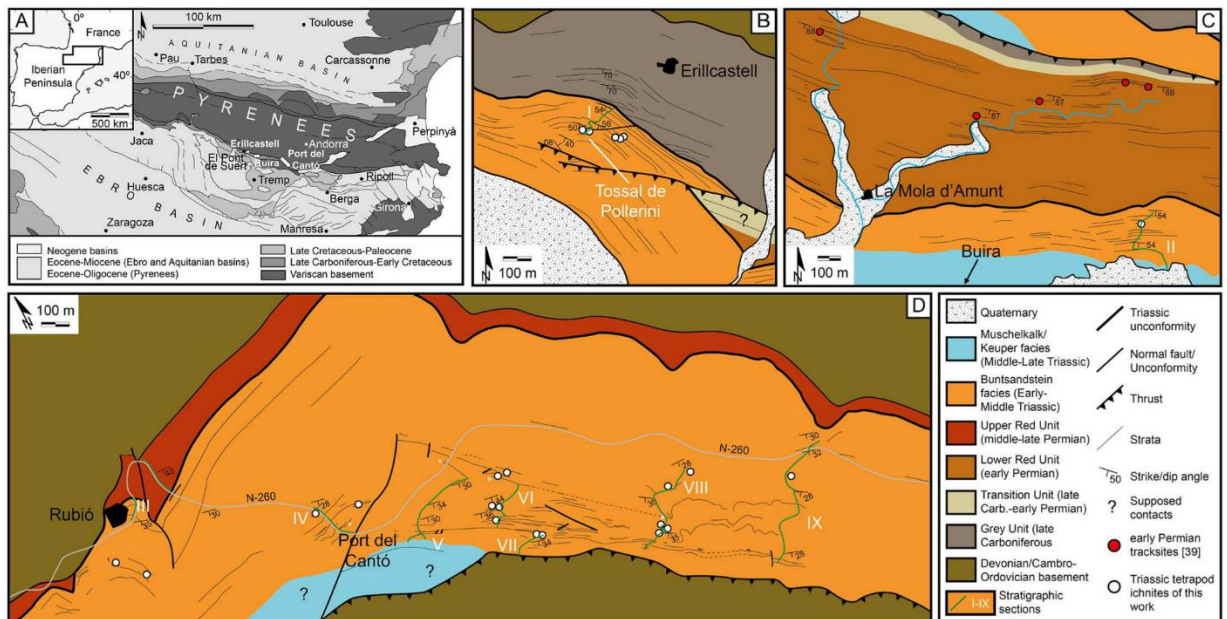


Fig 1. Regional setting and geological maps. (A) Situation of the localities in the Pyrenees. (B-D) Detailed geological maps of Erillcastell (B), Buira (C) and Port del Cantó (D) localities.

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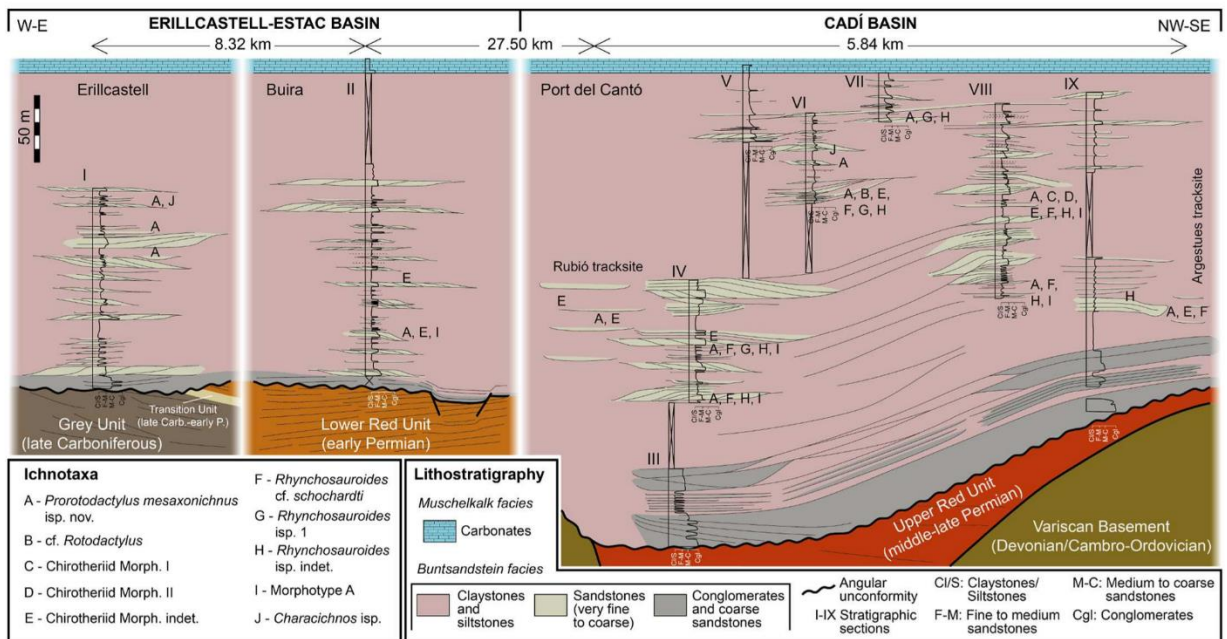


Fig 2. Stratigraphic correlation panel of the three studied localities. Triassic logged sections (I-IX) and location of tetrapod ichnotaxa (A-J).

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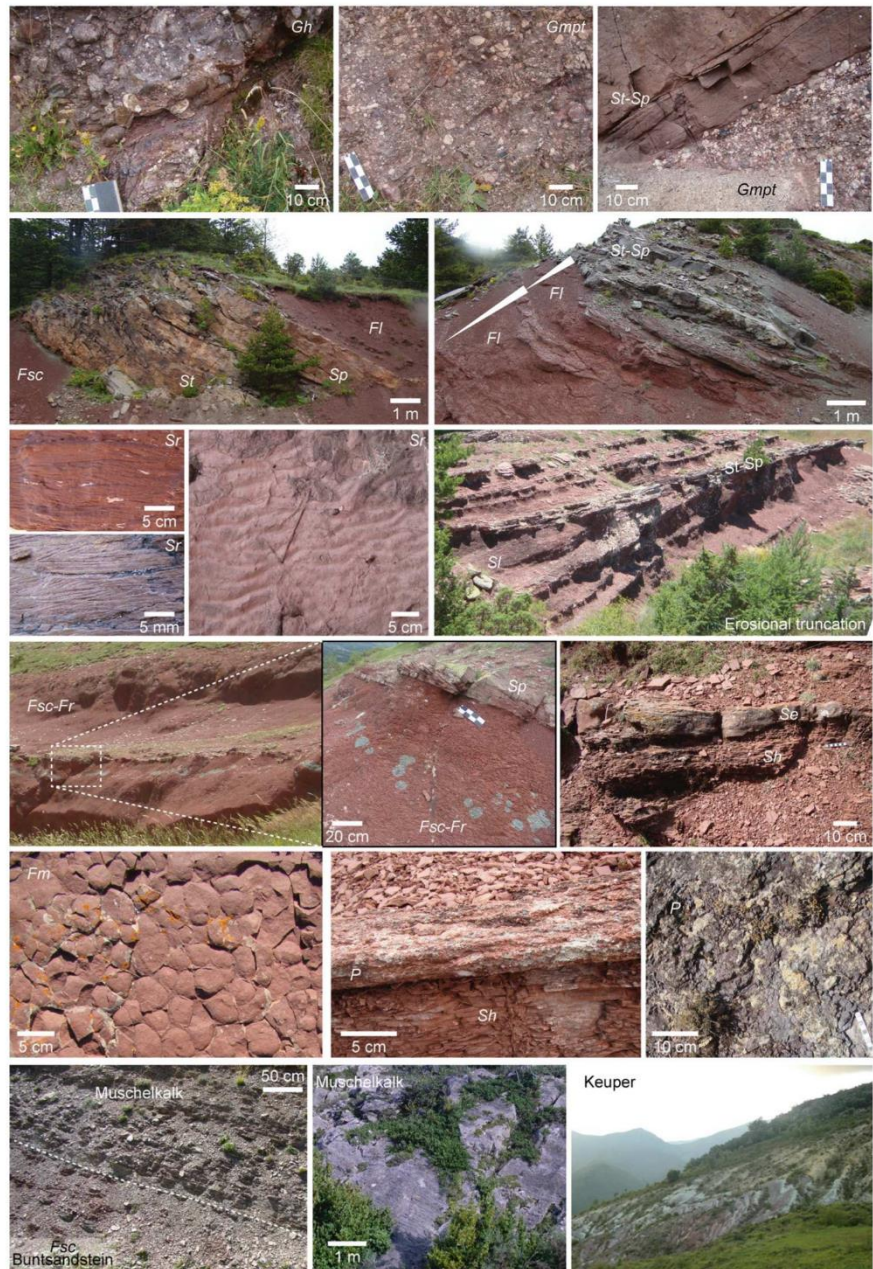


Fig 3. Triassic facies examples from the studied localities of the Catalan Pyrenees. Facies codes correspond to those of the text.

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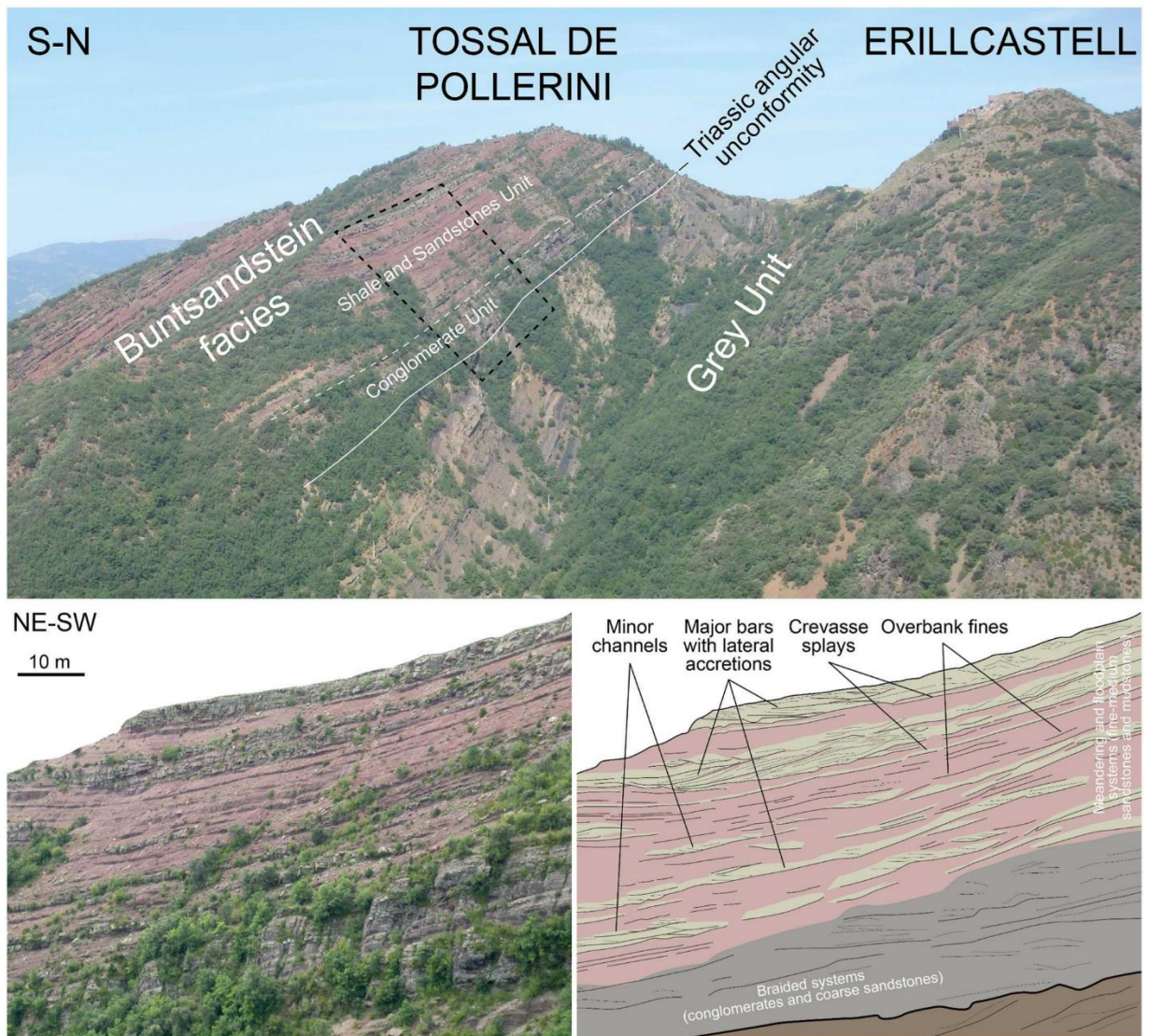


Fig 4. Buntsandstein fluvial facies at the Erillcastell locality, including the Tossal de Pollerini tracksite. The dashed black square in the top picture corresponds to the detail of the fluvial systems in the bottom photo.

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[35, 36], Leonardi [37] and Ptasiński [13]. Ichnites were outlined in transparency films and finally digitized with a vector-based drawing software. 3D photogrammetric models of selected specimens were performed using photographs obtained with a digital compact camera Sony T-200 8.1 megapixel following the procedures of Mallison and Wings [38] and processed with three open access software following the procedures of Mujal et al. [8, 39]: Visual SFM (v.0.5.22, <http://www.ccwu.me/vsfm/>) to generate the point cloud, MeshLab (v.1.3.2, <http://meshlab.sourceforge.net/>) to perform and edit the mesh (texture, scale, orientation) and

ParaView (v.4.1.0 <http://www.paraview.org>) to generate a color depth map and contour lines. High-resolution molds of tracks and trackways that could not be recovered were made with a two-component polyaddition silicone Harduplex[®] 23SH, acrylic resin (Acrysol Prima[®]) and glass-fiber. Once in the laboratory, a cast of each mold was produced with the same acrylic resin. Most of the studied specimens were found *in situ* and remained in the field, but those recovered and molds and casts are stored at the Institut Català de Paleontologia Miquel Crusafont.

Abbreviations

Institutional abbreviation: IPS, Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain. Studied specimens: IPS-73754, IPS-82611, IPS-82612, IPS-82613, IPS-82614, IPS-82615, IPS-82616, IPS-82617, IPS-82618, IPS-82619, IPS-82619, IPS-82620, IPS-82621, IPS-82622, IPS-82623, IPS-83739, IPS-83740, IPS-83743, IPS-83747, IPS-83748, IPS-83749, IPS-83750, IPS-83753, IPS-88716, IPS-88717, IPS-93867, IPS-93868, IPS-93869, IPS-93870, IPS-93872, IPS-93873, IPS-93874, IPS-93875

Sedimentary facies and architectural elements codes are modified from Miall [33, 34] and Gretter et al. [30]. Conglomerate facies: *Gh*, *Gmpt*. Sandstone facies: *St*, *Sp*, *Sr*, *Sh*, *Sl*, *Se*. Very fine-grained sandstone and mudstone (siltstone and claystone) facies: *Fl*, *Fsc*, *Fm*, *Fr*. Paleosol facies: *P*. Architectural elements: *CH1* (coarse-grained channels), *CH2* (medium- to fine-grained channels), *GB* (gravel bars), *SB* (sandy bedforms), *LA* (sand lateral accretions), *LS* (laminated sand sheets), *OF* (overbank fines).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "<http://zoobank.org/>". The LSID for this publication is: urn:lsid:zoobank.org:pub:B6C36C28-68EF-4F02-B6DD-3A0C8760CCD2. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Stratigraphy and sedimentology

The fossil-bearing unit corresponds to the redbed Buntsandstein facies, analyzed in three different areas, from W to E: Erillcastell (section I, of >151 m thick, including the Tossal de Polerini tracksite, Erillcastell-Estac basin), Buirra (section II, of >226 m, Erillcastell-Estac basin, at 8.32 km from Erillcastell) and Port del Cantó (sections III-IX, of 240 to 350 m, including the Rubió and Argestes tracksites, Cadí basin, at 27.52 km from Buirra) (Figs 1 and 2).

Three main units (*sensu* [28]) can be distinguished within the Buntsandstein sequences, from base to top: (a) conglomerate unit (oligomictic conglomerates of quartz pebbles and coarse sandstone with occasional breccia levels with lydite fragments), (b) shale and sandstones unit (reddish and greenish to greyish medium-coarse sandstones with some discontinuous conglomerate levels, reddish very fine to fine sandstones and reddish shales), and (c) shale unit (reddish shales with occasional thin but continuous sandstone beds as those of the shale and sandstones unit). It is worth noting that the thickness of each unit varies according to the basin configuration, and in some cases the conglomerate unit is even missing.

We identified 13 lithofacies (Fig 3), grouped in seven facies associations and constituting architectural elements characteristic from channel to floodplain environments (Fig 4). The sedimentological interpretations are based on our field observations and follow those of Miall [33, 34] and Gretter et al. [30]. Two facies (*Gh* and *Gmpt*) are conglomeratic (commonly of quartz pebbles, and either massive or with cross stratification and other water flow structures), mainly located and well developed in the basal conglomerate unit and constituting deposits of braided systems, such as channels and longitudinal bars (architectural element *CH1*) and gravel bars (architectural element *GB*). Six sandstone facies are found (*St*, *Sp*, *Sr*, *Sh*, *Sl* and *Se*), with grain sizes ranging from very coarse to very fine, and a wide variety of internal stratifications and water flow structures. In the conglomerate unit, facies *St* and *Sp* are in association with facies *Gh* and *Gmpt*, constituting the architectural element *CH1*, and all the sandstone facies constitute channel fills and minor bars of braided systems (architectural element *SB*). In the shale and sandstones unit, and occasionally in the shale unit, sandstone facies occur as meandering systems elements, constituting sandy bedforms (e.g., crevasse splay deposits) associated to lateral accretions (architectural elements *SB* and *LA*, respectively). Facies *St* and *Sp* are also displayed as small channels (in association with facies *Sr* and occasionally *Gh*; architectural element *CH2*). The laminated sand sheets (architectural element *LS*), such as crevasse splays, of the shale and sandstones unit are mainly constituted by facies *Sh* and *Sl*. Scour fill deposits are mostly constituted by facies *Se*. Four facies are related to siltstones and claystones with occasional very fine sandstones (*Fl*, *Fsc*, *Fm* and *Fr*). They mainly constitute floodplain deposits (with common greenish reduction marks associated to plant roots) associated to the meandering systems, which occasionally underwent subaerial exposure (identified by the desiccation structures). These facies are commonly displayed as overbank fines (architectural element *OF*). In the shale and sandstones unit and in the shale unit, levels related to pedogenic processes (paleosols, facies *P*) were identified: (1) scarce thin levels of carbonate nodules and (2) hardened intervals of facies *Fsc* with hydromorphic marks (large green mottles), root traces and slickensides.

A relevant association is the transition to the Muschelkalk facies. The facies *Fsc* of the shale unit are in transition to marls and fine laminated limestones corresponding to transitional/marine facies. At Port del Cantó, a thick sequence of dark red facies *Fsc* evolves to a laminated grey-greenish limestone/marl sequence. Although the top of the Buntsandstein sequence appears covered at Buira, the base of the Muschelkalk crops out and displays a breccia with Buntsandstein facies clasts embedded in a micritic limestone matrix.

The detailed descriptions and interpretations of facies and architectural elements are provided in the supplemental information (S1 Text). In general terms, the Buntsandstein fluvial succession is displayed as a fining upwards sequence grading from coarse-grained braided to finer meandering and floodplain fluvial systems (high to low energy) and is arranged as a growth strata onlapping onto the Carboniferous-Permian sequences or the Variscan basement (Fig 2). The long laterally-extended meandering sand bodies are interbedded within floodplain mudstone intervals.

Concerning the age of the Buntsandstein facies, Calvet et al. [40] provided palynological data from the shale unit, attributed to the early Anisian (early Middle Triassic). More recently, Mujal et al. [8] provided new palynological and ichnological data, giving an age of late Olenekian (late Early Triassic) for the lower-medium part of the shale and sandstones unit.

