# PALÆO VERTEBRATA

Special Volume 2-2023

EAVP
European Association of Vertebrate Palaeontologists

## Field trip guides of the 20th Annual Conference of the European Association of Vertebrate Palaeontologists, 26th June – 1st July 2023, Sabadell (Barcelona), Spain

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**Editor:**
Arnau Bolet

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# FIELD TRIP GUIDE TO THE PERMIAN TERRESTRIAL RED-BEDS OF THE CENTRAL-EASTERN CATALAN PYRENEES (NE IBERIAN PENINSULA) AND OVERVIEW OF THE CATALAN PERMIAN-TRIASSIC VERTEBRATE RECORD

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The end of the Palaeozoic and the beginning of the Mesozoic are marked by several drastic changes of global impact. They include severe climate shifts and the reorganisation of the landmasses forming Pangaea that triggered the most severe mass extinction of Earth's history, altogether prompting a profound and continuous remodelling of ecosystems (Fig. 1). In this field trip we are going to dive into the terrestrial vertebrate ecosystems of the Permian of the Catalan Pyrenees (NE Iberian Peninsula), spanning a time interval of almost 20 million years. The geological and palaeontological record that we are going to visit are fair representations of these past ecosystems, especially for central Pangaea, and contribute to our understanding of how they evolved through drastic global planetary changes. In addition, we are going to examine further vertebrate fossils from other Permian and Triassic Catalan localities in order to obtain a more complete picture. This field trip guide includes a general introduction of the Palaeozoic-Mesozoic transition, followed by a review of the fossil vertebrate record of Catalonia corresponding to this time interval, and finally a description of the outcrops and localities that will be visited.

## THE LATE PALAEOZOIC TO EARLY MESOZOIC VERTEBRATE ECOSYSTEMS

In order to understand the events characterising the Palaeozoic-Mesozoic transition we have to go back to the end of the Carboniferous period and its transition to the Permian, about 299 million years ago (Ma). The late Carboniferous to early Permian time interval is characterised by a marked climate change similar to that of the present, evolving from icehouse to greenhouse conditions accompanied by a stark aridification trend (Montañez *et al*., 2007). The continental configuration played an important role in the climate and hence the environmental settings (Chumakov and

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Zharkov, 2002; DiMichele *et al*., 2020; Richey *et al*., 2020). The continental landmasses were assembling the supercontinent Pangaea, with the Panthalassa ocean surrounding it and the Tethys sea forming a wedge at its eastern pantropical coast (Golonka and Ford, 2000; Domeier *et al*., 2012; Torsvik and Cocks, 2013; Scotese, 2014a). The collision of the southern landmasses, Gondwana, with the northern ones, Laurussia, implied the closure of the Rheic ocean (that entered from the West between the northern and southern landmasses), and the formation of the Variscan orogen, extending from West to East along the equator of Pangaea (Golonka and Ford, 2000; Domeier *et al*., 2012; Torsvik and Cocks, 2013).

The South of Gondwana (the late Palaeozoic South Pole) was covered by different, isolated ice sheets, directly related with atmospheric $CO_2$ fluctuations, which influenced the global climate and constituted the so-called late Palaeozoic ice age (LPIA) (Montañez *et al*., 2007, 2016; Fielding *et al*., 2008; Isbell *et al*., 2012; Montañez and Poulsen, 2013; Richey *et al*., 2020). During the late Carboniferous, atmospheric oxygen levels were relatively high and the climate was wet within the pantropical belt, although short dry periods also occurred (DiMichele, 2014; Michel *et al*., 2015; Montañez, 2016; Opluštil *et al*., 2017; Mujal *et al*., 2018a; DiMichele *et al*., 2020). These climatic and atmospheric conditions prompted the formation of vast, widespread vegetation landmasses through the pantropical belt (Opluštil *et al*., 2021) that in the present day are recorded by large coal deposits. Therefore, the Carboniferous terrestrial, paralic and shallow marine successions of these latitudes are featured by greyish deposits (low oxidation), commonly associated with coal intervals (e.g., Opluštil *et al*., 2021). Within the large plant diversity, the arborescent forms of horsetails and ferns, reaching heights of several metres, were notably abundant (DiMichele, 2014). These terrestrial environments were already inhabited by diverse tetrapod groups (e.g., non-amniote tetrapods, reptiliomorphs and basal synapsids), often linked to aquatic settings. Their distribution was also probably constrained by the climatic conditions (Pardo *et al*., 2019).