Systematic paleontology

The studied sequences yield a diverse tetrapod ichnoassemblage (Figs 2 and 5–13), including abundant footprints with extramorphological features (precluding ichnotaxonomic

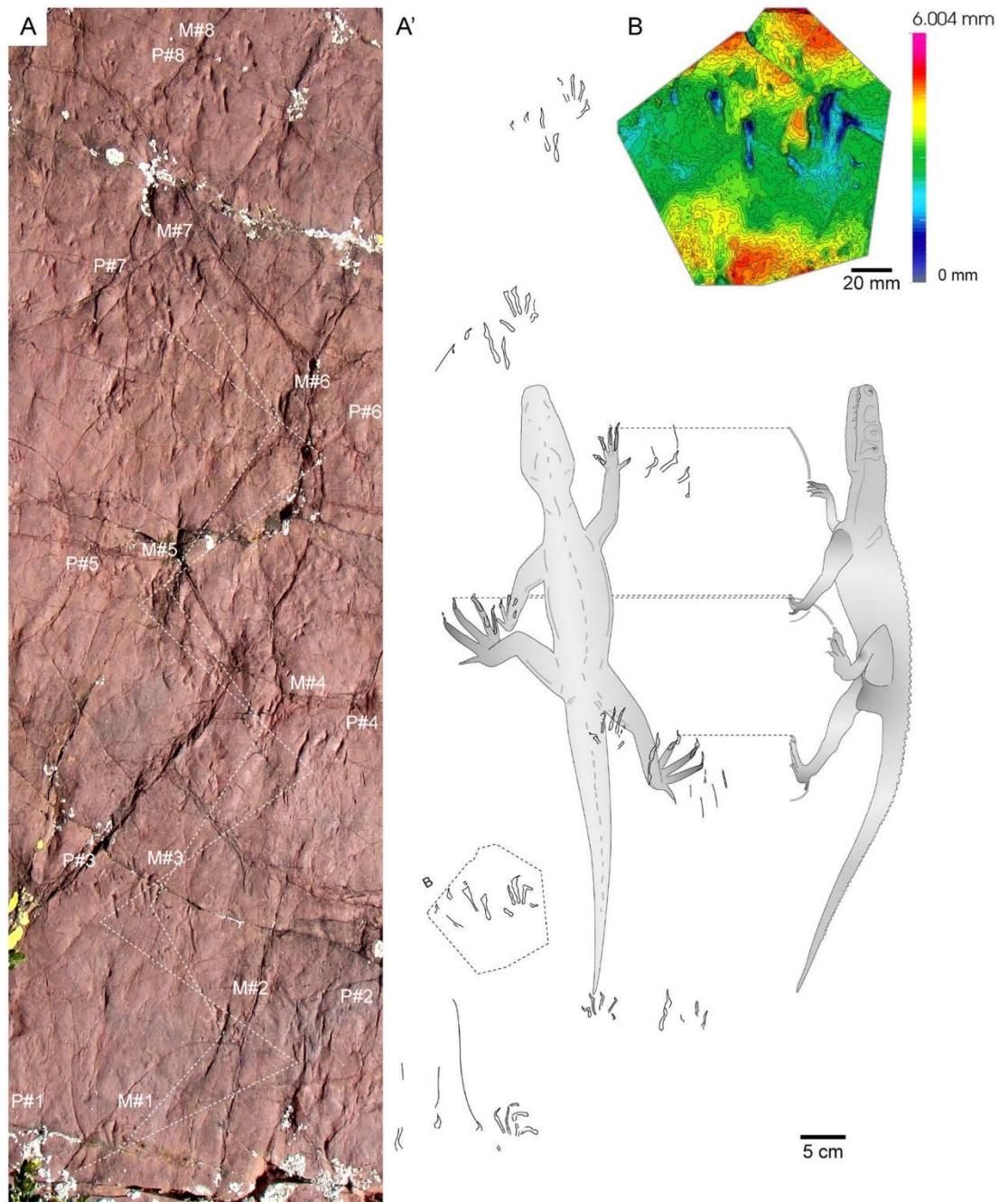


Fig 5. *Prorotodactylus mesaxonichnus* isp. nov. tracks I. (A) Trackway of the holotype (IPS-93870) and outline of the ichnites with the trackmaker (euparkeriid or basal archosauriform) silhouettes in plant view (idealized position in four consecutive tracks) and profile view (position during locomotion). (B) 3D photogrammetric model of a manus-pes set squared in (A).

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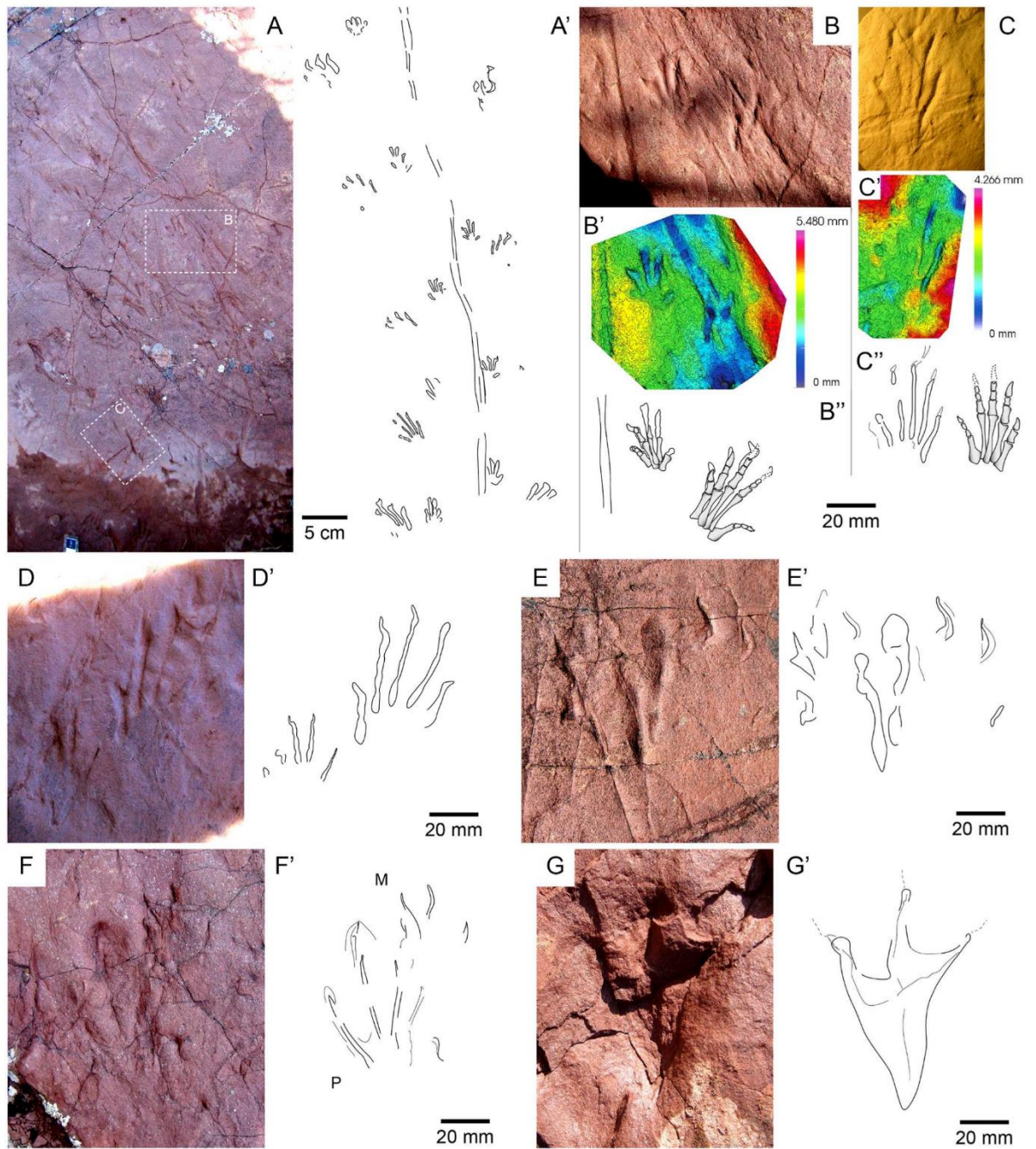


Fig 6. *Prorotodactylus mesaxonichnus* isp. nov. tracks II. (A) Trackway of the paratype IPS-93867 and outline of the ichnites. (B, C) Detail of a manus-pes set (B) and a pes track (C) of the trackway with the 3D models and correlated with the limbs of *Euparkeria capensis* (modified from Nesbitt, 2011 and Bernardi et al., 2015); note that bones and ichnites are at the same scale. (D) Paratype of a well-preserved pes completely overstepping the manus (IPS-93867). (E) Paratype of the manus-pes set of IPS-93871. (F, G) Right pes tracks with prevalence impression of digits II, III and IV (tridactyl function); M and P in (E) refer to manus and pes tracks, respectively.

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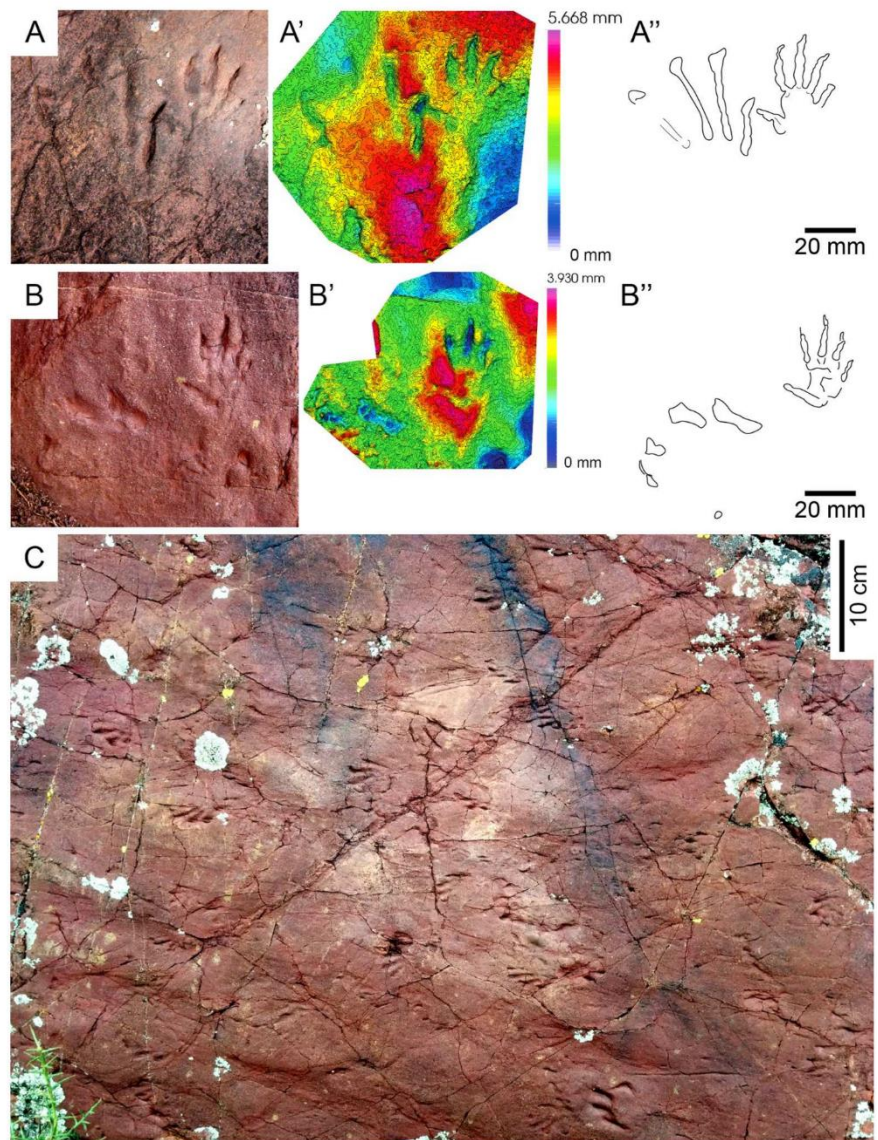


Fig 7. *Prorotodactylus mesaxonichnus* isp. nov. tracks III. (A, B) Manus-pes sets with 3D models and ichnites outline of the paratypes IPS-93868 (A) and IPS-93869 (B). (C) Trampled surface with most of the tracks advancing in the same direction (Westwards).

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assignment) related to locomotion and substrate conditions. Here we provide a detailed description of the identified tetrapod footprint morphotypes. We erect a new ichnospecies and emend the corresponding ichnogenus (monospecific until now), which was only known from the Central European Germanic Basin so far. Some ichnotaxa are equivalent to those of the Palanca de Noves tracksite (12 km Eastwards from Argestes tracksite) [8], thus here we provide additional remarks.

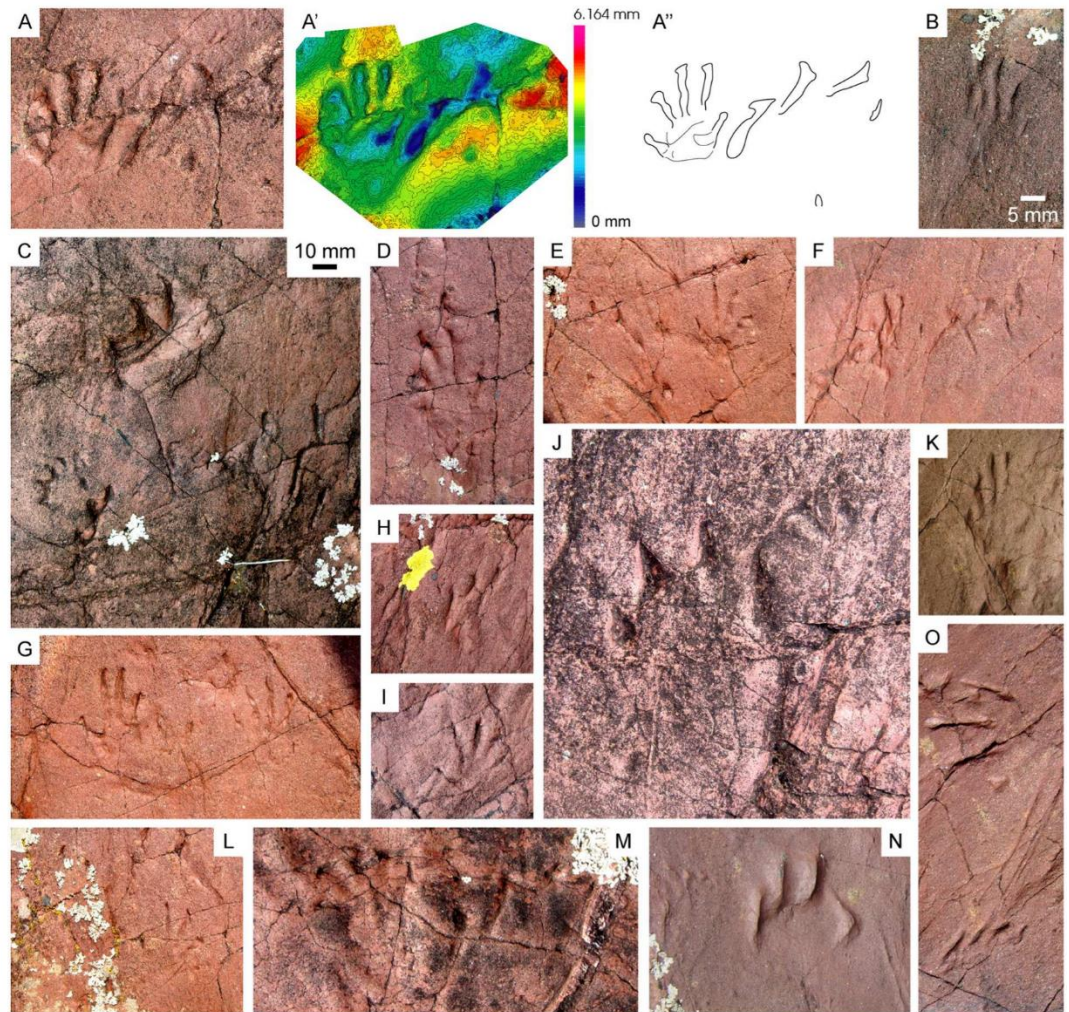


Fig 8. *Prorotodactylus mesaxonichnus* isp. nov. tracks IV. (A) Manus-pes set with the 3D model and ichnites outline. (B-N) Isolated sets, manus and pes tracks with different states of preservation. (O) Pes track with digit scratches and large pes with prevalence of digits II, III and IV. Note the characteristic hooked digit tips (D-G), tracks resembling *Rhynchosauroides* due to the dragging of digit tips (E, I). All tracks scaled at 10 mm except the manus in (B), which is at 5 mm. All tracks are from Tossal de Pollerini site (Erillcastell).

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The fossil assemblage of the studied localities also contains invertebrate trace fossils such as arthropod (limulid) body impressions (Fig 13L) and burrows (both horizontal and vertical; Fig 13M), root traces, trunk marks (Fig 13N) and plant stems (Fig 13O). Such remains deserve further analyses out of the scope of this work.

Ichnofamily Prorotodactylidae Ptaszyński, 2000

Ichnogenus. *Prorotodactylus* Ptaszyński, 2000

Type ichnospecies. *Prorotodactylus mirus* Ptaszyński, 2000

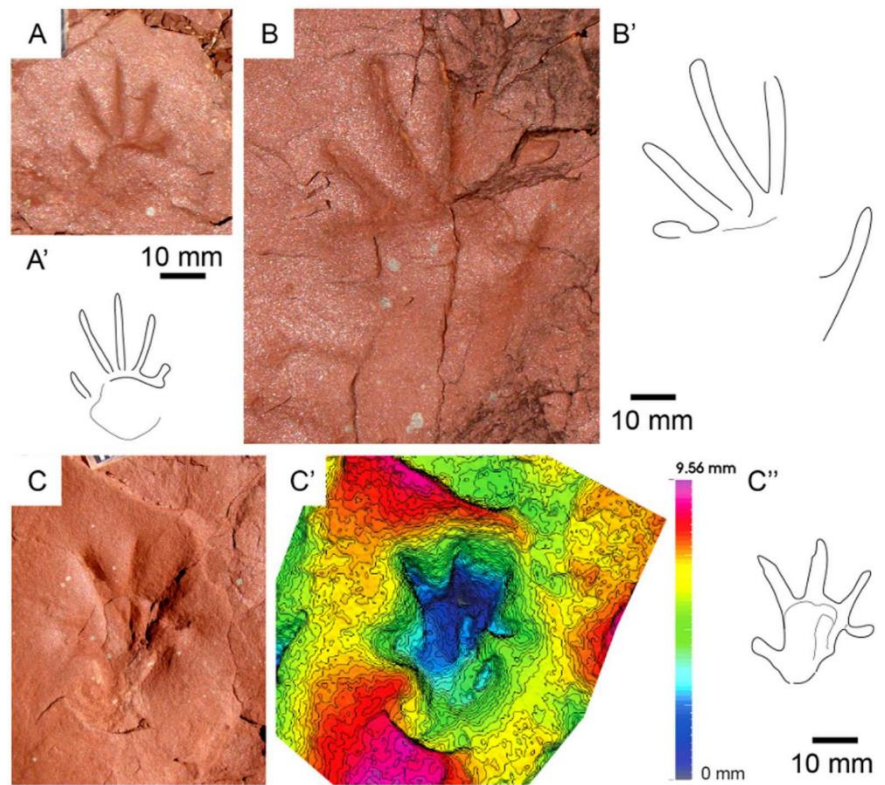


Fig 9. *Prorotodactylus mesaxonichnus* isp. nov. tracks V. Isolated impressions with a different preservation state (probably corresponding to undertracks or overtracks). Note the same kind of preservation despite tracks are small (A, C) or large (B). All tracks are from Port del Cantó, at sections VI (A), VIII (B) and VII (C).

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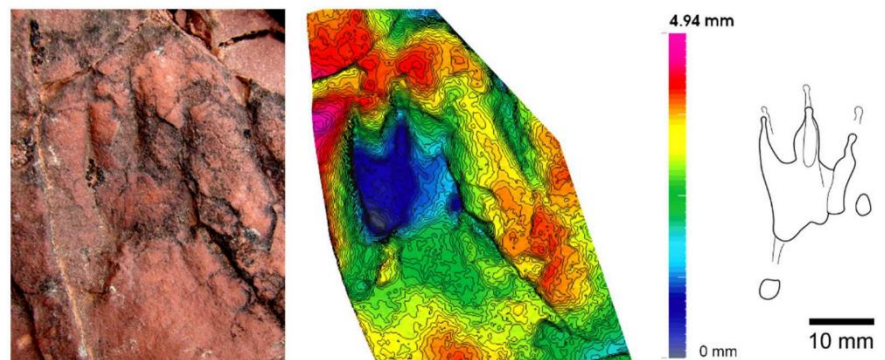


Fig 10. cf. *Rotodactylus* (Port del Cantó, section VI). Isolated manus track with the 3D model and ichnite outline. Note the longest digit III and the backwards rotated digit V.

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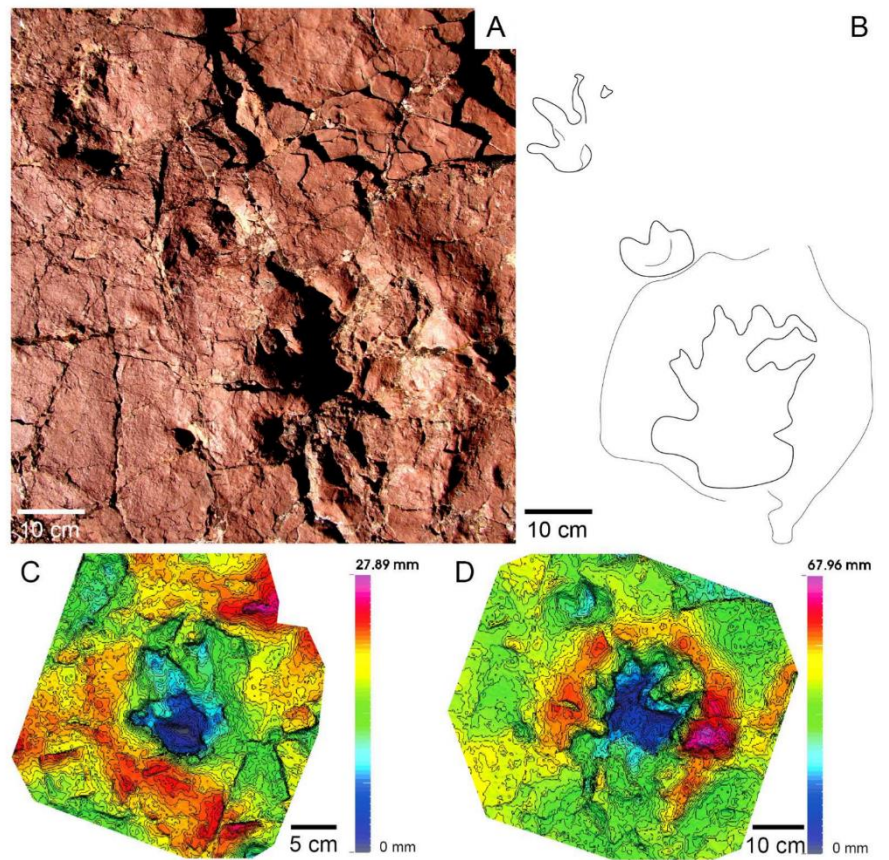


Fig 11. Chirotheriid Morphotype I (Port del Cantó, section VIII). (A) Manus-pes set (mold IPS-82616). (B) Ichinites outline. (C, D) 3D models of manus and pes tracks, respectively.

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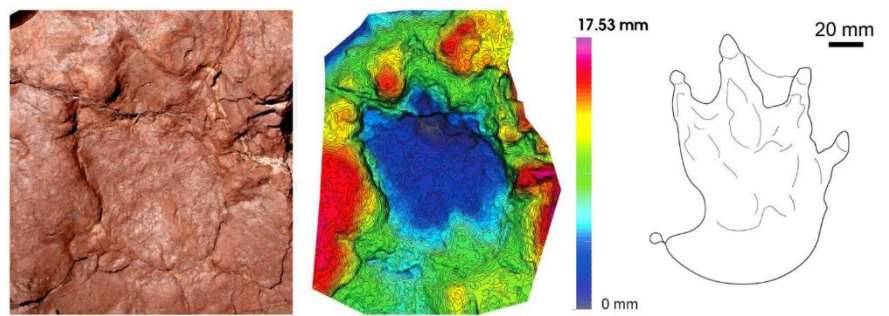


Fig 12. Chirotheriid Morphotype II (Port del Cantó, section VIII). Isolated ichnite with the 3D model and outline.

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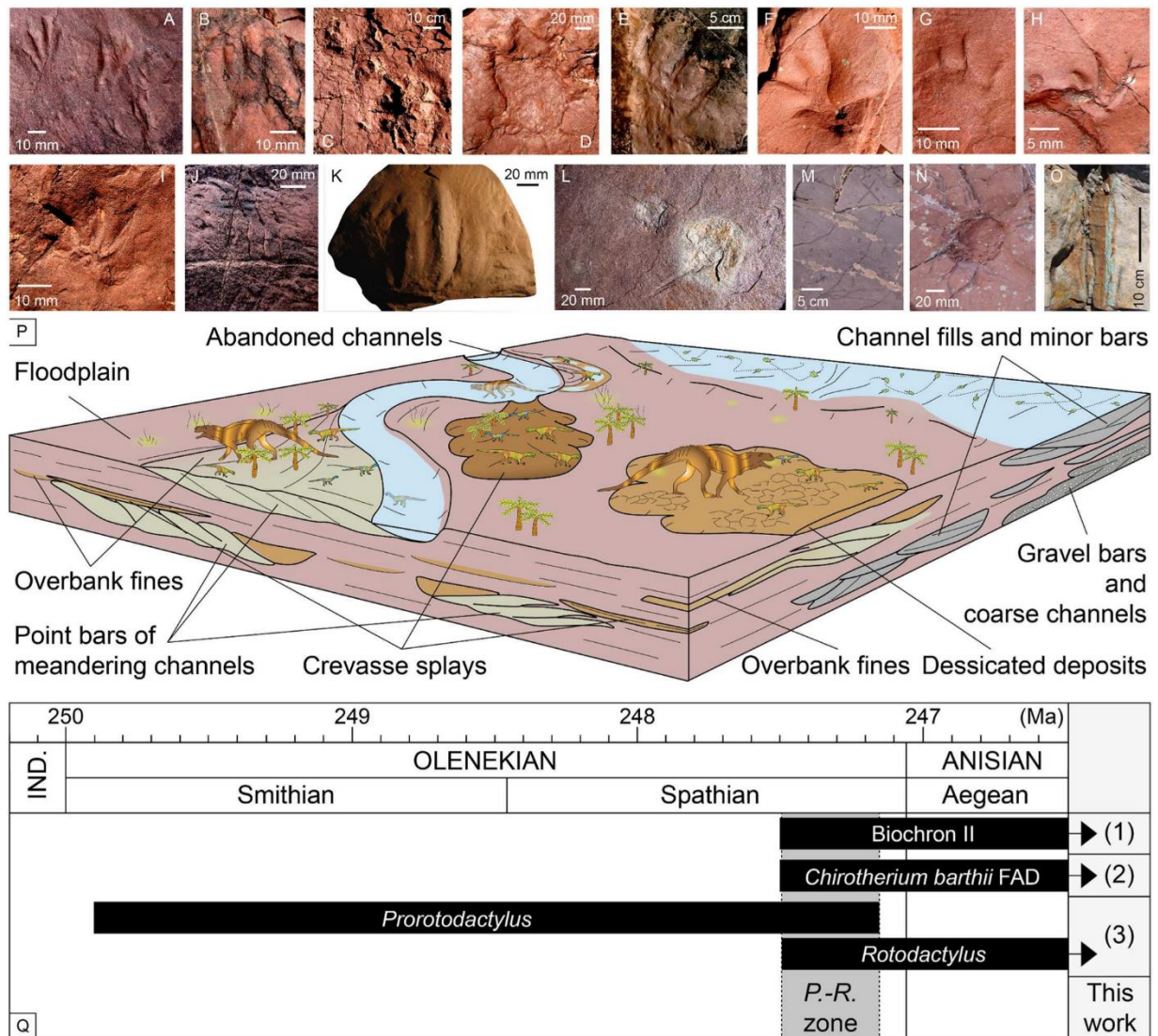


Fig 13. Fossil assemblage, paleoenvironment and biochronologic interval. (A) *Prorotodactylus mesaxonichnus* isp. nov. (B) cf. *Rotodactylus*. (C-E) Chirotheriid tracks: Morphotype I (C), Morphotype II (D) and Morphotype indet. (E). (F-H) *Rhynchosauroides* tracks: *R. cf. schochardti* (F), *R. isp. indet. 1* (G) and *R. isp. indet. (H)*. (I) Undetermined Morphotype A. (J, K) Swimming scratches of *Characichnos* isp. of small (J) and large (K) size. (L) Arthropod body impressions. (M) Invertebrate burrows. (N) Trunk mark. (O) Plant remain. (P) Paleoenvironmental reconstruction of the Triassic Pyrenean Basin (faunas and plants are not scaled). (Q) *Prorotodactylus*-*Rotodactylus* zone (P.-R. zone; grey interval) correlated with the Triassic biochronological intervals (see text for explanation of 1, 2 and 3). FAD: First Appearance Datum. IND.: Induan.

<https://doi.org/10.1371/journal.pone.0174693.g013>

Emended ichnogenus diagnosis. Trackways with small, lacertoid, pentadactyl pes and manus imprints. Manus overstepped laterally by the pes. Pace angulations of pes varying from 70° (low manus overstepping) to 135° (high manus overstepping). Pes outwardly and manus inwardly rotated with respect to the midline. Digits of both manus and pes are clawed. Digitigrade pes with digits I-III increasing in length, digit IV is either the longest or slightly shorter

Table 1. Minimum, maximum and mean values of the track parameters from the identified trackways of *Prorotodactylus mesaxonichnus* isp. nov.

Tracks	Length	Width	Digit I	Digit II	Digit III	Digit IV	Digit V	Length I-IV
Minimum Manus tracks	13.724	12.153	3.653	4.330	6.199	5.347	4.481	9.579
Maximum Manus tracks	50.288	35.813	14.831	23.128	33.219	27.521	18.878	41.791
Total Mean Manus tracks	37.167	24.088	13.190	17.425	22.953	21.014	12.447	31.248
Minimum Pes tracks	32.507	24.367	12.087	14.327	18.977	18.104	13.609*	25.649
Maximum Pes tracks	67.090	46.895	29.980	37.095	43.949	42.295	16.731*	57.781
Total Mean Pes tracks	45.453	29.989	18.147	22.988	27.475	25.215	15.170*	38.602
Tracks	Width I-IV	Div. I-II	Div. II-III	Div. III-IV	Div. IV-V	Div. II-IV	Div. I-IV	Div. I-V
Minimum Manus tracks	8.321	11.138	5.603	5.584	7.585	11.944	35.359	56.644
Maximum Manus tracks	26.957	40.409	23.523	21.858	83.372	40.771	68.518	142.220
Total Mean Manus tracks	22.867	20.748	15.731	11.883	33.477	27.494	48.606	84.424
Minimum Pes tracks	17.200	7.715	3.701	6.919	15.905	16.103	29.525	45.430
Maximum Pes tracks	53.513	19.818	21.135	20.917	57.596	40.805	58.114	87.825
Total Mean Pes tracks	29.657	14.348	13.240	12.744	33.768	25.941	40.177	71.865

*The mean length of the pedal digit V is not representative, as it is observed in few tracks and usually only preserved by the tip impression. Units in mm and degrees.

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than digit III, divarication angle between digits II and IV ranges from 10° (when digit IV is the longest) to 30° (when digit III is the longest). The metatarsal-phalangeal axis forming posterior end of digits II-IV is straight to slightly anteriorly convex. Digit I everted. Digit V rarely impressed, if present, in a postero-lateral position relative to digits I-IV. Manus semiplantigrade, of chirotheroid shape, compact and rounded with postero-laterally positioned digit V mostly impressed. Digit III always longest, followed by digits IV, II and I which is shortest.

New ichnospecies. *Prorotodactylus mesaxonichnus* isp. nov. urn:lsid:zoobank.org:act:B753A1A5-6946-49A5-9785-BA392F18842D (Figs 5–9 and 13A, Tables 1 and 2, S1 and S2 Tables, S1–S4 Figs).

Table 2. Mean values of the parameters from each identified trackway of *Prorotodactylus mesaxonichnus* isp. nov.

	IPS-93870	IPS-93867	S1A Fig	S1B Fig	S1C Fig	S1D Fig
Stride manus	294.884	136.039	277.403	250.021	374.792	-
Stride pes	286.771	138.725	267.456	250.335	-	-
Pace manus	182.603	89.830	156.814	144.288	202.42	72.23
Pace pes	257.069	156.955	204.186	228.978	-	82.615
Pace angulation manus	111.485	95.018	119.996	118.285	135.020	-
Pace angulation pes	69.668	53.437	78.700	66.246	-	-
Width pace manus	102.727	60.854	78.889	73.074	75.688	-
Width pace pes	211.174	138.184	160.036	189.776	-	-
Manus-Pes distance	62.802	49.778	46.597	59.786	49.782	32.072
Div. manus midline	7.074	-3.601	3.084	0.629	-6.629	0
Div. pes midline	51.073	46.983	30.608	49.283	72.552	-
Div. manus-pes digits III	38.361	42.867	29.567	48.497	92.439	-
Glenoacetabular distance	178.161	96.440	145.866	141.065	-	-
Glenoacetabular Standard deviation	21.537	5.581	10.014	5.563	-	-

Units in mm and degrees.

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Etymology. *mesaxonichnus* refers to the longest digit III (mesaxyony) of both manus and pes tracks.

Holotype. Trackway composed of 8 manus-pes sets (mold and cast IPS-93870; Fig 5).

Paratypes. Trackway with tail trace (mold and cast IPS-93867; Fig 6A and 6B), manus-pes sets settled in different trackways (molds and casts IPS-93867, IPS-93868 and IPS-93869; Figs 6D, 7A and 7B, respectively), isolated tracks and manus-pes sets corresponding to IPS-88716, IPS-88717, IPS-93872, IPS-93873 and IPS-93875.

Locality and horizon. Tossal de Pollerini tracksite (at 143.8 m of section I, Buntsandstein facies of Erillcastell, Pyrenean Basin), late Olenekian (Early Triassic). El Pont de Suert (Alta Ribagorça, Catalonia, Spain). GPS coordinates (WGS 84 UTM 31T): 318791E, 4698889N.

Referred specimens and stratigraphic position. At Erillcastell (Tossal de Pollerini tracksite), several trampled surfaces with five recognized trackways (including those of the holotype and paratypes), manus-pes sets and isolated tracks (>200 tracks) at 96.00 m, 115.00 m and 137.00–143.90 m of section I, and one *ex situ* isolated track (IPS-93874). At Buiria, one trackway and several manus-pes sets and isolated tracks at 31.00 m of section II. At Port del Cantó, several isolated ichnites and manus-pes sets (including IPS-82613, IPS-82617, IPS-82618, IPS-82623, IPS-83749), one poorly preserved trackway (mold IPS-82619) at 72.10 m of section VIII, and isolated tracks at 0–0.60 m and 41.30 m of section IV, at 2.00 m and 30.70 m of section VI, at 1.30 m and 2.40 m of section VII, at 0.70–1.20 m, 68.00 m (including mold IPS-82614 from a deformed ichnite), at 70.50 m and 72.10 m of section VIII, and at tracksites of Rubió (including IPS-83753) and Argestes (including IPS-83739 and IPS-83740).

Diagnosis. *Prorotodactylus mesaxonichnus* isp. nov. is distinguished from other specimens of the ichnogenus by the following combination of character-states: pes tracks digitigrade (digits I, II, III) to unguigrade (digit IV) with digit V rarely impressed and with a relative digits length of $I < V < II < IV < III$. Pedal digit impressions are straight to slightly curved and separated one of each other, with digit I slightly posteriorly positioned respect to digits II, III and IV and digit V rotated outwards. The metatarsal-phalangeal axis forming posterior end of digits II–IV is always slightly anteriorly convex. Mean pace angulation is about 118° in manus and 70° in pes tracks. A slightly sinuous tail trace is preserved in some trackways.

Description. *Tracks*—Pentadactyl longer than wide ichnites. Manus tracks (14–41 mm long) are usually semiplantigrade but also digitigrade, pes tracks (38–60 mm long) are digitigrade to unguigrade (Figs 5–8 and 13A, S1–S4 Figs, Table 1, S1 Table). The shape of the manus tracks is similar to that of chirotheriid pes footprints. Manus and pes footprints are similar in digit proportions, positions and angulations. In both, digit III is the longest, followed by digit IV and digit II. Digit I is much shorter than the other digits. The length of digit V is between digits I and II, and in some manus tracks digit V presents a relatively large pad impression, starting below digit IV. Digits I to IV are straight, digit V is also straight, but posteriorly positioned and directed outwards. Some manus tracks present scratches connecting to the digit tips, which became slightly curved inwards, and digit IV presents a slightly longer trailing scratch than digit III. Manus are usually deeper and commonly better preserved than pes tracks. In manus tracks, digits II, III and IV are the most deeply impressed (digits deepness: $III > IV \geq II$) and form a compact group with a slightly concave proximal line (i.e., the proximal margin of digit III is in a slightly more anterior position than those of digits II and IV; Figs 5B, 6B, 7A, 7B and 8A). In the manus tracks, digit I is close to digits II, III and IV, but posteriorly positioned. A large expulsion rim is observed between manus digits IV and V (Figs 5B, 7B and 8A). In pes tracks, digit I is posterior to digits II, III and IV (forming a slightly convex arch) as in manus tracks. The pedal digits I and II are “bottle-shaped” (the proximal part with an elongated oval-shape, the medial-distal part being the narrowest and the distal part and the tip nearly as wide as the proximal part). The deepness of digits decreases from I to V in pes

impressions, digits I and II being much deeper than the rest. Pedal digit IV is commonly preserved by the tip and a faint impression of the phalangeal portion (Figs 5B, 6B–6E, 7A, 7B and 8A). Pedal digit V is preserved in few tracks and mostly by the tip (Figs 6B, 6E, 6F, 7B and 8A), the phalangeal impression is rarely observed (Fig 6C and 6D), showing that digit V is slightly longer than digit I. Divarication of digits I–IV is relatively low (48.4° in manus and 40.7° in pes tracks; Table 1, S1 Table). Phalangeal pads are well-preserved in some manus tracks (formula 2-2-3-2-2; Fig 7A and 7B, S2 Fig). Some pes tracks also preserve faintly impressed phalangeal pads (Figs 6B, 6C and 7A). The tips of digits I to IV in both manus and pes tracks are often characteristically hooked (convex to the inner part), with an asymmetric T-shape. Some pes tracks present a particular shape, mostly preserving digits II, III and IV (being digit III the deepest), which are divergent and giving a symmetric shape to the impressions (Figs 6F, 6G and 8O). These pes footprints are mostly isolated or in manus-pes sets (but not included in trackways), but are found in surfaces with tracks with the previous described shape and with digit tip scratches. In the area of Port del Cantó several isolated tracks with the morphological traits described above can be identified (Fig 9, S3 and S4 Figs), although the footprints are smoothed as they probably correspond to undertracks or overtracks, and/or were possibly deformed or partially eroded by the water flow soon after their impression.

Trackways—Six trackways of alternating manus-pes sets are recognized (Figs 5A and 6A, S1 Fig). The pace angulation of the manus varies from 94.5° to 135° and is commonly about 118° . The pace angulation of the pes varies from 59° to 90° and is commonly of $64\text{--}74^\circ$ (Table 2, S2 Table). Pes tracks are commonly postero-laterally (but also laterally) positioned respect to manus, and rotated outwards (commonly $45\text{--}55^\circ$) from the midline. When settled in sets, the pes tracks with symmetric shape (prevalence of digits II, III and IV) completely overstep manus tracks (pes tracks are antero-laterally positioned with respect to the manus). Manus tracks are mostly parallel to the midline, but in some specimens are rotated either inwards or outwards (Figs 5A and 6A, S1 Fig). Some pes tracks have arched (convex outwards) digit scratches (Figs 5A and 8O). Relatively wide and slightly sinuous tail impressions are preserved in some trackways, as in the paratype IPS-93867 (Fig 6A, S1A and S1C Fig).

Discussion. The relative length of the manus digits ($I < V < II < IV < III$) and the general shape of the manus, being similar to the chirotheriid pes tracks, are diagnostic of *Prorotodactylus* [13, 16, 19]. Nevertheless, several features substantially differ from the unique well-established ichnospecies, *Prorotodactylus mirus*, as well as from the resembling ichnogenera *Rotodactylus* and *Rhynchosauroides*: (a) The pedal digit proportions (with digit III the longest) and their relative deepness (decreasing from I to V), (b) the pes tracks much larger than manus, (c) the pedal digit impressions separated on from each other, (d) the characteristically hooked (convex to the inner part) or also T-shaped digit tips (clawed) of both manus and pedes, (e) the low pace angulations (about 118° in manus and $64\text{--}74^\circ$ in pedes), (f) the postero-lateral position of the pes respect to the manus tracks, (g) the outwardly rotated pedes and the parallel manus from the midline, and (h) the presence of slightly sinuous tail impressions. The trackway parameters (relatively low pace angulations) are similar to those of *Rhynchosauroides*. However, a diagnostic feature of *Rhynchosauroides* is the longest digit IV in both manus and pes tracks, whereas in the Pyrenean tracks digit III is the longest, thus precluding the assignation to *Rhynchosauroides*. Similarly, the chirotheriid pes-like shape of manus tracks is a character shared by both *Prorotodactylus* and the herein reported tracks, but not found in *Rhynchosauroides*. Trackway parameters are linked to the body plan and relative length of trackmakers limbs, but are also highly influenced by the locomotion gait, as well as by the substrate conditions. Thus, the morphological characters of the tracks (e.g., length, width, relative length of the digits, etc.) present less variation than trackway parameters. In all, the

combination of features of these Pyrenean tracks is consistent with the existence of a different and new morphotype for *Prorotodactylus*.

Until now, *Prorotodactylus* tracks were only known from the Germanic Basin [13, 15–19], and possibly from the French Lodève Basin [13, 41]. Ptaszyński [13] reassigned “*Rhynchosauroides lutevensis*” of Demathieu [41] to *Prorotodactylus lutevensis* based on the similarity of the manus tracks with the Polish *Prorotodactylus*. “*Rhynchosauroides lutevensis*” was erected upon a single trackway composed of three manus-pes sets. The characters of the French tracks are also similar to those herein reported (e.g., shape of pedal digits and pes pace angulation of 96°), but differ in the pedal digit IV, which is the longest in the French tracks, as in the Polish *Prorotodactylus*. We agree with Ptaszyński [13] on the assignation of the French trackway to *Prorotodactylus*, but with an open ichnospecies nomenclature, because further and more complete specimens and trackways are needed (e.g., no impressions of the pedal digit V are recognized) [41] and so other features (e.g., pace angulation, relative manus-pes position and relative digits length) are possibly linked to extramorphologies (i.e., substrate conditions and speed locomotion). In the nearby Palanca de Noves site (12 km eastwards from Argestues tracksite), Mujal et al. [8] identified an isolated manus-pes set referred to a *Prorotodactylus-Rotodactylus* plexus. The new Pyrenean tracks described here confirm the presence of *Prorotodactylus* in the Western Tethys, which present differences with the specimens from the Central European Germanic Basin.

The slightly outwardly rotation of some manus, the high expulsion rim in the outer side and the hooked digit tips indicate that the forelimbs were directed outwards during the impression and inwards during the rising, describing a sinusoidal movement. The scratches in some pedal digits describe a laterally-arched movement of the hindlimbs, being similar to that of the elongated trailing traces of the manus digit IV. The wide standard deviation of the glenoacetabular distances (Table 2, S2 Table) and the sinusoidal shape of the tail impression suggest a lateral torsion of the trackmaker body trunk. Together with the low pace angulations and the relative wide trackways, a quadrupedal sprawling to semi-erect locomotion is inferred (Fig 5). The tail impressions, mostly associated to trackways with low pace angulations, would indicate a relatively slow locomotion. Noteworthy, the pedal impressions with a prevalence function of digits II, III and IV (tridactyl shape similar to dinosaur tracks), anteriorly positioned to manus impressions, or not being associated with manus (nor other tracks) suggest a potential occasional faster (i.e., cursorial) locomotion with a tridactyl function of hindlimbs, differing from that of the recognized trackways.

The potential trackmakers. In order to correlate the footprints of *Prorotodactylus mesaxonichnus* sp. nov. with their potential trackmaker, a synapomorphy-based approach is carried out by following the methods of Carrano and Wilson [42]. First, these footprints must be compared with other ichnological records. The most similar known ichnotaxa are the Triassic *Prorotodactylus*, *Rotodactylus* and *Rhynchosauroides*. The chirotheriid pes-like shape of the manus is diagnostic of *Prorotodactylus*, whereas the trackway parameters (low pace angulations, relative manus-pes distance) resemble those of *Rhynchosauroides*. Therefore, the trackmaker most probably presented morphological similarities (by phylogenetic relation and/or morphological convergence) to the trackmakers of these ichnogenera. The claw marks exclude amphibians, and point to a diapsid trackmaker instead.