The transition from the Carboniferous to the Permian featured a peak of glaciation (Montañez and Poulsen, 2013). Afterwards, during the Sakmarian (early Permian), an aridification process started, and the ice sheets in the South Pole were drastically reduced due to a global warming, resulting in the end of the LPIA (Roscher and Schneider, 2006; Tabor and Poulsen, 2008; Isbell *et al*., 2012; Montañez and Poulsen, 2013). All these changes are recorded by globally distributed terrestrial deposits, often of alluvial origin and commonly reddish due to oxidising conditions, the so-called red-beds, and by a nearly total absence of coal (Chumakov and Zharkov, 2002). Notably, these changes appear to be slightly diachronous from East to West along the pantropical Pangaean belt (Michel *et al*., 2015), possibly due to the drifting of the landmasses (e.g., Roscher and Schneider, 2006). As a result, the Permian is characterised by dominant dry climates with shorter humid periods (Roscher and Schneider, 2006; Michel *et al*., 2015; Mujal *et al*., 2018a). Regarding the continental distribution, northern Euramerica and part of Asia collided, forming Laurasia (Golonka and Ford, 2000; Scotese, 2014a, 2014b). Towards the end of the Permian, the Palaeotethys gradually closed until its disappearance, while the Neotethys (generally, the Tethys sea) opened.