Nevertheless, the less inclusive feature is mesaxony (i.e., digit III the longest) in both manus and pes tracks. Regarding the Triassic amniote tetrapod groups, mesaxony in both fore- and hindlimbs is most commonly found in archosauromorphs and derived groups [43, 44]. Brusatte et al. [15] provided a comprehensive review of characters of the Triassic terrestrial tetrapods in their supplementary material. Based on their work, the mesaxony character excludes the Triassic groups of rhynchosaurs, sphenodontians, drepanosaurids, kuehneosaurids,

parareptiles and basal diapsids. Other potential trackmakers would be the dicynodont and cynodont synapsids, but their limbs are relatively shorter and thicker (i.e., more robust or stubbier) than their potential impressions. Similarly, the relatively short hindlimbs of dicynodonts and cynodonts would not overstep the forelimbs, and their tails would not be impressed during locomotion. Brusatte et al. [15] concluded that the Polish *Prorotodactylus*, as well as *Rotodactylus*, were probably impressed by dinosauromorphs [19] (but see [16, 17, 45, 46] for an alternative discussion). On the contrary, the quadrupedal trackways of *Prorotodactylus mesaxonichnus* isp. nov. present low pace angulations (i.e., a sprawling or semi-erect posture of the trackmaker). This feature excludes archosaurs as trackmakers, as the narrow gauge trackway is a synapomorphy of the group [15].

Consequently, the most reliable trackmakers of *Prorotodactylus mesaxonichnus* isp. nov. are non-archosaurian archosauromorphs with mesaxonic limbs. Based on the detailed archosauromorph analyses by Nesbitt [43], in *Euparkeria* both metacarpal and metatarsal III are the longest among them, denoting mesaxonic limbs. In a morphological comparison, the manus-pes proportions and the pedal digits relative length are the same for both *P. mesaxonichnus* isp. nov. and *Euparkeria*, and thus equivalent points can be identified in both ichnites and bones (Figs 5A, 6B and 6C). Noteworthy, *Euparkeria* presented a sprawling to semi-erect posture of the humerus during locomotion, and the femur was held in a horizontal position during slow locomotion, being able to reach a semi-erect gait in faster locomotion [47, 48]. The glenoacetabular distance of *Euparkeria* [48] correlates with those of the trackways of *P. mesaxonichnus* isp. nov. (between 90 to 150 mm; Table 2, S2 Table). The relatively large head of *Euparkeria* also correlates with the better and relatively deeper preservation of manus than pes tracks in *P. mesaxonichnus* isp. nov. Sookias and Butler [48] also suggested a potential facultative bipedalism, which may fit with the pedal tracks with prevalence function of digits II, III and IV, linked to occasional cursorial locomotion (Figs 6D, 6F, 6G, 8N and 8O). Therefore, given all these evidences, we suggest euparkeriids (*sensu* [49]) and similar basal archosauriforms as potential trackmakers of *Prorotodactylus mesaxonichnus* isp. nov.

Ichnofamily Rotodactylidae Peabody, 1948

Ichnogenus. *Rotodactylus* Peabody, 1948

cf. *Rotodactylus* (Figs 10 and 13B).

Referred specimens and stratigraphic position. At Port del Cantó, isolated tracks (including mold IPS-82611) at 2.00 m of section VI.

Description. Small elongated pentadactyl ichnites. The digits relative length is $I < II < IV \leq III$. Digit V is rotated posteriorly, preserved mostly by the tip. Digit I is reduced, preserved as a rounded tip impression. Digits II, III and IV are much longer than digit I, and present small claw marks. The proximal parts of digits II, III and IV are deeper impressed than the tips. The digits deepness increases from II to IV.

Discussion. The longer than wide footprints, the relative digits length, and the position and shape of digit V are diagnostic traits of *Rotodactylus* [16, 19, 50]. The scarcity of footprints and lack of trackways prevent a confident assignment, being preferable its confer to *Rotodactylus*. The slightly longer digit III than digit IV indicates that this footprint may correspond to a manus impression, as in *Rotodactylus* only in some manus tracks the digit III has been identified as the longest [16, 19]. In the Early and Middle Triassic of Poland, Germany, France, Eastern Spain and the USA this ichnogenus is much more abundant [16, 31, 35, 36, 50, 51], being the dominant ichnotaxon in some Middle Triassic localities [19]. The potential trackmakers are still matter of discussion, *Rotodactylus* has been referred to dinosauromorphs [15, 19], but also to non-dinosauromorph archosauromorphs [16] such as basal archosauromorphs [46].

Ichnofamily Chirotheriidae Abel, 1935

Morphotype indet. I. Chirotheriidae Morphotype I (Figs 11 and 13C).

Referred specimens and stratigraphic position. At Port del Cantó, one manus-pes set and another associated manus track (mold IPS-82616) at 68.00 m of section VIII.

Description. The pes track is pentadactyl and plantigrade to semiplantigrade, of approximately 25 cm long. Digit III is the longest, and digit I the shortest. Digits I to IV are wide, of triangular shape, straight and subparallel, with clawed tips. Digit V is in a posterior position, curved outwards, and preserving a large pad impression. The two small tracks correspond to manus impressions. The closest manus to the pes is semiplantigrade, and preserves three digits, most probably digits II, III (the longest) and IV. The other manus track is semiplantigrade and of approximately 10 cm long, with four digits preserved. The shape is similar to that of the pes track, but with slender digits and with an angle between the digits II, III and IV higher than in those of the pes track.

Discussion. The shape of the tracks, and the manus-pes proportions are features diagnostic of the chirotheriid ichnofamily [35]. The lack of trackways and the poor footprint preservation preclude a confident assignment, but regarding the late Early—early Middle Triassic ichnoassemblages [9, 14, 16, 52, 53], the pedal footprint outline, the robustness of digits I to IV and the large pad of digit V, these tracks show some affinities to *Protochirotherium*. The potential trackmakers of such tracks may correspond to basal archosauriforms, such as erythrosuchids or crocodylian-stem archosaurs [53].

Morphotype indet. II. Chirotheriidae Morphotype II (Figs 12 and 13D).

Referred specimens and stratigraphic position. At Port del Cantó, one isolated track in concave epirelief at 68.00 m of section VIII.

Description. Pentadactyl, semiplantigrade-digitigrade, and longer than wide track (about 13 cm long). Digit III is the longest, followed by digit IV and digit II. Digit I is the shortest, being 1/3 in length of digit III. Digits I to IV form a group, separated from digit V. Digit V presents a wide pad, and is outwardly oriented. The angulation of digits I-II and II-III is higher than that of digits III and IV, which are nearly parallel. Claw marks are observed in all the digit tips. The footprint is deeper in the anterior and central part (the heel is the shallowest part).

Discussion. The concave posterior margin is similar to that of archosaur footprints, corresponding to the overlap of the metatarsals II and IV [16, 54]. The reduced and posterior position of digit I, as well as the position of digit V, are characteristic of manus tracks of *Protochirotherium* [53, 54], but as no other tracks are associated, the assignment remains open.

Morphotypes indet. Chirotheriidae Morphotypes indet. (Fig 13E, S5 Fig).

Referred specimens and stratigraphic position. At Buira, one isolated track in concave epirelief at 31.00 m and 69.00 m of section II. At Port del Cantó, one manus-pes set and about a total of 10 isolated ichnites at tracksites of Rubió and Argestues (including IPS-83739), at 48.00 m of section IV, at 0.60 m of section VI, and at 68.00 m of section VIII (including IPS-83750).

Description. The footprint of Buira (Fig 13E) corresponds to a large impression (>12 cm long) with three long digits. The middle digit is the longest. The three preserved digits are nearly parallel, they present triangular shape with clawed tips, and are slightly curved toward middle digit axis (which is straight). The isolated manus-pes set of Port del Cantó corresponds to two rounded impressions (S5A Fig), one much larger than the other (of 8 and 20 cm long), with high expulsion rims similar to those of the chirotheriid Morphotype I. The IPS-83750 of Port del Cantó corresponds to a partial track preserving three smooth digits, probably corresponding to III, IV and V (S5C Fig). The estimated size of the track is equivalent to that of Morphotype I (20–25 cm long).

Discussion. These tracks preserve few features to confidently be assigned to any ichnogenus. Nevertheless, the size and digit shapes are that of the chirotheriid ichnofamily [35, 54]. The footprint of Buirra resembles those of chirotheriids from the nearby Palanca de Noves tracksite [8].

Ichnofamily Rhynchosauroidae Haubold, 1966

Ichnogenus. *Rhynchosauroides* Maidwell, 1911

Ichnospecies—I. *Rhynchosauroides* cf. *schochardti* (Rühle von Lilienstern, 1939) (Fig 13F, S6A–S6C Fig).

Referred specimens and stratigraphic position. At Port del Cantó, isolated tracks at 0–0.60 m and 41.30 m of section IV, at 2.00 m of section VI (including molds IPS-82612, IPS-82619), at 0.70–1.20 m, 68.00 m, 70.50 m and 72.10 m of section VIII, and isolated tracks *ex situ* at Argestes tracksite.

Remarks. The characteristically asymmetrical footprints, with the long and slender digits I to IV (in increasing length) curved inwards and digit V curved and rotated outwards, the digits angulation, and the relatively sharp, hooked-shape heel are features of *Rhynchosauroides schochardti* manus tracks. This ichnospecies characteristic from the Early–Middle Triassic [11, 20, 35, 36, 55]. These footprints present the same shape as those manus tracks conferred to *R. schochardti* at Palanca de Noves. The *Rhynchosauroides* ichnogenus is commonly related to archosauromorph and lepidosauromorph trackmakers [16, 20].

Ichnospecies—II. Undetermined *Rhynchosauroides* ichnospecies 1 of [8] (Fig 13G, S6D Fig).

Referred specimens and stratigraphic position. At Port del Cantó, several isolated tracks at 41.30 m of section IV, at 2.00 m of section VI, and at 1.30 m of section VII (including molds IPS-82620, IPS-82621, IPS-82622).

Remarks. The slightly longer than wide footprints, the deepness of the digits and the outwardly curved digits (especially digit IV) are features of the *Rhynchosauroides* isp. 1 described at Palanca de Noves [8]. The lack of track couples or sets precludes assigning these tracks to manus or pes impressions.

Ichnospecies—III. Undetermined *Rhynchosauroides* ichnospecies of [8] (Fig 13H, S6E–S6G Fig).

Referred specimens and stratigraphic position. At Port del Cantó, several isolated ichnites at 0–0.60 m and 41.30 m of section IV, at 2.00 m of section VI, at 2.40 m of section VII (including IPS-83747 and IPS-83748), and at 0.70–1.20 m and 68.00 m (including mold IPS-82615) of section VIII.

Remarks. These *Rhynchosauroides* footprints are characterized by their small size and the angulation of digits IV–V at approximately 90°. As at Palanca de Noves [8], these footprints could correspond to juvenile specimens of other *Rhynchosauroides* forms. As no sets nor trackways are preserved, impressions cannot be assigned to pes or manus, and ichnospecies cannot be determined.

Morphotype indet. A

Undetermined Morphotype A of [8] (Fig 13I, S7 Fig).

Referred specimens and stratigraphic position. At Buirra, isolated ichnites at 31.00 m of section II. At Port del Cantó, isolated ichnites (including IPS-73754) at 0–0.60 m and 41.30 m of section IV, 0.70–1.20 m and 68.00 m of section VIII.

Remarks. Ichnites are pentadactyl, with digit IV slightly shorter than digit III (the longest). Digit I is preserved by a shallow tip impression. Digit V is posteriorly positioned from

digit group I-IV and slightly rotated outwards. Digits are slightly curved inwards, with clawed tips. Despite some impressions are digitigrade, they are commonly plantigrade to semiplantigrade, with a wide oval-shaped palm with an elevated ridge separating it from digits II, III and IV. These tracks correspond to manus impressions [8]. Digit proportions are those of *Prorotodactylus*, but the wide oval palm is not observed in this ichnogenus. At the analogous Palanca de Noves tracksite, Mujal et al. [8] reported several footprints and a faint trackway attributable to an archosauromorph trackmaker.

Ichnogenus *Characichnos* Whyte and Romano, 2001

Characichnos isp. indet. (Fig 13J and 13K).

Referred specimens and stratigraphic position. At Erillcastell, small scratches at 138.20 m, 142 m and 143.90 m of section I. At Port del Cantó, large track (IPS-83743) at 39.50 m of section VI.

Description. Two main track sizes are recognized. The traces from Erillcastell correspond to small digit tip scratches, with widths of 2–3 cm and variable lengths (from 4–5 cm to up to 30 cm; Fig 13J). The marks are long and continuous, being straight to sinuous, and in groups of three scratches. IPS-83743 corresponds to a large (7 cm wide and 10 cm long) crocodile-like track composed of four sigmoid-shaped digit scratches (Fig 13K).

Discussion. These kinds of scratches are interpreted as swimming traces [21, 22, 56]. The small scratches from Erillcastell may have been impressed during a flooding event, as are associated with other walking-gait ichnites of *Prorotodactylus mesaxonichnus* isp. nov. The size of these small scratches is comparable to the tracks of *P. mesaxonichnus* isp. nov., thus they were probably impressed by the same trackmaker. The large track IPS-83743 of Port del Cantó fits with the size of chirotheriid tracks [22]. It was found at the base of a meandering channel (facies *St*), hence impressed under a relatively deep water column considering the size of the track.

Discussion

Paleoenvironmental reconstruction of the Triassic Pyrenean fossil record

Stratigraphic and sedimentological data allow to determine the environmental conditions of the studied successions (Fig 13P, Table 3). The upper part of the basal conglomerate unit is constituted by sequences of facies *St-Sp* (Fig 2), where cylindrical burrows (mostly vertical) are common and scarce plant remains are also present, demonstrating the general high energy water flow of the braided system. Some surfaces yield abundant arthropod (limulid) body and trace fossils (Fig 13L), indicating episodes of relatively low water flow energy on the braided systems. Deeper environmental affinities of such arthropods in Early Triassic deposits deserve further analyses out of the scope of this work.

In the floodplain deposits of the shale and sandstones unit and shale unit, root traces are evidenced by greenish reduction marks that at some points define horizons parallel to the stratification, sometimes related to paleosols (Fig 3). This last feature indicate soil stabilization and energy decrease of the depositional system (final phases of the syn-rift). In the upper surfaces of crevasse splay deposits of 10–15 cm thick plant stem impressions and rounded trunk marks are preserved (Fig 13N), sometimes associated to capped root traces, indicating episodic flooding events of the meandering streams. The thick sandstone deposits of Port del Cantó (section IV), interpreted as large point bars of meandering systems, preserve large plant stems (Fig 13O), probably transported in episodic high energetic flow events of the main rivers

Table 3. Facies with tetrapod footprints, plant stems and impressions, and invertebrate ichnites.

Port del Cantó		
Facies associations	Architectural elements	Fossils
St-Sp	Sandy bedforms (SB)	Limulid body and trail impressions, invertebrate cylindrical burrows, plant stems
FI	Overbank fines and abandoned channels (OF)	<i>Rhynchosauroides</i> isp. indet.
Sl-Fm	Crevasse splays (SB) and abandoned channels (OF), some surfaces are mud-cracked	<i>Prorotodactylus mesaxonichnus</i> isp. nov., all <i>Rhynchosauroides</i> morphotypes, plant stems and trunk marks, and abundant burrows (in the uppermost level, with trough cross stratification and flow ripples)
St → Sh → St	Point bars (LA) of grey sandstones	Plant stems (with abundant malachite)
FI-Fm	Abandoned channels (OF)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., cf. <i>Rotodactylus</i> isp. <i>Chirotheriid</i> Morph. indet., <i>Rhynchosauroides</i> cf. <i>schochardti</i> , <i>R. isp.</i> indet., Morphotype A
Sp	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., Morphotype A, <i>Chirotheriid</i> Morph. indet., trunk marks
Sr → Fsc	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., plant stems
FI	Abandoned channels (OF)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., cf. <i>Rotodactylus</i> isp. <i>Chirotheriid</i> Morph. indet., <i>Rhynchosauroides</i> cf. <i>schochardti</i> , <i>R. isp.</i> indet.
St → Sr	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov.
St	Point bars (LA)	Large scratch track of <i>Characichnos</i> isp.
Sl	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Rhynchosauroides</i> isp. indet.
Sr/FI → FI	Crevasse splays (SB) and overbank fines (OF)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Rhynchosauroides</i> cf. <i>schochardti</i> , <i>R. isp.</i> indet., and Morphotype A
St → Sl → Fsc (interbedded Sl)	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., all <i>Rhynchosauroides</i> morphotypes, and Morphotype A
St/Sr	Crevasse splays (SB)	<i>Chirotheriid</i> Morph. indet.
Buira		
Facies associations	Architectural elements	Fossils
St → Sp → Sr → Fsc (Se)	Point bars (LA) and crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Chirotheriid</i> Morph. indet., <i>Rhynchosauroides</i> cf. <i>schochardti</i> , <i>R. isp.</i> indet., Morphotype A, invertebrate burrows
St → Fsc	Crevasse splays	Deformed indet. tetrapod tracks
Erillcastell		
Facies associations	Architectural elements	Fossils
Sp → Fsc	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., plant stems and trunk marks
Fm	Overbank fines and abandoned channels (OF)	<i>Prorotodactylus mesaxonichnus</i> isp. nov.
Sp-Sr → Se-Fsc	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Characichnos</i> isp.
Sr → FI	Crevasse splays (SB)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Characichnos</i> isp.
St → Fsc (Se)	Crevasse splays (often mud-cracked; SB) and small point bars (LA)	<i>Prorotodactylus mesaxonichnus</i> isp. nov., <i>Characichnos</i> isp.

Facies (see codes in corresponding text section and in [S1 Text](#)) in bold are those bearing fossils. Conglomeratic and massive mudstone facies do not contain fossils. Arrows indicate gradation of facies.

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streams. Invertebrate burrows are common in fluvial bars of the shale and sandstones unit. In deposits associated to occasional and rapid events (i.e., crevasse splays and scour fill deposits) burrows are vertical, whereas in abandoned channels (low energy systems) burrows are horizontal, long and sinuous (Fig 13M).

The tetrapod footprints are found in the shale and sandstones unit (Figs 2, 4 and 13P, Table 3). They are abundantly preserved in abandoned channels (at facies *FI* and facies association *Sl-Fm*) and even in small point bars (at facies associations *St-Fsc*, *St-Sr*, and *St-Sp*), as well as in crevasse splay deposits (at facies *Sl* and facies associations *Sr-Sl*, *Sp-Fsc*, and *St-Sl-Fsc*) (Table 3). The low number of swimming scratches may indicate that trackmakers passed through the deposits with a low water level. Only the large chirotheriid scratch is found in

well-developed point bar facies (*St-Sp*), thus suggesting that relatively large archosauromorphs probably had swimming faculties and possible water-living activity. Some *Prorotodactylus mesaxonichnus* isp. nov. trackways have asymmetric manus-pes distances (i.e., in one side the fore- and hindlimbs of the trackmaker were closer than in the other during locomotion; Figs 5A and 6A, S1 Fig, S2 Table), suggesting surface sloping towards the side of the more spaced tracks.

Several trampled surfaces with hundreds of *Prorotodactylus mesaxonichnus* isp. nov. footprints advancing in the same direction (westwards) occur in Erillcastell (Fig 7C). This also occurs in Buirá, although footprints are not so abundant and an isolated chirotheriid track is also preserved. The trampled surfaces may indicate gregarious behavior and increased activity [15]. Similarly, such abundance of footprints, as well as their wide distribution along the different facies (Table 3), may also denote generalist faunas [8] occupying a wide range of ecological niches. In the same way, different states of footprint preservation (i.e., unguigrade, digitigrade, semiplantigrade, plantigrade) are observed (Figs 5–9, S2–S4 Figs), both in different levels and in the same surfaces. Footprints with large dragging component denote soft substrates, while faint digit tip impressions or claw marks were recorded in relatively dry or hard substrates. Some track-bearing surfaces present either flow structures (e.g., facies *St*, *Sr* and *Se*) or mud-cracks (e.g., facies *Fm*). In sum, this would be the result of substrate varying moisture, a recurrent process in small ponds and crevasses with sporadic flooding (Fig 13P).

Early Triassic biostratigraphy and paleobiogeography

The Triassic Pyrenean tetrapod ichnoassemblage contributes to the knowledge of the general frame and distribution of the ichnofaunal record. Until now, occurrences of *Prorotodactylus*, which are always associated with *Rotodactylus*, were restricted to the Central European Germanic Basin [15–19], and possibly to the French Lodève Basin [13]. This association of ichnogenes indicates a late Olenekian age [19]. Recently, Mujal et al. [8] provided palynological data giving a late Olenekian age for the basal portion of the Pyrenean Buntsandstein facies. Similarly, Calvet et al. [40] dated as early Anisian the shale unit (uppermost Buntsandstein). Together, these works support a latest Olenekian age of the tetrapod ichnoassociation. In this way, the Pyrenean ichnoassemblage points to a Central Pangean distribution of *Prorotodactylus*, although it could be similar to that of *Rotodactylus*. Therefore, we suggest the *Prorotodactylus-Rotodactylus* zone as a new Triassic biochronological interval for, at least, Central Pangea, constituted by deposits with both ichnogenes (Fig 13Q). This zone probably corresponds to the lower parts of the Triassic biochron II [57] (1 in Fig 13Q) and the First Appearance Datum of *Rotodactylus* and *Chirotherium barthii* [52] (2 in Fig 13Q), coinciding with the overlapping interval of *Prorotodactylus* and *Rotodactylus* (3 in Fig 13; see [19]). Other characteristic late Early Triassic ichnotaxa are *Rhynchosauroides* and large chirotheriid tracks, such as *Protochirotherium* [16, 53], being potentially similar ichnotaxa to those of the Triassic Pyrenean assemblage and denoting a Central Pangean homogeneity of ichnofaunas. The trackmakers of all these ichnotaxa most probably correspond to archosauromorphs. This group radiated in the late Permian [1, 43, 58, 59], and several clades evolved along Pangea, probably in the aftermath of the different Permian extinctions [60].