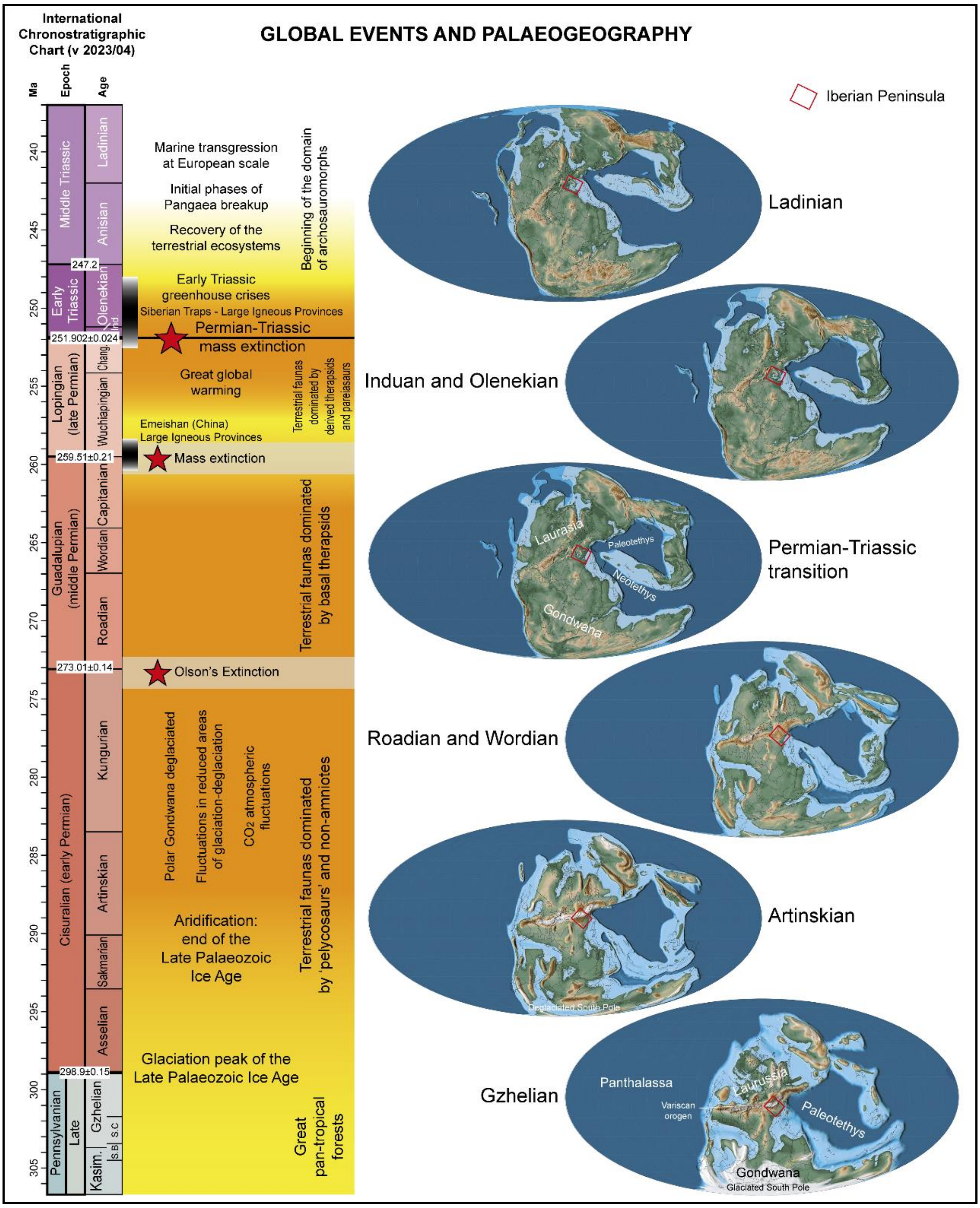


**Figure 1.** Global context. Main events and palaeogeography during the late Palaeozoic and early Mesozoic (see Mujal, 2017, and text for references). Palaeogeographic maps from Scotese (2014a, b).

With this distribution, the continental landmasses displayed a relatively symmetric shape, with the equator of the planet as the plane of reference (Fig. 1). The atmospheric circulation patterns tended to a symmetrical distribution that implied the establishment of different climatic biomes approximately parallel or subparallel to Earth's equator (Parrish and Peterson, 1988; Rees *et al.*, 2002; Tabor and Poulsen, 2008). Specifically, since the early Permian, a monsoonal climate was established in the equatorial zone (Tabor and Montañez, 2002). During the Permian, ecosystems underwent profound changes: the generally dominant wet periods switched to dominantly dry periods. Despite aridification and global warming, terrestrial ecosystems were still rich and diverse. Early Permian (Cisuralian) terrestrial faunas were dominated by non-amniote tetrapods (such as temnospondyls) and synapsids (‘pelycosaurs’), displaying a wide size variation, from few centimetres to several metres long. Other tetrapod groups, such as basal amniotes (e.g., seymouriamorphs and diadectomorphs) and several groups of basal reptiles (e.g., captorhinomorphs, bolosaurids and araeoscelids), were also present (Dunne *et al*., 2018). The transition to the middle Permian (Guadalupian) is characterised by the Olson’s Extinction, which implied a terrestrial faunal replacement that was unequal and heterochronic along Pangaea. Such replacement brought to the dominance of basal therapsids (e.g., dinocephalians), together with diverse parareptile groups, and a diminishing of non-amniote faunas (Brocklehurst *et al*., 2017). This trend is not only recorded by tetrapod direct remains, but also by footprints, as well as plant remains (Marchetti *et al*., 2022a). This is particularly relevant considering that the most part of the Permian tetrapod record is based on ichnites, many of which with biostratigraphic value (Gand and Durand, 2006; Lucas, 2019; Mujal *et al*., 2020; Schneider *et al*., 2020; Marchetti *et al*., 2022a, b), as is the case of the Catalan Pyrenees (Fig. 2). Towards the end of the Guadalupian, a great mass extinction has been identified, possibly coinciding with the emission of large amounts of basalt (large igneous provinces, LIP) in Emeishan, southwest of China (Retallack *et al*., 2006; Sheldon *et al*., 2014; Day *et al*., 2015 and references therein). In the aftermath of the mass extinction, during the late Permian (Lopingian), faunas were dominated by derived therapsids and pareiasaurs (Sahney and Benton, 2008; Day *et al*., 2015; Day and Rubidge, 2021). Another relevant event from that time interval is the appearance of the first archosauromorphs, a group of primary importance during the Triassic (Ezcurra *et al*., 2014). Although continents were assembled in one, faunas were not homogeneously distributed because the different climatic biomes induced faunal endemism (Sidor *et al*., 2005, 2013).