The pedal and trackway pattern differences of the Pyrenean and Polish *Prorotodactylus* indicate that this ichnogenus includes different trackmakers, being in accordance with the late Early Triassic archosauromorph diversification in the aftermath of the end-Permian extinction event. The mesaxononic pedes and the low pace angulations of *Prorotodactylus mesaxonichnus* isp. nov. are possibly correlated to euparkeriids and basal archosauriforms (*sensu* [44, 49]), whereas *P. mirus* (ectaxononic pedes and higher pace angulations) has been referred to small

dinosauromorphs [13, 15, 19], although such attribution is controversial [16, 17, 45, 46]. The Polish *Prorotodactylus* (and also *Rotodactylus*) tracks were compared with the limbs of the dinosauromorph *Lagerpeton* [15] and a potential *Lagerpeton*-like dinosauromorph [61]. Nevertheless, the relative digits length and proportions of *Lagerpeton* do not match the relative depths of *Prorotodactylus* digit impressions (e.g., digit I would not be impressed) [46]. Interestingly, the similar manus impressions of the Pyrenean and Polish *Prorotodactylus* may be related to the low morphological disparity of archosauriforms suggested by Ezcurra and Butler [62]. In summary, we suggest stem archosauriforms as potential trackmakers of *Prorotodactylus*, such as euparkeriids for *P. mesaxonichnus* isp. nov.

The Triassic vertebrate recovery

In recent years, several works focused on the diversification of archosauromorphs during the Triassic [43, 44, 49, 60, 62]. Early Triassic footprints are much more abundant than body fossils, as is the case of the Western Tethys region [20, 52, 59], hence the ichnological record plays an important role to understand the vertebrate recovery. The new findings represent the earliest evidence of Mesozoic Iberian vertebrates, and one of the few and the most complete record from the Western Tethys.

The correlation between ichnites and sedimentary environments in the Catalan localities (Table 3) shows that archosauromorph footprints occur throughout the different sub-environments of the fluvial systems (Fig 13P). Similarly, Bernardi et al. [59] also suggested that the preferential habitats of archosauromorphs were the fluvial environments. Therefore, the Early Triassic archosauromorph radiation, increasing in diversity and final dominance [60, 63], may be linked to the widely extended and well-developed fluvial settings along Pangea after the end-Permian extinction event. On the instable Early Triassic ecosystems [3, 4], archosauromorph faunas were probably generalist [8, 11], taking advantage and occupying a widespread range of ecologic niches (see [3] for other groups). Key ecological innovations, such as those related to locomotion [49], permitted a rapid radiation and dominance of archosauromorphs, also hampering the radiation of other groups.

Conclusions

The Triassic Pyrenean Basin is a key region of Western Tethys to understand the early Mesozoic non-marine evolution in terms of paleoenvironment and (ichno-) faunal diversity. The red-bed Buntsandstein deposits of the Catalan Pyrenees correspond to a fluvial setting evolving from high-energy braided systems to low-energy meandering and floodplain systems that infilled the depocenters generated during the Triassic rifting. In our case, the Buntsandstein facies are arranged as a fining-upwards sequence culminated by the marine transgression of the Muschelkalk facies. A relatively diverse fossil record is yielded in the red-beds, and tetrapod footprints are especially abundant. We identified an ichnoassemblage composed by *Prorotodactylus mesaxonichnus* isp. nov., cf. *Rotodactylus*, at least two different chirotheriid morphotypes, *Rhynchosauroides* cf. *schochardti* and two other *Rhynchosauroides* forms, an undetermined Morphotype A, and two types of swimming scratches corresponding to *Characichnos* isp. The potential trackmakers of *P. mesaxonichnus* isp. nov. are archosauriform euparkeriids, suggesting, together with the other ichnotaxa, an ichnofaunal homogeneity at least along Central Pangea. *Prorotodactylus* and *Rotodactylus* may characterize the late Early Triassic continental deposits. The trackmakers of all these ichnotaxa probably correspond to archosauromorphs, suggesting that this group became dominant in the instable terrestrial settings after the end-Permian mass extinction. Archosauromorphs may represent the main pull of

vertebrate recovery that lead to the further ecosystem stabilization of the Middle Triassic, with a turnover to larger archosaurian faunas and the radiation of this lineage.

Supporting information

S1 Text. Sedimentology. Facies Description and Interpretation. Architectural Elements. (DOCX)

S1 Table. Track measurements of *Prorotodactylus mesaxonichnus* isp. nov. trackways. (DOCX)

S2 Table. Trackway measurements of *Prorotodactylus mesaxonichnus* isp. nov. (DOCX)

S1 Fig. Trackways of *Prorotodactylus mesaxonichnus* isp. nov. (A-C) Specimens from Erillcastell; dashed squares from A and C are correspond to manus-pes sets from Fig 7A and 7B, respectively. (D) Specimen from Buira. (TIF)

S2 Fig. Tracks of *Prorotodactylus mesaxonichnus* isp. nov. from Buira. (TIF)

S3 Fig. Tracks of *Prorotodactylus mesaxonichnus* isp. nov. from Port del Cantó. Ichnites from sections IV (A) and VII (B). (TIF)

S4 Fig. Tracks of *Prorotodactylus mesaxonichnus* isp. nov. from Port del Cantó. (A) IPS-83740 from Argestes tracksite. (B-E) Isolated ichnites from Rubió tracksite. Note the relatively bad preservation of the ichnites, all in convex hyporelief, preserved in the bases of small meandering channels (facies St). (TIF)

S5 Fig. Tracks of chirotheriid morphotype indet. from Port del Cantó. (A) Manus-pes set (M-P). (B) Scratch-like track. (C) Partial track of IPS-83750. (TIF)

S6 Fig. Tracks of *Rhynchosauroides* morphotypes from Port del Cantó. (A-C) *Rhynchosauroides* cf. *schochardti*. (D) *Rhynchosauroides* isp. indet. 1. (E-G) *Rhynchosauroides* isp. indet. (TIF)

S7 Fig. Isolated and partially preserved tracks of the undetermined Morphotype A from Port del Cantó (section IV). (TIF)

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Author Contributions

Conceptualization: EM JF OO.

Funding acquisition: JF.

Investigation: EM JF AB OO JÁL.

Methodology: EM JF AB OO JÁL.

Project administration: JF EM.

Resources: JF OO.

Visualization: EM.

Writing – original draft: EM JF.

Writing – review & editing: EM JF AB OO JÁL.

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Capítol 8. *First archosauromorph direct remains from the Early–Middle Triassic transition of the Iberian Peninsula*

El capítol 8 correspon al treball provisionalment acceptat per publicació a la revista *Palaeontologia Electronica*, revisat i reenviat l'11 d'octubre de 2016:

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En aquest article l'autor E. M. ha contribuït en: tasques de camp, incloent elaboració del mapa geològic i de la columna estratigràfica, i prospecció, excavació i documentació de les restes fòssils de Port del Cantó; anàlisi de sedimentologia; discussió dels resultats; redacció del context geològic i revisió del manuscrit; preparació de la figura 2; maquetació de les figures 1 i 2.

First archosauromorph direct remains from the Early–Middle Triassic transition of the Iberian Peninsula

Martín D. Ezcurra^{*1,2}, Josep Fortuny^{3,4}, Eudald Mujal⁵, and Arnau Bolet³

¹Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales, Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina.

²School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom.

³Institut Català de Paleontologia M. Crusafont. Z building, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain.

⁴Centre de Recherches en Paléobiodiversité et Paléoenvironnements, UMR 7207, Muséum National d'Histoire Naturelle, Bâtiment de Paléontologie, CP38, 8 rue Buffon, 75005 Paris, France.

⁵Departament de Geologia, Universitat Autònoma de Barcelona, 08193, Bellaterra, Barcelona, Spain.

*Corresponding author: martindezcurra@yahoo.com.ar

Abstract

Here we describe and discuss the taxonomic affinities of three isolated teeth discovered in the Buntsandstein facies of the Catalan Coastal ranges and central-eastern Pyrenean basins that crop out in Catalonia, north-eastern Spain. The tooth crowns are blade-like, labiolingually compressed, distally recurved and proportionally apicobasally tall, in which the most complete of them is at least 2.4 times taller than its mesiodistal depth at base. The distal margins possess a densely serrated carina, and the mesial margins lack carina and serrations. The enamel of the crowns lacks ornamentation (e.g., wrinkles, ridges) or macroscopic wear-facets. The three teeth are referred to indeterminate crocopodan archosauromorphs based on the presence of labiolingually compressed and serrated crowns. The absence of mesial denticles resembles the condition in the non-archosauriform archosauromorph *Teyujagua*, proterosuchids, and some more crownward archosauriforms (e.g., some proterochampsids). We could not find evidence to determine if these teeth belong to a single or multiple closely related species. These remains represent the first archosauromorph direct remains from Lower–Middle Triassic beds of the Iberian Peninsula and add information about the geographic distribution of the group during the dawn of the evolutionary radiation of the group.

Key words

Diapsida; Archosauromorpha; Crocophoda; teeth; Early–Middle Triassic.

Introduction

The Permo-Triassic mass extinction (ca. 251 m.y.a.) allowed the flourishing of multiple vertebrate clades that were minor components of Palaeozoic assemblages or originated in the aftermath of this event. One of the clades that radiated during the Triassic was Archosauromorpha, which includes the diapsids more closely related to crocodiles and dinosaurs (including birds) than to lepidosaurs (Gauthier et al., 1988). The oldest archosauromorphs are middle-late Permian in age (Ezcurra et al., 2014; Martinelli et al., 2016) and during the Triassic achieved disparate morphologies and ecological habits, including the specialized herbivorous rhynchosaurs, allokotosaurians, ornithischians, and sauropodomorphs, the bulky carnivorous erythrosuchids and “rauisuchians”, the aquatic or semi-aquatic tanystropheids and at least some proterochampsids and poposauroids, and the flying pterosaurs (Nesbitt, 2011; Ezcurra, 2016). The clade suffered several biotic crises during its evolutionary history, such as those of the Triassic-Jurassic and Cretaceous-Palaeogene mass extinctions, but they are abundantly represented in extant ecosystems by more than 10,000 species, mostly corresponding to birds. The Early Triassic archosauromorph record is mainly restricted to species with a low morphological diversity (Ezcurra and Butler, 2015). Otherwise, during the Anisian (247–242 m.y.a.) several of the above-mentioned eco-morphotypes appear or become more abundant probably as a result of the stabilization of ecosystems recovered from the mass extinction event (Irmis and Whiteside, 2012; Lau et al., 2016). As a result, the Early–Middle Triassic transition is a key interval to understand the subsequent evolutionary success of archosauromorphs.

The European late Olenekian–Anisian archosauromorph record is relatively rich, but that of the Iberian Peninsula is restricted to ichnites from the Buntsandstein and Muschelkalk facies (Lapparent et al., 1965; Calafat et al., 1987; Fortuny et al., 2011a; Mujal et al., 2016). The only named Iberian Middle Triassic archosauromorph species is the tanystropheid *Cosesaurus aviceps* from the Ladinian of the Montral-Alcover Basin (Ellenberger and Villalta, 1974; Sanz and López-Martínez, 1984). *Cosesaurus aviceps* is based on a fairly complete skeleton preserved as natural moulds and is probably closely related to derived tanystropheids (e.g., *Amotosaurus rotfeldensis*, *Tanystropheus longobardicus*) based on the presence of an elongated, metatarsal-like pedal phalanx V-1 (MGB-V1, see synapomorphies within Tanystropheidae in Ezcurra, 2016). Here we describe and discuss the taxonomic affinities of three isolated archosauromorph teeth discovered in the Buntsandstein facies of the Catalan Coastal Ranges and Catalan Pyrenees, north-eastern Iberian Peninsula (Spain) (Fig. 1). These fossils represent the first archosauromorph direct remains fossils from Early–Middle Triassic beds of the Iberian Peninsula.

Geological and palaeontological setting

The archosauromorph teeth were recovered in two outcrops from the north-eastern region of the Iberian Peninsula (Catalonia, Spain). In the Iberian Peninsula the Triassic is composed of the classic German lithofacies: Buntsandstein, Muschelkalk, and Keuper. All the remains here reported come from the Buntsandstein facies.

The tooth IPS-90631 comes from the La Mora site of the Catalan Basin, the Triassic beds of the current Catalan Coastal Ranges, and was collected during fieldwork conducted in 2008. This site

yielded hundreds of fossil bones assigned mainly to temnospondyl amphibians and to a lesser degree amniotes (Fortuny et al., 2011a,b, 2014). La Mora site belongs to the Montseny-Llobregat domain of the Catalan Basin (Calvet and Marzo, 1994). The Buntsandstein facies in this area (lower part of the Areniscas y Lutitas del Figaró unit) are formed by continental deposits, mainly composed of sandstones, mudstones, and red clays, being interpreted as fluvial deposits (Calvet and Marzo, 1994). The age of this unit is unclear, but based on palynological, palaeomagnetostratigraphic, and biostratigraphic evidence the lower part of this unit (including the La Mora site) is considered as early to middle Anisian (Middle Triassic) (see Dinarès-Turell et al., 2005; Fortuny et al., 2011b and references therein for further stratigraphic and sedimentological details).

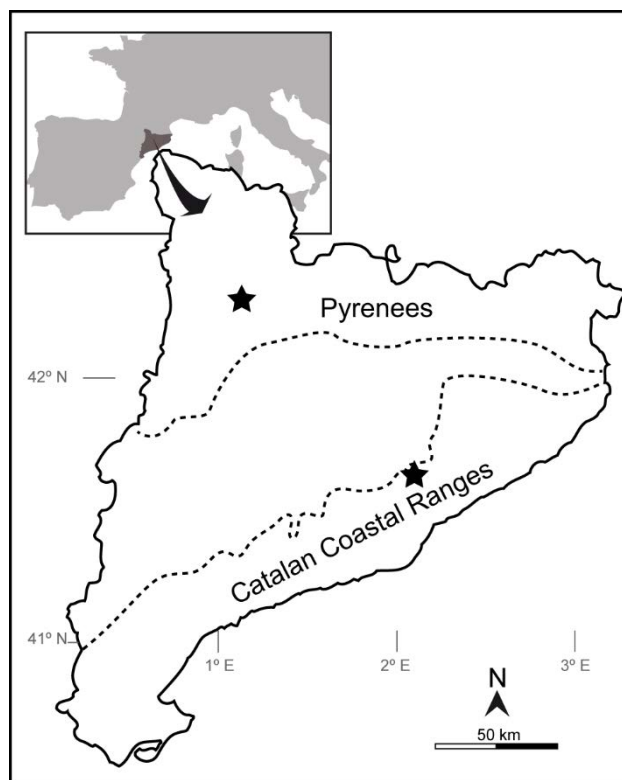


Figure 1. Map of Catalonia showing the geographic occurrence of the archosauromorph teeth described here. Dashed lines indicate the boundary of each mountain range.

The teeth IPS-73757 and IPS-90188 and a few bone fragments were recovered from the Triassic levels of the Pyrenean Basin that crop out in the Port del Cantó site in fieldworks corresponding to years 2012 (for IPS-73757) and 2014 (for IPS-90188). In the earliest Triassic, the Pyrenees were composed of several continental sedimentary basins developed in the latest phases of the Variscan cycle, resulting from a strike-slip (transtensional) tectonic activity (Speksnijder, 1985; Saura, 2004; Saura and Teixell, 2006; Izquierdo-Llavall et al., 2014; Gretter et al., 2015). In this extensional regime the Triassic sediments covered the Variscan basement and the Permo-Carboniferous vulcanosedimentary sequences, configuring an erosive angular unconformity. The region of Port del Cantó belongs to the central Noguera structural zone (Saura, 2004). The reference studies by Mey et al. (1968) and Nagtegaal (1969) defined the “post-hercynian” units of the Catalan Pyrenees. Séguret (1972) and Zwart (1979) conducted the basic regional geology and mapping, and recent structural works are those of

Saura (2004) and Saura and Teixell (2006). The basin architecture and evolution has been largely studied (Speksnijder, 1985; Saura and Teixell, 2006; Izquierdo-Llavall et al., 2014; Gretter et al., 2015). A revision of the Triassic vertebrate content has been addressed by Fortuny et al. (2011a), and more recently Mujal et al. (2016) revised and provided new data on the Permo-Triassic transition.

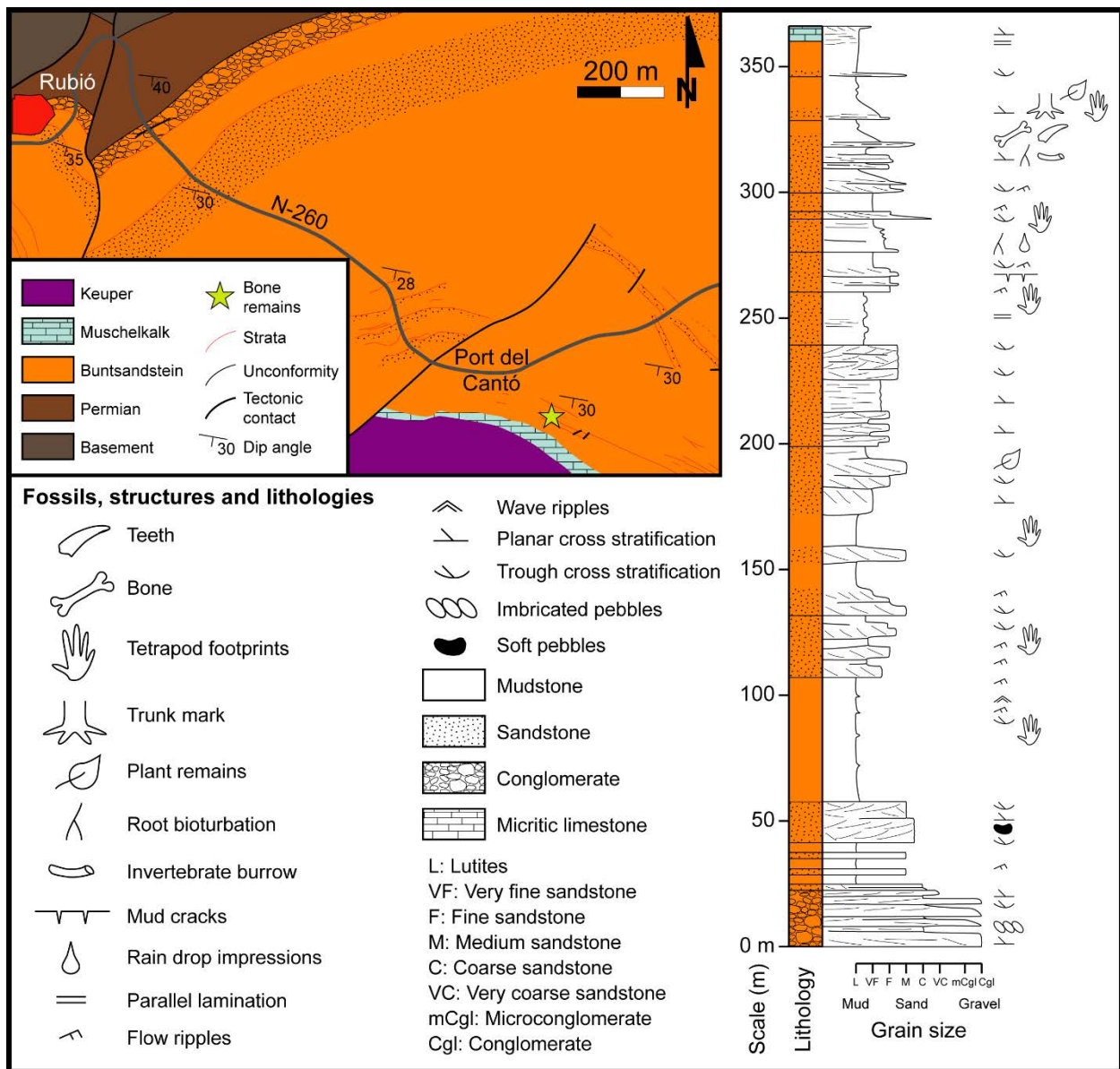


Figure 2. Geological map and stratigraphic profile of the Port del Cantó locality where IPS-73757 and IPS-90188 were collected.

In Port del Cantó, the Buntsandstein facies reach a maximum thickness of 350 metres, and the sequence is divided in three main units (sensu of Calvet et al., 1993), from base to top: (1) conglomerate unit, composed of fluvial braided oligomictic conglomerates (mostly of quartz pebbles) and medium to very coarse channel-fill sandstones; (2) shale and sandstones unit, composed of reddish and greenish to greyish medium-coarse sandstones, with some discontinuous conglomerate levels, of meandering fluvial settings, and reddish very fine to fine sandstones and shales of floodplain systems; and (3) shale unit, composed of reddish shales with occasional thin but continuous sandstone beds (as those of the shale and sandstones unit) corresponding to floodplain deposits and minor channels.

The Buntsandstein facies represent the thickest Triassic sequences of the Catalan Pyrenean Basin, followed by the transitional to marine Muschelkalk and Keuper facies (Fig. 2).

The reported teeth were recovered in the uppermost part of the Buntsandstein shale and sandstones unit, 42 metres below the transition to the Muschelkalk facies. They were found in a fining upwards interval composed of fine- to medium-grained cross laminated sandstones displayed in thin (ca. 5 cm) layers of low lateral extension interbedded with reddish mudstones. Root traces, invertebrate burrows, and low-developed palaeosols (thin mudstone levels with carbonate nodules) are also present. This interval is interpreted as small crevasse splay deposits of floodplain systems. The teeth and bone fragments were in close association (less than two square metres in horizontal axis, and a few centimetres in stratigraphic level).

The palynological analysis of Calvet et al. (1993) indicated an early Anisian (early Middle Triassic) age for the shale unit of the Buntsandstein facies (see also Diez et al., 2005, 2010). Mujal et al. (2016) described a palynological assemblage from the base of the shale and sandstones unit corresponding to the late Olenekian (late Early Triassic). Therefore, the age interval for the teeth IPS-73757 and IPS-90188 is late Early–early Middle Triassic.

Institutional abbreviations. **BP**, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **IPS**, Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCZ**, Museum of Comparative Zoology, Cambridge, USA; **MGB**, Nat-Museu de Ciències Naturals de Barcelona, Barcelona, Spain; **RC**, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; **SAM-PK**, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **UA**, University of Antananarivo, Antananarivo, Madagascar.

Systematic palaeontology

Diapsida Osborn, 1903 sensu Laurin, 1991

Sauria Gauthier, 1984 sensu Gauthier, Kluge and Rowe, 1988

Archosauromorpha Huene, 1946 sensu Dilkes, 1998

Crocopoda Ezcurra, 2016

Gen. et sp. indet.

Figure 3

Material. IPS-90631: isolated tooth crown missing its apex, probably from the anterior region of the mouth (Fig. 3.1).

Locality and horizon. La Mora site, Catalonia, Spain. Buntsandstein facies (lower part of the Areniscas y Lutitas del Figaró unit), Montseny-Llobregat domain of the Catalan Basin, dated as early to middle Anisian (Fortuny et al., 2011b).

Description. IPS-90631 is identified as a possible shed tooth, detached from the tooth series when the animal was alive, because the crown is broken around its base and, as a result, the root is missing

(Fig. 3.1). Nevertheless, no resorption pit is preserved to unambiguously confirm this interpretation. The apex of the crown is missing and the most apically preserved portion possesses a fresh broken surface, indicating that its apex was probably lost after exposure of the specimen. The crown is asymmetric in distal view, in which the inferred labial surface is more convex apicobasally than the lingual surface. The distal carina of the crown is slightly lingually displaced from the main mesiodistal axis of the tooth and, as a result, this dental element would have belonged to the anterior region of the mouth (where the alveolar margin of the snout arches medially). The preserved portion of the crown is blade-like, being slightly distally recurved in side view and distinctly labiolingually compressed. The crown possesses a serrated distal carina, in which the main axis of the denticles is perpendicular to that of the crown. The distal margin of the denticles is straight to slightly apicobasally convex. The interdenticular sulci are shallow and not extend onto the rest of the crown as blood grooves. The serrations extend along most of the distal margin of the crown, with a density of five denticles per millimetre, and they are absent at its base. The mesial margin of the crown lacks a carina and serrations, being continuously labiolingually convex. The enamel of the crown lacks ornamentation (e.g., wrinkles, ridges) or macroscopic wear-facets in its preserved portion.

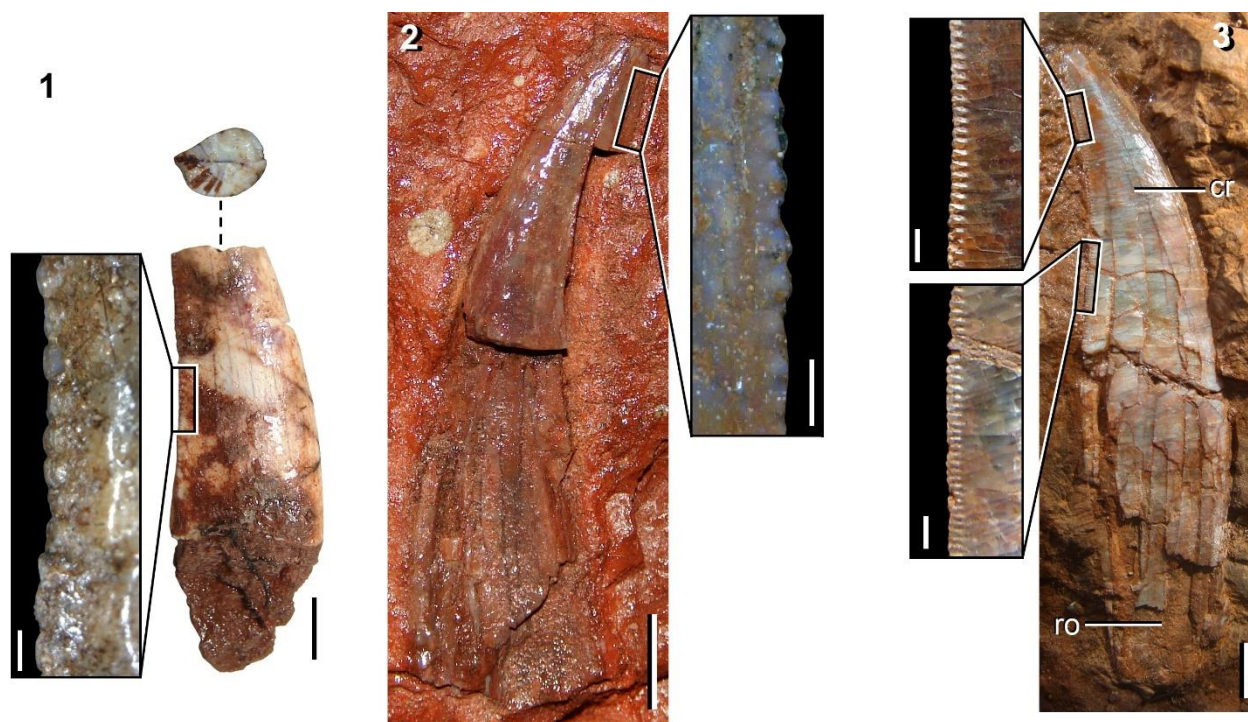


Figure 3. Isolated crocoid archosauromorph teeth from the Early–Middle Triassic of Catalonia. 1, IPS-90631 in apical (top) and lingual (bottom) views and close up of distal denticles; 2, IPS-73757 in labial view and close up of distal denticles; 3, IPS-90188 in side view and close up of distal denticles. Abbreviations: cr, crown; ro, root. Scale bars equal 2 mm in (1), 5 mm in (2, 3), 0.2 mm in close up of (1), 0.5 mm in close up of (2), and 1 mm in close ups of (3).

Material. IPS-73757: isolated tooth crown from the middle or posterior region of the mouth, with its apical half – missing the tip and part of the distal margin – exposed in probable labial view and distal half preserved as the natural mould of its lingual surface (Fig. 3.2); IPS-90188: isolated complete tooth exposed in probable labial view (Fig. 3.3).

Locality and horizon. Port del Cantó site, Catalonia, Spain. Buntsandstein facies of the Pyrenean Basin dated as late Olenekian-early Anisian (Calvet et al., 1993; Fortuny et al., 2011a; Mujal et al., 2016).

Description. IPS-73757 is an isolated tooth probably exposed in labial view because it possesses a faint bowing towards the side that is covered with matrix in mesial or distal view (Fig. 3.2). The apical half of the preserved portion of the tooth lacks its tip and part of the distal margin. The distal half is preserved as the natural mould of the probable lingual surface. The preserved portion continuously expands mesiodistally towards its base and the boundary between the crown and root (if present) cannot be determined. IPS-90188 is a complete tooth, preserving crown and root, exposed probably in labial view because the crown bows towards the rock (Fig. 3.3). In both specimens there is a series of longitudinal cracks (also present in the natural mould of IPS-73757), but otherwise they are well preserved. The two specimens from the Port del Cantó site possess a fairly congruent morphology between each other and they are described together as follows.

Table 1. Measurements of the crocopodan archosauromorph teeth here described in millimetres. Values between brackets indicate incomplete measurements. Maximum deviation of the digital calliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.

Measurements	La Mora tooth (IPS-90631)	Port del Cantó tooth (IPS-73757)	Port del Cantó tooth (IPS-90188)
Apicobasal height of crown+root	?	?	(58.7)
Apicobasal height of crown	(10.0)	(38.7)	(29.8)
Mesiodistal depth of crown at base	4.9	ca. 13	12.9
Labiolingual width of crown at base	3.4	?	?

The crowns are distally recurved along their entire extension and, as a result, their apexes are placed distally to the distal margin of their bases. The crowns are labiolingually compressed, with a more acute distal margin than the mesial margin. The crowns are proportionally tall, being at least 2.4 times taller than its mesiodistal depth at base in IPS-90188 (Fig. 3.3: cr). The distal margin possesses a sharp and serrated carina and, at least, in IPS-73757 there are no carina and serrations on the mesial margin of the preserved portion of the crown. The distal carina of IPS-73757 is aligned with the mesiodistal axis of the crown, indicating that it is not a tooth from the anterior region of the mouth. This feature cannot be determined confidently in IPS-90188. The denticles extend along the entire preserved portion of the distal margin of the crown in IPS-90188 and this condition cannot be determined in IPS-73757 because the actual distal half of the crown is missing. The morphology of the distal denticles of IPS-73757 closely resembles that of IPS-90631. The latter two specimens possess squared denticles, but in IPS-90188 they are proportionally mesiodistally longer, being subrectangular. The interdenticular sulci are shallow and not extend onto the rest of the crown as blood grooves. In both specimens, the most apical third of the crown possesses three denticles per millimetre, whereas around mid-height there are four denticles per millimetre. The enamel of the crown lacks ornamentation (e.g., wrinkles,

ridges) or macroscopic wear-facets in its preserved portion. The root of IPS-90188 is probably complete and there is no evidence of reabsorption at least in the exposed side (Fig. 3.3: ro). The root expands gently mesiodistally along its most apical portion, as a continuation of the expansion towards the base present in the crown, and more basally it narrows gradually as a result of the convergence of the straight mesial and distal margins. The basal margin of the root is straight and, as a result, the root acquires an overall trapezoidal contour in side view.

Discussion

The morphology of the three isolated teeth described here is rather consistent between each other, but they differ in the density and shape of the distal denticles. These features have not been used as characters in phylogenetic analyses focused on basal archosauromorphs (e.g., Dilkes, 1998; Nesbitt, 2011; Nesbitt et al., 2015; Pritchard et al., 2015; Ezcurra, 2016) and they seem to be taxonomically uninformative. In addition, the subtle differences observed in the morphology of the denticles may be attributable to variations within the dental series or intraspecific variability. Therefore, we could not find evidence to determine if the teeth described here belong to a single or multiple closely related species.

The three teeth share the presence of a labiolingually compressed and serrated crown, which are two character-states found in lesser inclusive clades of Archosauromorpha. Compressed crowns are present in several crocopodan archosauromorphs (sensu Ezcurra, 2016), namely azendohsaurids (e.g., *Azendohsaurus madagaskarensis*: UA 10603, 10604, 8-29-97-160), prolacertids (e.g., *Prolacerta broomi*: BP/1/2675), *Teyujagua* (Pinheiro et al., 2016), *Tasmaniosaurus* (Ezcurra, 2014) and archosauriforms (e.g., *Proterosuchus fergusi*: RC 846; *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis*: SAM-PK-5867). By contrast, the crowns are conical, with a circular cross-section, in non-crocopodan archosauromorphs and more basal diapsids, such as *Youngina* (BP/1/3859), tanystropheids (e.g., *Tanystropheus*: SMNS 54147), and *Prolacertoides* (IVPP V3233). The presence of small serrations is a more taxonomically restricted feature, being present in *Teyujagua*, *Tasmaniosaurus*, and archosauriforms among archosauromorphs (Ezcurra, 2016; Pinheiro et al., 2016). By contrast, other archosauromorphs lack finely serrated crowns (e.g., tanystropheids, prolacertids, trilophosaurids, rhynchosaurs; Benton and Clark, 1988; Juul, 1994; Dilkes, 1998; Nesbitt et al., 2015; Ezcurra, 2016; Pinheiro et al., 2016) and, although azendohsaurids possess denticles in the crown, they are considerably larger and coarser (with a lower density; Flynn et al., 2010; Nesbitt et al., 2015). As a result, recent quantitative phylogenetic analyses found compressed and finely serrated crowns as synapomorphies of lesser inclusive clades within Crocopoda (Ezcurra, 2016; Pinheiro et al., 2016) and support the assignment of the three teeth from the late Early to Middle Triassic of Catalonia to this clade.

The teeth described here also share the absence of mesial denticles in the crown. The occurrence of apically restricted, incipient or absent mesial denticles has been scored for proterosuchids (e.g., *Proterosuchus fergusi*, “*Chasmatosaurus*” *yuani*) (Ezcurra, 2016) and more recently *Teyujagua* (Pinheiro et al., 2016) among basal archosauromorphs, whereas *Kalisuchus rewanensis*, *Sarmatosuchus otschevi*, erythrosuchids and the vast majority of Triassic eucrocopodan archosauriforms possess densely serrated mesial carinae (Ezcurra, 2016). However, the presence of crowns with a serrated distal margin

and lacking serrations in the mesial one convergently occur in disparate archosauriform groups, such as in some proterochampsids (e.g., *Chanaresuchus bonapartei*: MCZ 4686) and early dinosauriforms (MDE personal obs.). As a result, the absence of mesial denticles is not a character-state useful to unambiguously constrain the taxonomic assignment of blade-like, serrated archosauromorph teeth. Therefore, the three teeth described here for the late Early to Middle Triassic of Catalonia are assigned to indeterminate crocoid archosauromorphs. The teeth described here indicate the presence of small-sized predatory archosauromorphs in the late Olenekian–early Anisian tetrapod assemblage of the Iberian Peninsula. The currently available sample is very low and restricted to morphologically similar crowns, but it is a first step towards a better knowledge of the late Early–early Middle Triassic archosauromorph diversity in this part of Europe. These remains represent the first archosauromorph direct fossils from beds of this age in the Iberian Peninsula and add information about the geographic distribution of the group during the dawn of the evolutionary radiation of the group.

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Capítol 9. *Integrated discussion*

The long terrestrial succession from the late Carboniferous to the Middle Triassic of the Catalan Pyrenees (NE Iberian Peninsula): paleoenvironmental crises and paleoclimatic trend at the equator of Pangea

Along the terrestrial successions cropping out in the narrow but continuous W-E oriented belt located at the southern margin of the axial Catalan Pyrenees, the Paleozoic–Mesozoic transition is recorded. These successions were deposited from the late Carboniferous to the Middle Triassic in a strike-slip transtensional system known as the Pyrenean Basin. The new paleontological and sedimentological data presented shed light on ecosystems evolution and contribute to the knowledge of the major global events (i.e., climatic changes and mass extinctions) of these periods (Figs. 9.1, 9.2). Distinct paleoenvironments and fossils (plants, invertebrate trace fossils, tetrapod footprints composing different ichnoassemblages and ichnoassociations, and sparse bone remains) have been identified throughout the sedimentary and volcanosedimentary units, which are linked to different paleoclimates. From base to top, depositional units are (Fig. 9.2): Grey Unit (GU; late Carboniferous), Transition Unit (TU; late Carboniferous–early Permian), Lower Red Unit (LRU; early Permian), Upper Red Unit (URU; middle–late Permian), Buntsandstein facies unit (Early–Middle Triassic). Contacts between units are often unconformable and/or paraconformable, but here are newly reported some areas and localities where contacts are transitional, i.e., conformable. Therefore, the studied areas allow to establish a continuous record. The long and continuous record of the GU, TU and LRU is studied in detail in the Erillcastell-Estac sub-basin, whereas the revisited URU is analyzed in the Cadí sub-basin, and different successions from the Buntsandstein facies are studied in both sub-basins.

9.1. Age and paleoenvironmental changes

The lowermost succession studied in the present PhD thesis corresponds to the uppermost part of the Grey Unit (GU), equivalent to the lower part of the Malpàs Formation (see **chapter 3**). The uppermost GU overlies a volcanic sequence and is composed of volcanoclastic deposits reworked in fluvio-lacustrine systems. Such deposits are typically grey (and greenish) and are composed of abundant floodplain coal and carbonaceous mudstones with interbedded relatively small meandering sandstone channel deposits, indicative of short-lived stream flows. Abundant plant remains in these sandstone deposits also suggest a relatively low energy of the system. A large diversity of plants grew up in the dominant floodplain environments. Sudden lateral changes in facies and lateral variations in interval thickness indicate an uneven paleorelief. The sedimentological and paleopedological succession, together with the characteristic fossil macroflora, suggest a generally humid climate. Nevertheless, specific (and sporadic) features in pedotypes and plant taxa demonstrate the occurrence of short periods with low water availability. The plant fossil assemblage allows to age the succession as Stephanian C (**chapter 3**; Fig. 9.1; see section 9.2.1 below for paleobiogeography).

The subsequent Transition Unit (TU) is composed of reworked volcanic deposits in fluvial (meandering channels and floodplain) and lacustrine systems. The large slickensides identified within the grey-greenish floodplain mudstones were formed due to a high variation of water content, being indicative of strong seasonality. In the studied section (see **chapter 3**) the TU is almost barren of fossils,

precluding any biostratigraphic inference. Nevertheless, this unit has potential to preserve fossils, thus future prospections in other areas will focus in equivalent successions. In fact, in the eastern Castellar de n'Hug sub-basin, Broutin and Gisbert (1985) described a fossil flora assemblage from the lower part of the TU suggesting a late Carboniferous age.

The onset of the Lower Red Unit (LRU), conformably overlying the TU, is featured by a sudden shift from grey-beds to red-beds and the disappearance of coal (see **chapter 3**). The LRU consists of a long volcanosedimentary succession characterized by relatively thick ignimbrite deposits and occasional thin grey cinerites, the emission source being far (eastwards, in the Castellar de n'Hug sub-basin) from the studied area (Martí, 1996). A change in the paleorelief from the GU and TU to the LRU is indicated by the high lateral continuity of the LRU strata, denoting a relatively flat landscape (i.e., strata progressively expanded throughout the basin). The succession exhibits a high abundance of carbonate pedotypes that, together with reddish color and the coal absence, indicate more arid (semi-arid and arid paleoclimate) and more oxidizing conditions than in the GU and TU. Nevertheless, some well-differentiated intervals corresponding to meandering fluvial systems with greenish mottling and/or horizons (reducing conditions) with few or absent carbonate pedotypes denote more humid conditions (sub-humid climate). These intervals yield an abundant and diverse ichnofauna, often related to water-dependent trackmakers, that confirm the suggested humid conditions (see **chapter 4**). The age of the LRU is well-constrained by different means: (1) the tetrapod ichnoassemblage is characteristic of the Artinskian; (2) the reverse paleomagnetic polarity found along the ~750 m analyzed in the LRU is correlated to the early Permian Kiaman superchron; (3) the ignimbrite above the lowermost ichnoassociation corresponds to a Pyrenean-scale event (Martí, 1996) dated as 290 Ma by Pereira et al. (2014). Therefore, the entire LRU was most probably deposited during the early Permian (see **chapters 3**). The top of the LRU is unknown because, in all reported Pyrenean localities, it is unconformably overlaid by the URU (in the Cadí sub-basin) or by the Buntsandstein facies unit (in the Erillcastell-Estac sub-basin) (see also Gisbert, 1981; Gisbert et al., 1985). After the results presented in **chapters 3 and 6** and discussed in the section 9.2.3 below, the estimated time gap between the LRU and URU would extend from the middle–late Kungurian (late early Permian) to the early Roadian (earliest middle Permian) (Fig. 9.2).

The Upper Red Unit (URU) is studied in newly uncovered localities from the Cadí sub-basin (it is not found in the Erillcastell-Estac sub-basin; see **chapters 5, 6**). At the Port del Cantó area (western margin of the Cadí sub-basin), the URU overlies the Variscan basement (see **chapter 7**); however, in the eastwards areas studied (Palanca de Noves, Coll de Terrers and La Trava) the URU overlies the LRU by means of an angular unconformity. The URU constitutes a fining- and thinning-upwards sequence. The lowermost part is composed of relatively coarse alluvial braided facies (Gisbert, 1981; Gretter et al., 2015) grading to floodplain and distal meandering fluvial systems (lower URU). After a long period of pedogenesis represented by a laterally continuous interval of carbonate nodules, a succession of playa-lake/ephemeral lacustrine deposits sedimented. This succession was deposited under a monsoonal regime (indicating strong seasonality) with a potential cyclic recurrence of eccentricities (100 kyr and 400 kyr) and obliquity (~1-1.2 Myr) (see **chapter 6**). This is the first report of an orbital control in a Permian succession of the Iberian Peninsula. The sedimentological and mineralogical

analyses conducted in the URU indicate a climatic change from the lower to the upper deposits. The coupled increase of albite and depletion of kaolinite suggests a shift from humid (lower URU) to semi-arid (upper URU) conditions. Similarly, the quartz depletion indicates a decrease in weathering. The new fossil data (bones in the lower URU and footprints in both lower and upper URU; Fig. 9.1), together with the sedimentary stacking (i.e., cyclic sedimentation), suggest a middle Permian age for the lower URU and a late Permian age for the upper URU. Thus, a potential, previously unknown, stratigraphic gap, possibly including most part of the Capitanian (late middle Permian) and the basal Wuchiapingian (earliest late Permian) exists between the lower and upper URU (Fig. 9.2).

The Buntsandstein facies unit of the Catalan Pyrenees (see **chapters 5–8**) consists in a fining-upwards, red-bed alluvial sequence with: (1) predominance of fluvial braided deposits in the lower part (conglomerate unit), (2) predominance of meandering fluvial and floodplain deposits in the middle part (shale and sandstones unit), and (3) predominance of floodplain deposits, with occasional meandering fluvial channels, in the upper part (shale unit). The measure of up to 11 stratigraphic sections of the Buntsandstein facies throughout both sub-basins shows a great variation of each distinguished interval. Similarly, the thickness of each Buntsandstein succession varies according to the basin configuration. In the studied areas, the total thickness ranges from 103 m to 350 m. The Buntsandstein often overlies the previous units or the Variscan basement by means of an angular unconformity (Fig. 9.2), representing a large scale onlap (Gisbert et al., 1985) deposited in a distensive regime (Saura, 2004), probably representing the final phases of the syn-rift interval.