Towards the end of the Permian, about 252 Ma, an important increase in aridification, together with marine acidification and anoxia, occurred (Algeo *et al*., 2011; Payne and Clapham, 2012). This situation was possibly the result of large emissions of methane and sulphur compounds derived from the Siberian volcanic activity that produced massive deposits, the large igneous provinces known as Siberian Traps (Retallack *et al*., 2006; Svetlitskaya and Nevolko, 2016; Dal Corso *et al*., 2022). This set of environmental changes and disasters culminated with what has been acknowledged as the greatest mass extinction of Earth’s history, in which the disappearance of about the 70% of terrestrial vertebrate families is estimated, as well as deforestation of the ecosystems (Erwin, 1994; Benton, 2003, 2016; Hallam, 2004; Sahney and Benton, 2008; Benton and Newell, 2014). It should be remarked that the magnitude of the different Permian extinctions has been lately debated, especially on terrestrial ecosystems (see previous references and Lucas, 2017, 2018), though clear faunal turnovers have been identified (Smith and Botha-Brink, 2014; Dal Corso *et al*., 2022).

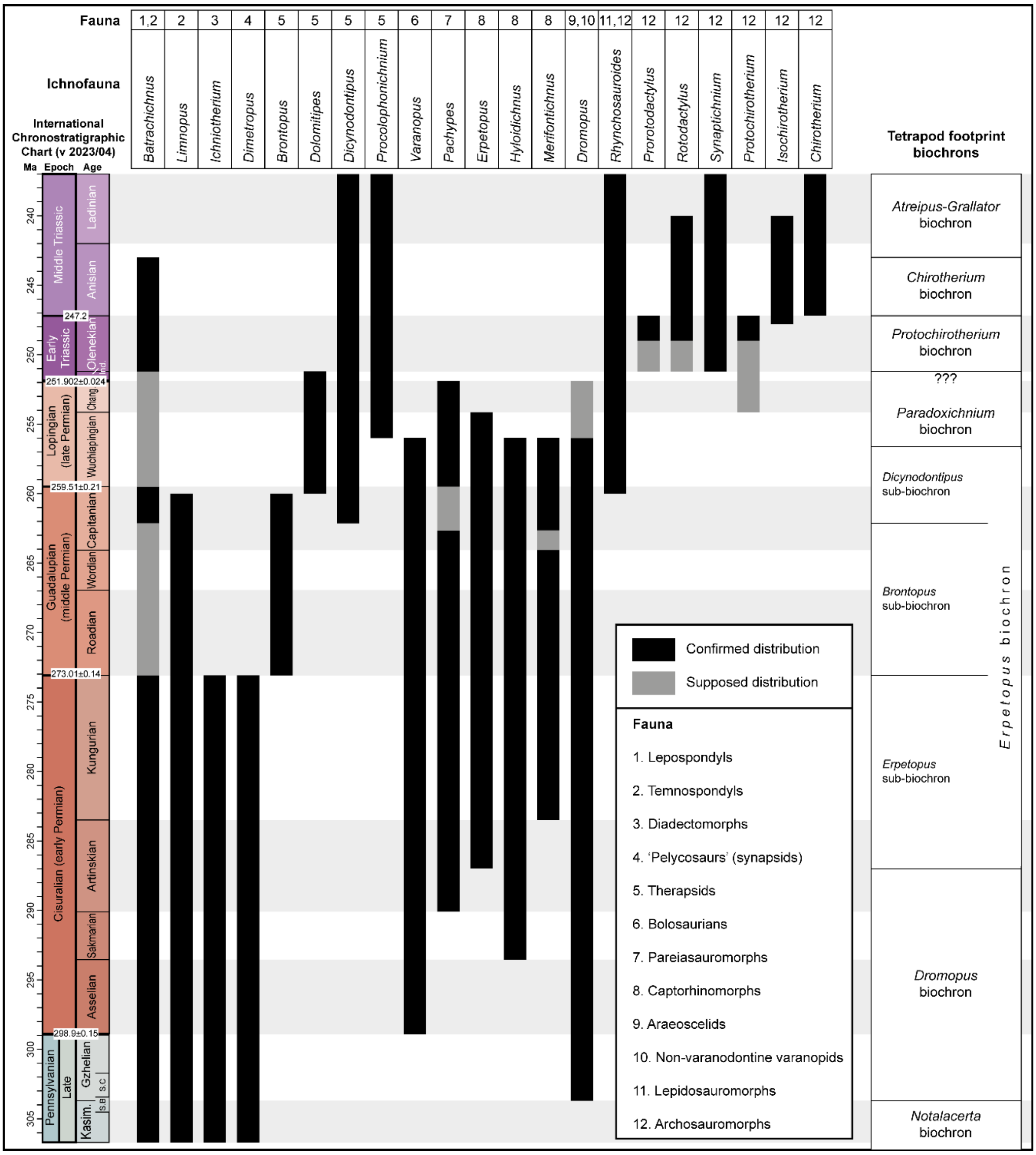


**Figure 2.** Tetrapod ichnostratigraphy depicting ichnotaxa present in the Permian and Triassic of Catalonia (including those identified as cf.). Biostratigraphic ranges and biochrons after Schneider *et al*. (2020) and Marchetti *et al*. (2021, 2022b).

The beginning of the Triassic is characterised by the persistence of conditions of extreme aridity (Retallack *et al*., 2011; Retallack, 2013; Rey *et al*., 2016) and many empty ecological niches that led to the restructuration of terrestrial ecosystems and the establishment of modern faunas (Benton *et al*., 2004). It has been hypothesised that recovery of ecosystems was slow and it was not until the transition from the