The new palynological results presented in **chapter 5** attribute the lower portion of the Buntsandstein facies unit (for the first time in the Catalan Pyrenees) to the late Olenekian (late Early Triassic). This age is in agreement with the palynological data of Calvet et al. (1993), who suggested an early Anisian age (earliest Middle Triassic) for the base of the shale unit. These ages also agree with the tetrapod ichnoassemblages described in **chapters 5 and 7**. Notably, in Coll de Terrers (see **chapter 6**), the Buntsandstein facies are in continuity (i.e., conformable contact) with the upper URU succession, as supported by the preliminary cyclostratigraphic results. In addition, the basal portion of the unit in this area differs from that of the others: the conglomerate unit is represented by a thin breccia, which is overlaid by playa lake/ephemeral lacustrine deposits as those of the upper URU. Therefore, the oldest Triassic (Induan) is possibly recorded (Fig. 9.2). This is exceptional not only regarding the Catalan Pyrenees, but also regarding the Western Tethys domain, where a stratigraphic gap often exists between Permian and Triassic successions (Bourquin et al., 2011).

The onset of the coastal/marine Muschelkalk and Keuper facies above the Buntsandstein facies units represent the end of the terrestrial succession in the early Mesozoic from the Catalan Pyrenees. The Catalan Pyrenean Muschelkalk facies are aged as Middle–Late Triassic (late Ladinian–early Carnian) by palynology (Calvet et al., 1993) and actinopterygian fossil remains (Cartanyà et al., 2011, 2015; Fortuny et al., 2011a). These facies, diachronous throughout the European successions, represent the Middle Triassic marine transgression of European scale (Escudero-Mozo et al., 2015 and references therein). Whereas in the Pyrenean Basin a single unit of the Muschelkalk facies is distinguished, in the southwards Catalan Basin such marine deposits, much more developed, display three well-distinguished intervals or sub-units: Lower, Middle and Upper Muschelkalk (Calvet and Marzo, 1994). The

Middle Muschelkalk unit, of late Anisian–early Ladinian age (Solé de Porta et al., 1987; Dinarès-Turell et al., 2005), is composed by distal alluvial and coastal deposits corresponding to a short regression interval within the transgression. This succession yields tetrapod footprints (see **Annexes 1 and 2**) that complete the general framework of the terrestrial tetrapod ichnoassemblages evolution, closely related to the paleoenvironmental setting.

9.2. Significance of the fossil content and paleobiogeography

The studied volcanosedimentary and sedimentary terrestrial successions yield an unsuspected abundant and diverse fossil record well-differentiated and characteristic for each unit (Figs. 9.1, 9.2). The paleoenvironmental implications and significance for the end-Carboniferous, Permian and Triassic continental ecosystems are discussed.

9.2.1. *Plant fossils*

The new plant fossil assemblage of the Grey Unit (late Carboniferous, Stephanian C) indicates proper conditions (humid climate) for the development of hygrophile and mesophile floral elements, with abundant tree ferns and sphenopsids. Nevertheless, the presence of plants adapted to water-stressed habitats (i.e., Zygopteridales) denote periods of dry conditions. The preliminary taphonomic results presented in **chapter 3** suggest that floodplains were mainly inhabited by marattialean tree ferns and medullosan pteridosperms; sphenopsids grew up in fluvial channels; and the distal areas of alluvial fans were inhabited by cordaitaleans.

The plant taxa identified in the studied succession is similar to that of assemblages from other Catalan Pyrenean localities (e.g., Dalloni, 1930; Broutin and Gisbert, 1985; Talens and Wagner, 1995; Martín-Closas and Martínez-Roig, 2007), as well as from other regions of equivalent paleolatitudes. Several European localities yield similar floras, especially those from the French Montceau-les-Mines basin (Charbonnier et al., 2008; Charbonnier, 2014), the Germanic Saar-Nahe basin (Kerp and Fichter, 1985; Uhl and Jasper, 2016), and the Czech Republic Carboniferous basins (Opluštil et al., 2013, 2017). The North American Carboniferous floras are also equivalent to the previously mentioned ones (including that here studied) sharing most of the taxa (DiMichele, 2014; DiMichele et al., 2017 and references therein).

Notably, plant fossils in the red-bed sequences (Lower and Upper Red Unit, LRU and URU, respectively; and Buntsandstein facies unit) are sparse and mostly represented by unidentifiable plant fragments and stem impressions, sometimes carbonized. As an exception, in the LRU impressions of *walchia* conifer-like fronds, a common floral element of the early Permian red-beds, are recognized. In all red-bed units root traces and carbonatic rhizoliths are recognized in mudstone deposits from floodplain environments, indicating substrate stabilization and initial phases of pedogenic processes. Large plant stems and trunks are often preserved in the large meandering fluvial sandstone channel deposits from the Buntsandstein facies unit. Similarly, in the Buntsandstein crevasse splay deposits

rounded molds of vertical trunks denote that plants growing up in floodplains were covered in episodic flooding events. These differences suggest a drastic environmental change from the GU to the LRU, which is also evidenced by the facies succession (see **chapter 3**).

9.2.2. *Invertebrate trace fossils*

In this PhD thesis, invertebrate trace fossils have been preliminary identified and interpreted, although future works will analyze them in detail. Invertebrate trace fossils, abundant in the red-bed units and most commonly associated to tetrapod footprints, provide further insights to the paleoenvironmental setting. The meandering fluvial systems of the Lower Red Unit (LRU) as well as the lower surfaces of the thin sandstone from the upper Upper Red Unit (upper URU) are dominated by *Rusophycus* and *Acripes*, ichnogenera associated to resting (cubichnia) and locomotion (repichnia) traces of arthropod triopsids (or notostracans). The great abundance of such triopsid trace fossils and their nearly continuous distribution suggest that these arthropods were common, and possibly dominant, organisms of their ecosystems. In fact, such ichnofossils have a Pangean distribution, being especially common in Permian and Triassic terrestrial red-bed successions. Notably, they indicate relatively permanent or constant presence of waters (Gand et al., 2008). Thus, red-bed successions bearing such arthropod trace fossils underwent periods of relatively perennial waters. In the case of the Catalan Pyrenees, this is in accordance to the seasonality found throughout the Permian red-beds. Cylindrical burrows (*Skolithos*-like) exist in all red-bed sequences; with respect to strata surfaces, they are either horizontal or vertical, indicating quiet flow conditions and sudden deposition, respectively. Further comparisons between the record of these ichnofossils in the studied units will contribute to untangle the ichnonetwork evolution during the Permian and Triassic, which has already been related to the environmental crisis of this transition (Baucon et al., 2014).

9.2.3. *Tetrapod trace fossils and bone remains*

The studied Permian and Triassic successions yield an exceptional record of tetrapod footprints, being largely abundant and diverse throughout the three red-bed units. Moreover, bone remains have been recovered for the first time in the Catalan Pyrenees. Bones are sparse and often fragmentary, and they are only identified in the lower Upper Red Unit (lower URU) and in the Buntsandstein facies unit so far. As tetrapod footprints are much more abundant than bones, it is suggested that the Permian and Triassic environments from the Catalan Pyrenean Basin were conducive for footprint preservation but difficulted bone preservation. This is a common feature of late Paleozoic terrestrial successions worldwide, where tetrapod footprints are much more abundant than bone remains (Falcon-Lang et al., 2010).

The poor bone record prevents deep analyses related with the paleoenvironmental setting. Nevertheless, two main types of bone preservation are identified in the Buntsandstein facies unit: (1) fragmentary unidentifiable bones occur in fluvial channel deposits (see **chapter 5**), indicating that they were probably transported and fragmented (like pebbles) by a relatively high water flow; (2) the two well-preserved archosauromorph teeth were found close each other (separated few decimeters) in the same thin-bedded sequence (but not in the same layer) of a crevasse splay deposit composed of fine-

to very fine-grained sandstones displaying small ripples and parallel lamination (see **chapter 8**), suggesting relatively low water flow.

The vast and diverse tetrapod footprint record of the Catalan Pyrenees allows to decipher the paleoenvironmental affinities and behavior of the trackmakers, also contributing in the knowledge of the potential composition of tetrapod communities and in paleoenvironmental analyses (e.g., Melchor, 2015). Footprints are found either isolated or forming trampled surfaces. The LRU ichnoassemblage evidences a clear link of ichnotaxa with the paleoenvironmental setting (see **chapter 4**). On one side, the meandering fluvial deposits record abundant ichnites, most of them associated to amphibian trackmakers and swimming trace fossils, indicating relatively high water availability. On the other side, the lack of amphibian tracks and the relatively low number of footprints in the unconfined runoff surfaces suggest low water availability (see **chapter 4**). Therefore, environmental conditions constrained tetrapod distribution, especially those depending on aquatic environments. Similar ichnotaxa associations are attributed to the *Batrachichnus* ichnofacies (Hunt and Lucas, 2007), thus the observed ichnotaxa distribution in the LRU may correspond to different ichnocoenosis of the mentioned ichnofacies (see **Annex 2** and below for further discussion on ichnocoenosis). Tetrapod footprints in the upper URU at Coll de Terrers are relatively sparse if compared with the large, well-exposed surfaces of the locality (see **chapter 6**). In these playa-lake/ephemeral lacustrine settings, periods of desiccation were dominant, precluding a wide distribution of tetrapods. The paleoenvironmental data of the lower URU footprints (Robles and Llompart, 1987) suggest a similar scenario as that of the upper URU. Due to the poorly known worldwide record, middle and late Permian footprints have not been related to the tetrapod ichnofacies so far, although late Permian footprints have been used in paleoenvironmental analyses (e.g., Kustatscher et al., 2017). Exceptional trampled surfaces exist in the Buntsandstein facies unit, especially at the Erillcastell locality (see **chapter 7**). Most of the footprints in these surfaces are oriented in the same direction, suggesting a gregarious behavior of the trackmakers (small-sized archosauromorphs). On the contrary, large archosaur footprints (i.e., Chirotheriidae morphotypes) are isolated. Preliminary data of ongoing studies suggests a potential relationship between paleoflow, sloping (i.e., paleosurface inclination) and footprint orientation.

Besides tracks and trackways of terrestrial locomotion, swimming trace fossils are also present. The thickest LRU meandering fluvial deposits preserve abundant swimming ichnites (scratches, i.e., dragged digit impressions; see **chapter 4**), confirming a persistent and relatively high water table (with respect to the size of the trackmakers). Consequently, scratches are less abundant in relatively thin fluvial channel deposits and in crevasse splay deposits, where water tables were lower (see **chapter 7**). Thomson and Droser (2015) discussed that the preservation of particularly abundant swimming scratches in Early Triassic deposits is derived from a low bioturbation of the substrate, related to a low population of benthic invertebrate fauna due to a delayed recovery from the end-Permian mass extinction. Nevertheless, after the present study, such ecological situation appears to be not exclusive of a post-extinction scenario. Notably, tetrapod swimming scratches of the LRU meandering fluvial deposits display tiny, well-preserved details (see **chapter 4**). These meandering fluvial systems correspond to short humid periods within the early Permian semi-arid and arid climate (see **chapter 3**);

therefore, benthic communities were low in abundance, implying a low level of bioturbation and an enhanced preservation of tetrapod swimming scratches.

These paleoenvironmental affinities of the Permian and Triassic tetrapod track record from the Catalan Pyrenees are coupled by the two newly documented ichnoassociations from the Middle Triassic Muschelkalk detrital unit of the Catalan Basin (see **Annexes 1 and 2**). The relationship between track preservation type (*Rhynchosauroides* isp.) and substrate rheology (conditioned by moisture and thus by the specific environmental setting) is well-documented in the sabkha settings of the Middle Muschelkalk (see **Annex 2**): (1) deep, deformed tracks occur in soft, saturated substrates; (2) trampled surfaces with well-impressed tracks occur in substrates of intermediate moisture that did not undergo desiccation; (3) optimally-preserved tracks (i.e., including pad and claw impressions) and faint impressions (i.e., tracks only preserving claw impressions) are found in substrates that underwent desiccation. A similar case occurs in the fluvial settings of the Pyrenean LRU and Buntsandstein facies (see **chapter 4 and 7**, respectively), where swimming scratches (*Characichnos* isp.) are associated to different tracks derived from a walking locomotion (i.e., associated to different ichnogenera: *Batrachichnus*, *Limnopus* and cf. *Amphisauropus* in the LRU, and *Prorotodactylus* and Chirotheriidae in the Buntsandstein facies unit). In summary, all these examples denote a wide distribution of the trackmakers throughout the environmental settings that point to a wide distribution of: (1) lepospondyls and/or small temnospondyls (potential *Batrachichnus* trackmakers) and large temnospondyls (potential *Limnopus* trackmakers) during the early Permian, and (2) archosauromorphs during the late Early and Middle Triassic. Furthermore, the two studied Middle Muschelkalk localities preserve well-differentiated tetrapod ichnoassociations, suggesting an environmental constrain on the tetrapod distribution: large archosauromorph footprints are more abundant in terrestrial paleoenvironments with low influence of coastal or marine systems, whereas small archosauromorph footprints dominate in the coastal settings. Future works will eventually confirm the use of tetrapod ichnofacies and ichnocoenosis in paleoenvironmental analyses (e.g., Hunt and Lucas, 2007, 2016; Melchor, 2015). In these studies, time may appear as a constraining factor because, in many cases, different tetrapod ichnogenera from different geological periods are found in the same settings. This is the case of the Catalan Pyrenees, where both ichnoassociations from the LRU (early Permian) and the Buntsandstein facies unit (late Early Triassic) are settled in meandering fluvial deposits, though ichnotaxa and their potential trackmakers are completely different.

The long succession of tetrapod ichnoassemblages and their potential trackmakers, together with bone remains, show a spatial and temporal distribution throughout the studied localities, as well as a successive replacement of tetrapod ecosystems from the early Permian to the Middle Triassic (Fig. 9.1):

- **Ichnoassemblage I:** The LRU tetrapod ichnoassociations (see **chapter 4**) are similar to those of the early Permian footprint record from France (Gand and Durand, 2006), Morocco (Voigt et al., 2011a), New Mexico (Van Allen et al., 2005; Voigt and Lucas, 2016a) and Argentina (Melchor and Sarjeant, 2004). Potential trackmakers correspond to lepospondyls and/or small temnospondyls (*Batrachichnus*), large temnospondyls (*Limnopus*), basal amniotes (i.e., seymouriamorphs, cf. *Amphisauropus*, and diadectomorphs, cf. *Ichniotherium*), synapsid

“pelycosaurs” (*Dimetropus*), captorhinomorphs (cf. *Varanopus* and *Hyloidichnus*) and bolosaurids or araeoscelids (*Dromopus*).

- **Ichnoassemblage II:** The lower URU footprints (see Robles and Llompart, 1987) are most probably equivalent to the ichnogenus *Merifontichnus*, recovered from the Wordian (middle Permian) of the French Lodève Basin (Gand et al., 2000; Michel et al., 2015), and probably from the Kungurian (late early Permian) of the Italian Orobic Basin (Marchetti, 2016). This ichnogenus suggests the presence of derived captorhinids, possibly a non-diapsid reptilian (Marchetti, 2016). Similarly, the vertebra recovered from lower URU is tentatively attributed to cf. *Ennatosaurus tecton*, a synapsid caseid known from the early Wordian of Russia, although the Pyrenean vertebra suggests that such specimen was larger than those from Russia (see **chapter 5**). Noteworthy, this vertebra is stratigraphically above the tetrapod footprints, thus the latter might be older than Wordian. Regarding similar caseid record in nearing basins, large specimens are known from the Permian localities of Sardinia (Ronchi et al., 2011; Romano and Nicosia, 2014) and the French La Lieude (Reisz et al., 2011). Additionally, the large footprints of *Planipes*, ichnogenus from the middle Permian of France (Lodève Basin, Gand et al., 2000; Saint-Raphaël Estérel Basin, Gand et al., 1995) and South Africa (Tapinocephalus assemblage zone, Valentini et al., 2009), are assigned to caseids and/or therapsid trackmakers. In summary, all these remains suggest a Pangean distribution of large caseids and, at least, a paleoequatorial distribution of derived captorhinids during the middle Permian.
- **Ichnoassemblage III:** The upper URU footprint morphotypes (see chapter 6) suggests the potential presence of large therapsids and pareiasaurs by similarities to the late Permian *Dicynodontipus* (recovered from the *Cistecephalus* assemblage zone of South Africa, de Klerk, 2002, and Northern Italy, Kustatscher et al., 2017 and references therein) and *Pachypes* (recovered from Northern Italy, Valentini et al., 2009, Russia, Valentini et al., 2009 after Gubin et al., 2003 and Surkov et al., 2007, Morocco, Voigt et al., 2010, and Niger, Smith et al., 2015), respectively. The small lacertoid-like footprint morphotype of the upper URU, tentatively assigned to *Rhynchosauroides* or *Dromopus* (of Pangean distribution), would potentially correspond to small basal archosauromorphs or basal lepidosauromorphs. Araeoscelids and bolosaurids, the potential trackmakers of *Dromopus*, are not included, as they do not reach the late Permian, although *Dromopus* does (Voigt and Lucas, 2016b). Therefore, *Dromopus* possibly is possibly linked to several trackmakers, which is also suggested by its widespread distribution, being the most common Permian ichnotaxon. In summary, all these remains support a Pangean distribution of large therapsid and pareiasaurs and of small diapsids. It is remarkably that Sidor et al. (2005) suggested a potential endemism prompted by the climate during the late Permian. The herein inferred Pangean distribution is compatible with such endemism, because footprint trackmakers refer to major taxonomic groups (e.g., families; Falcon-Lang et al., 2010).
- **Ichnoassemblage IV:** The widely distributed ichnoassociations throughout the Buntsandstein facies unit of the Catalan Pyrenees (see **chapters 5 and 7**) are dominated by archosauromorph and basal archosauriform tracks. Most of the trackmakers were generally small-sized (body length of ca. 50 cm), and larger specimens (2-3 m long) were present in lesser proportion. Similarly, the recovered teeth indicate the presence of predatory archosauromorphs (see **chapter 8**). Along Central Pangea, similar ichnoassemblages dominated by archosauromorph

tracks are found. Future findings, including direct remains, would demonstrate whether such distribution is wider or if it responds to the provincialization of terrestrial faunas in the aftermath of the end-Permian extinction (Sidor et al., 2013; see section 9.3 below). At this point, it is suggested that archosauromorphs took an important role on the recovery of the terrestrial ecosystems. As noted by Bernardi et al. (2015), fluvial settings were the preferential habitats of this group. These settings were widespread during Early (and Middle) Triassic times, facilitating a wide distribution of archosauromorphs.

- **Ichnoassemblage V:** The Buntsandstein fossil-sites of the Catalan Basin yield tetrapod footprints (Valdiserri et al., 2009; Fortuny et al., 2011a and references therein) mostly attributed to archosauromorphs and archosaurs, but also to therapsids. These ichnites deserve further studies, which would contribute to the reconstruction of the terrestrial ecosystems during the early Middle Triassic, where temnospondyls and procolophonids were also present (Fortuny et al., 2011b, 2014).
- **Ichnoassemblage VI:** The Middle Muschelkalk footprints correspond to relatively large chirotheriids (*Chirotherium* and *Isochirotherium*, see **Annex 1**), attributed to rauisuchian archosaurs, and *Rhynchosauroides*, attributed to small archosauromorphs, possibly tanystropheids (see **Annex 2**). Throughout the European Middle Triassic Muschelkalk tracksites, similar or equivalent ichnoassociations are found, being linked to the paleoenvironmental setting and indicating a global distribution of the archosauromorph lineage.

The successive ichnoassemblages demonstrate several replacements of tetrapod communities from the early Permian to the Middle Triassic (Fig. 9.1). The paleoenvironmental succession shows that fluvial systems (mostly meandering channels and associated floodplain deposits) and distal alluvial systems dominate. Therefore, as discussed in section 9.3 below, these faunal replacements are linked to major global events, such as climate changes, that prompted different mass extinctions (Fig. 9.2).

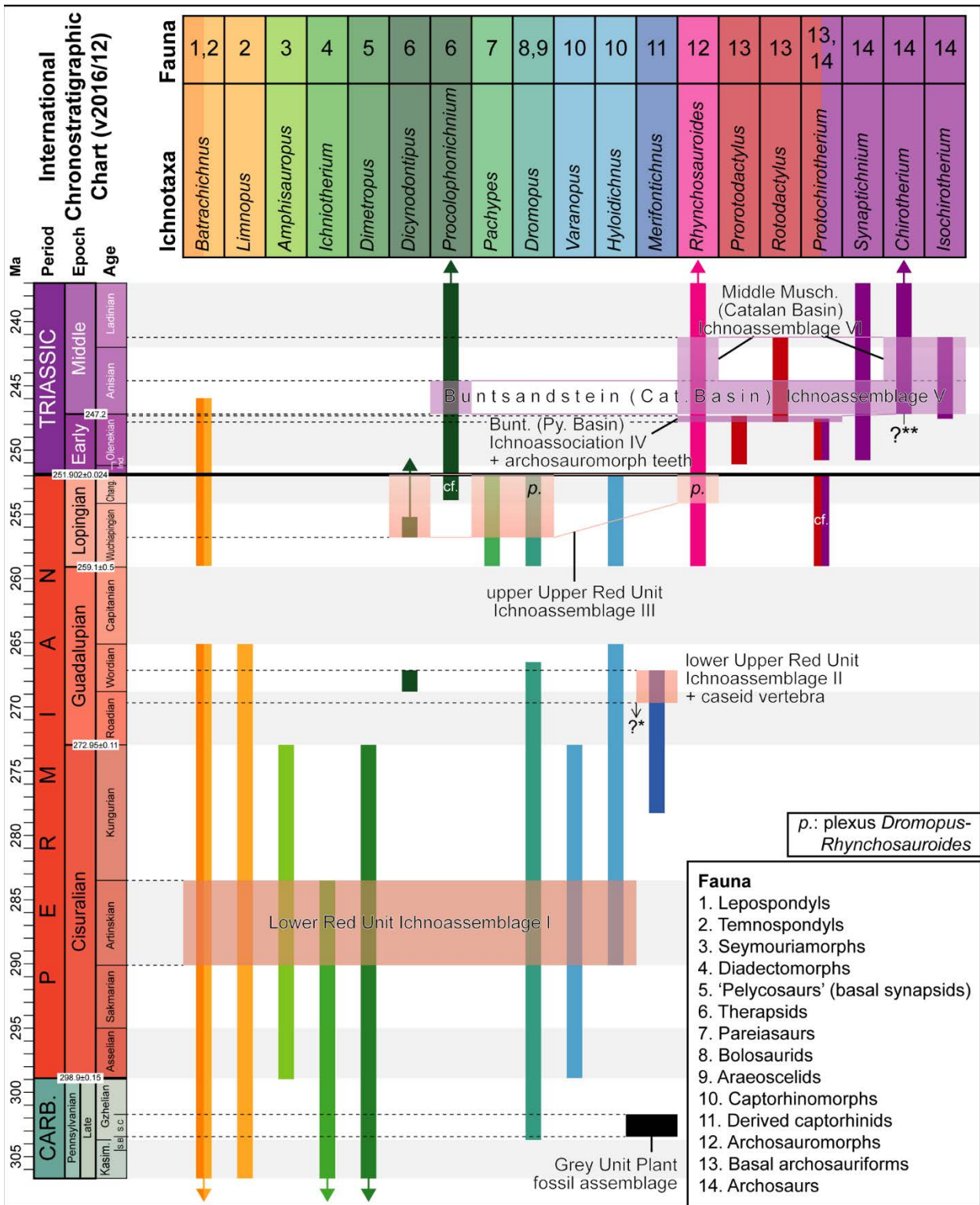


Figure 9.1. Biostratigraphy of the late Carboniferous–Middle Triassic continental fossils from the Catalan Pyrenean Basin (Py. Basin) and the Catalan Basin (Cat. Basin). Global distribution of tetrapod ichnotaxa compiled from: de Klerk (2002), Gand and Durand (2006), Klein and Lucas (2010b), Klein et al. (2013, 2015), Niedźwiedzki et al. (2013), Bernardi et al. (2015), Marchetti (2016), Voigt and Lucas (2016b). Ichnoassemblage V (Buntsandstein of the Catalan Basin) based on Calzada (1987), Valdiserri et al. (2009) and Fortuny et al. (2011a). ?* indicates uncertainty on the basal age of the Ichnoassemblage II. ?** indicates the potential presence of *Chirotherium* in Ichnoassemblage IV. cf.'s indicate uncertainty on the ichnotaxon identification (for *Procolophonichnium* see Klein et al., 2015; for *Protochirotherium* see Bernardi et al., 2015). CARB.: Carboniferous. S.B and S.C: Stephanian B and C, respectively. Chang.: Changhsingian. Ind.: Induan.

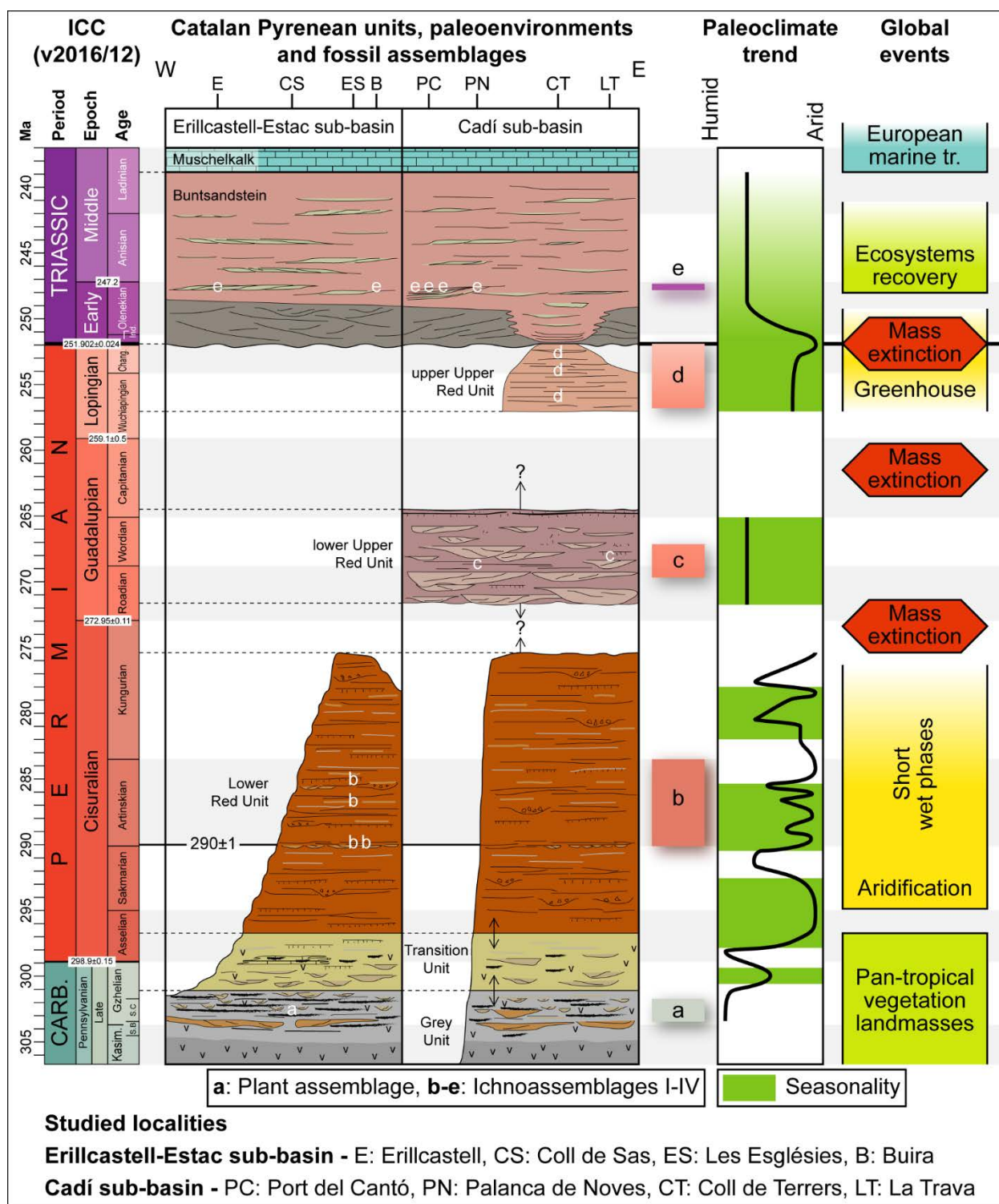


Figure 9.2. Data compilation from the Catalan Pyrenean localities studied showing the paleoenvironmental evolution, the time extension of the depositional units after the bio- and geochronological data (plant and ichnite assemblages, magneto- and cyclostratigraphy), the main paleoclimatic trend and the global events recorded. Localities are ordered from West to East, but distance between them is not at scale (see corresponding chapters for details). Arrows and question marks indicate uncertainty on the age of unit boundaries. Note the large time gap between the lower and upper Upper Red Unit and the different facies at the base of Coll de Terrers, where a conformable contact between Permian and Triassic deposits is observed. Abbreviations of the International Chronostratigraphic Chart (ICC) are as in Fig. 9.1.

9.3. The Paleozoic–Mesozoic transition events

The long terrestrial successions of the Catalan Pyrenees allow to constrain the paleoenvironmental and paleoclimatic evolution from the late Carboniferous to the Middle Triassic, shedding light on the global events that completely remodeled the terrestrial ecosystems (Fig. 9.2).

The exceptionally well-exposed GU-TU-LRU succession records the Carboniferous–Permian (C–P) transition and sheds light on climatic fluctuations during the pan-tropical aridification of Pangea. This global warming coincided with the end of the late Paleozoic ice age (LPIA; Montañez and Poulsen, 2013). The vast, widespread tropical forests of the late Carboniferous are represented by the GU plant fossil assemblage. The TU records the increasing seasonality occurring in the late Carboniferous–early Permian transition. The onset of the LRU red-beds represent the early Permian aridification, when the late Carboniferous mass vegetation depleted due to climatic conditions, also precluding coal accumulation. The distinct vertic features of the LRU demonstrate strong seasonality, linked to the monsoonal climate regime (Tabor and Montañez, 2002; Tabor and Poulsen, 2008). The rich LRU tetrapod ichnoassemblage supports the previously suggested dominance of amphibians and basal synapsids in terrestrial ecosystems (Sahney and Benton, 2008; Brocklehurst et al., 2017). Noteworthy, tetrapod footprints are found in specific LRU intervals, those corresponding to meandering fluvial systems and unconfined runoff waters. These intervals are possibly related with wet phases (cf. Roscher and Schneider, 2006) tentatively linked to short periods of relatively low concentrations of atmospheric CO₂ and peaks of glaciation in Southern Gondwana.

The paleoenvironmental setting of the lower URU denote more humid conditions than in the LRU. Otherwise, vertic features are also recognized throughout this unit, indicating that the early Permian seasonality persisted. Here it is suggested that this relatively humid climate correlates with the Guadalupian wet phase detected in the Iberian Basin (De la Horra et al., 2012) as well as in Northern European basins and the USA (Roscher and Schneider, 2006; Slowakiewicz et al., 2006) and Southern Gondwanan basins (Retallack et al., 2006). The revisited lower URU tetrapod remains, although sparse, evidence a replacement of faunas from the early to the middle Permian. Such replacement has been attributed to the debated Olson’s Extinction (see Brocklehurst et al., 2017 and Lucas, 2017).

The sudden sedimentological and mineralogical shifts from the lower to the upper URU denote an environmental change from relatively humid (sub-humid) to semi-arid conditions related to the late Permian aridification. The strong seasonality documented in the upper URU could correspond to the late Permian wet and dry phases of Slowakiewicz et al. (2009) and the uppermost Permian record of the Iberian Basin (De la Horra et al., 2012). The tetrapod remains recorded in this cyclic sequence are different from those of the lower URU. This tetrapod replacement is most probably due to the end-Guadalupian extinction (Retallack et al., 2006; Day et al., 2015; Lucas, 2017; or mid-Capitanian *sensu* Sheldon et al., 2014). The newly reported localities in this study allow to constrain in detail the Permian–Triassic (P–T) transition, occurring in the transition from the upper URU to the Buntsandstein facies unit (Fig. 9.2).

On one side, the basal braided fluvial deposits of the Buntsandstein facies correspond to the environmental shift and increased energy of the system during the P–T transition (Ward et al., 2000; Arche

and López-Gómez, 2005; Newell et al., 2010; Benton and Newell, 2014). These coarse-grained, commonly thick, deposits at the base of the Triassic record denote erosion of Permian strata, implying a time gap (see **chapter 5 and 7**). Nevertheless, on the other hand, the singular Coll de Terrers area (see **chapter 6**) is free from any major erosion and records a continuous sequence. Therefore, the P–T transition can be constrained in detail. In fact, the mineralogical results from Coll de Terrers show a potential increase in aridity from the uppermost URU to the basalmost Buntsandstein, possibly related with the greenhouse crises of this time interval (Retallack et al., 2011; Retallack, 2013; Rey et al., 2016). In the same way, the large derived therapsids and pareiasaurs, potentially recorded in the upper URU, are absent in the Buntsandstein deposits. Instead, when ecosystems began to stabilize after the end-Permian extinction, during the late Early Triassic, archosauromorphs started their domain, being an important group for the recovery of the remodeled ecosystems. Notably, as Lucas (2017) stated, this change from therapsid- and pareiasaur-dominated to archosaur-dominated assemblages do not characterize the P–T boundary itself, as archosauriforms possibly appeared already in the late Permian (Bernardi et al., 2015). As the Middle Triassic fossil record of the Catalan Basin indicates, the archosauromorph lineage persisted and dominated all the terrestrial Mesozoic ecosystems from the Late Triassic onwards.

In summary, the Catalan Pyrenees exceptionally record two major transitions of Earth history: (1) the Carboniferous–Permian aridification, representing a unique transition from icehouse to greenhouse; (2) the Permian–Triassic transition, corresponding to the most devastating mass extinction and the transition to the so-called modern ecosystems.

Capítol 10. *Conclusions*

The multidisciplinary study of the terrestrial end-Carboniferous, Permian and Triassic from the Catalan Pyrenees allowed to obtain new data about the paleoenvironmental and paleoclimatic evolution, as well as changes in the terrestrial ecosystems during the Paleozoic–Mesozoic transition.

- Geological fieldwork and paleontological prospection implied the discovery and characterization of many fossil sites. The integration of these fossil sites in a physical correlation frame allowed to establish their relative succession. This frame is given by the measurement of stratigraphic sections, their cartography and integration in the regional geology. A total of 10 fossil sites (most of them bearing tetrapod ichnites) within 18 sections, representing a total of 2370 m measured and covering a West-Est oriented belt of 59 km, have been situated in stratigraphic continuity. Previously, only two ichnite fossil sites, both from the same section, were known.
- The sedimentological data associated to the paleontological sites allowed to characterize features that influenced the taphonomic bias such as substrate rheology, the presence of water inferred from the preservation of tetrapod swimming trace fossils, the amount of trace fossils in each surface, the presence of true tracks and undertracks and their morphological variation, etc.
- Tetrapod ichnite diversity and associated ichnotaxa were identified thanks to photogrammetry, being a useful technique for ichnological studies. The 3D models of the footprints reveal features unperceived under traditional techniques and allow defining depth patterns, which are directly related with the trackmaker locomotion. This implies the improvement of the track-trackmaker correlation. In the same way, the 3D models allow to distinguish the (extra-) morphological and preservation variability of tetrapod ichnites.
- The studied fossil content shows diverse associations related with specific environments and of biochronologic value. Seven fossil assemblages are defined (Fig. 9.1): a plant fossil assemblage and four ichnoassemblages (I-IV) are defined in the Pyrenean Basin, and two ichnoassemblages (V and VI) are defined in the Catalan Basin. The ichnoassemblage V was studied in previous works, and here it is integrated to completed the fossil assemblage succession. Bone remains complement the tetrapod record.
 1. The plant fossil assemblage is found in the Grey Unit, it is composed of several taxa showing the presence of: horsetails (equisetophids, including Calamitales and Sphenophyllales), ferns (Marattiales and Zygopteridales in a lesser degree), abundant pteridosperms (Medullosales), Cordaitales, and lycophids (Lepidondendrales, although sparse). The set of taxa indicates a Stephanian C age (late Carboniferous).
 2. The ichnoassemblage I is found in the Lower Red Unit, it is composed of: *Batrachichnus salamandroides*, *Limnopus* isp., cf. *Amphisauropus*, cf. *Ichniotherium*, *Dromopus* isp., cf. *Varanopus*, *Hyloidichnus* isp., *Dimetropus leisnerianus* and three types of *Characichnos* (swimming trace fossils) associated with the first three ichnotaxa. These ichnotaxa indicate the potential presence of: small temnospondyls and lepospondyls, large temnospondyls, seymouriamorphs, diadectomorphs, araeoscelids and/or bolosaurids, captorhinomorphs and basal synapsids (“pelycosaurs”). Biostratigraphically, this ichnoassemblages indicates an Artinskian age (early Permian). Otherwise, abundant arthropod

trace fossils (mostly corresponding to triopsids) are common, mainly including the ichnogenera *Rusophycus* and *Acripes*.

3. The ichnoassemblage II is found in the lower part of the Upper Red Unit, it is composed by a set of footprints that could not be first hand studied because they are currently lost. The review of the previously published data suggests the potential presence of *Merifontichnus*, which is attributed to derived captorhinids. This unit also includes a caseid vertebra attributed to cf. *Ennatosaurus tecton*, which suggest an early Wordian age (middle Permian). This age agrees with the biostratigraphic interval of the aforementioned ichnogenus.
4. The ichnoassemblage III is found in the upper part of the Upper Red Unit, it is composed of a set of footprints differentiated in four morphotypes (I-IV): morphotype I shows some similarities with *Dicynodontipus* (ichnogenus associated to therapsids); morphotype II shows some similarities with *Pachypes* (ichnogenus associated to pareiasaurs); morphotype III is an unknown form, possibly corresponding to deformed footprints due to substrate consistency; morphotype IV shows some similarities with *Dromopus* and *Rhynchosauroides* (ichnogenera associated to small eureptiles and possibly to basal archosauromorphs). Otherwise, abundant arthropod trace fossils are common, most of them similar to those from the Lower Red Unit (*Rusophycus* and *Acripes*).
5. The ichnoassemblage IV is found in the Buntsandstein facies unit, and it extends throughout nearly all the studied localities. The identified ichnotaxa include: *Prorotodactylus mesaxonichnus* (recently erected as a new ichnospecies), cf. *Rotodactylus*, *Rhynchosauroides* cf. *schochardti*, other undetermined *Rhynchosauroides* specimens, diverse chirotheriid morphotypes, possibly related with *Protochirotherium* and *Chirotherium*, an unknown morphotype (Morphotype A), and *Characichnos* associated with the recently erected *Prorotodactylus* ichnospecies and the chirotheriids. These ichnotaxa are attributed to small archosauromorphs and basal archosauriforms, except chirotheriids, which are attributed to large archosauriforms and archosaurs. Similarly, the two recovered teeth belong to predatory archosauromorphs. The corresponding biostratigraphic interval is from the late Olenekian to the basal Anisian (Early–Middle Triassic), which is in agreement with the identified palynological association (lycopod spores and other bisaccate and taeniate pollen types).
6. The identified tooth from the Buntsandstein facies (early Anisian, Middle Triassic) from the Catalan Basin represents the first direct evidence of archosauromorphs from this region, enriching and completing the previously known ichnite record of this group. Based on ichnotaxonomic differences with the Catalan Pyrenees and with the Middle Muschelkalk facies (see below), the ichnoassemblage V (composed of *Procolophonichnium*, *Rhynchosauroides*, *Synaptichnium*, *Chirotherium* and *Isochirotherium*) is constituted.

7. The ichnoassemblage VI is found in the Middle Muschelkalk facies (late Anisian–middle Ladinian, Middle Triassic) from the Catalan Basin. Ichnotaxa include *Isochirotherium* isp., *Chirotherium* isp. and *Rhynchosauroides* isp. A distribution of tetrapod ichnotaxa controlled by facies types is established, suggesting a potential differentiation of vertebrate ichnofacies and ichnocoenosis. This fact makes tetrapod footprints a useful tool in paleoenvironmental analyses.
- The dating of the succession frame and the consequent calibration of the biozones is here based on magnetostratigraphy. The Lower Red Unit results allowed to identify the Kiaman superchron (early Permian), of inverse polarity. These data agree with absolute dating of this unit conducted by other authors. The paleomagnetic data of the Grey Unit and Upper Red Unit indicate a secondary remagnetization, precluding any correlation to the global magnetostratigraphy scale.
 - Preliminary cyclostratigraphic analyses from the Upper Red Unit suggest an orbital forcing, with possible eccentricity (of 100 and 400 kyr) and obliquity (of ~1-1.2 Myr) cycles, allowing a calibration of the relative time of sedimentation.
 - Therefore, the bio- and geochronological data give a chronostratigraphic value to the lithological units and indicate the presence of sedimentary hiatuses different from those published in previous works (Fig. 9.2).
 1. The uppermost part of the Grey Unit is of late Carboniferous age.
 2. The Transition Unit ranges from the latest Carboniferous to the earliest early Permian. The few chronological markers known so far from this unit preclude a better precision of the temporal boundaries.
 3. The Lower Red Unit comprises most of the early Permian, possibly until the middle–late Kungurian.
 4. The lower part of the Upper Red Unit is of middle Permian age, possibly ranging from the early Roadian to the earliest middle Capitanian.
 5. The upper part of the Upper Red Unit probably ranges from the early–middle Wuchiapingian to the end of the Changhsingian (late Permian).
 6. The Buntsandstein facies unit of the Pyrenean Basin probably ranges from the Induan to the middle–late Ladinian (Early–Middle Triassic).
 - The sedimentological data obtained by the measurement of stratigraphic sections allowed to characterize the paleoenvironmental and paleoclimatic succession. On one hand, the study of paleosols from the Grey, Transition and Lower Red units allowed to identify up to four pedotypes: Histosols, ferric horizons, Vertisols and Calcisols. Within these pedotypes, different subgroups have been identified and, in stratigraphic succession, they show the general paleoclimatic trend. On the other hand, X ray diffraction and fluorescence analyses allowed to identify the mineralogical and elemental variations of the Upper Red Unit (from the lower to the upper part of the unit) and the transition from the Upper Red Unit to the Buntsandstein facies unit. The set of mineralogical variations, such as those of quartz, albite, chlorite group, hematite, kaolinite

and muscovite/illite, together with the elemental trends of Al, K, Fe, Cu, Rb, Sr, Ni and Pb, show the climatic changes and the successive environmental conditions, such as possible acidifications and anoxia.

- All these analyses result in a model of paleoclimatic and paleoenvironmental changes for the studied succession, as well as for the tetrapod ecosystems evolution. Therefore, the following events have been identified: (1) aridification across the Carboniferous–Permian transition; (2) faunal replacement between the early and middle Permian; (3) faunal replacement between the middle and late Permian (late Guadalupian extinction); (4) aridification across the Permian–Triassic transition and faunal replacement (end-Permian extinction); (5) terrestrial ecosystems recovery during the Early–Middle Triassic.
- The detailed stratigraphic study, together with the sedimentological, ichnological, cyclostratigraphic and mineralogical analyses, as well as the regional lithostratigraphic correlation, allowed to identify (for the first time in southwestern Europe) a terrestrial succession where the Permian and Triassic are in sedimentary continuity. This section, called Coll de Terrers, opens the window to new detailed studies to define the Permian–Triassic transition in continental environments.
- The long and rich geological and paleontological records situate the Catalan Pyrenees as a global reference region to understand and characterize the successions of events that featured the terrestrial late Carboniferous, Permian and Triassic. The studied sedimentological and paleontological records allow to establish the paleoenvironmental evolution and crises at the equator of Pangea. This PhD thesis documents some of the most dramatic changes of Earth's history, such as a long term climatic change, the greatest mass extinction and the subsequent ecosystems recovery.

Agraïments

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