Early to the Middle Triassic (Olenekian-Anisian), about 5 Myr after the end-Permian mass extinction, when they began to regenerate and stabilise (Sahney and Benton, 2008; Irmis and Whiteside 2012; Smith and Botha-Brink, 2014; Benton, 2016). At a planetary scale, the initial phases of the breakup of Pangaea started, although the clear fragmentation of the supercontinent occurred by the end of the Triassic and the beginning of the Jurassic (Golonka and Ford, 2000), linked to the end of the Variscan cycle (Torsvik and Cocks, 2013). The Triassic terrestrial deposits often display reddish colouration, similar to the Permian red-beds, as it is indeed the case in the Catalan Pyrenees. Generally, in successions encompassing the Permian-Triassic transition an increase of the energy of the continental sedimentary systems is observed, with coarser deposits, linked to the loss of vegetation mass in the aftermath of the extinction (Ward *et al*., 2000; Michaelsen, 2002; Arche and López-Gómez, 2005; Newell *et al*., 2010; Benton and Newell, 2014; Dal Corso *et al*., 2022). As a result, the Permian-Triassic boundary is recorded in few localities around the planet, Russia and South-Africa among others, but also in Europe (e.g., Scholze *et al*., 2017) and possibly also in the Catalan Pyrenees (Mujal *et al*., 2017a). The earliest Triassic faunas in terrestrial environments were dominated by 'disaster taxa', survivors of the mass extinction, such as *Lystrosaurus* (e.g., Romano *et al*., 2020; Smith *et al*., 2022). In any case, stereospondyl temnospondyls and basal archosauromorphs were abundant in aquatic environments (Sahney and Benton, 2008; Romano *et al*., 2020). As ecosystems became stable, archosauromorphs diversified, occupying a large variety of ecological niches and increasing in percentage (Foth *et al*., 2016; Ezcurra and Butler, 2018). This is also observed in the rich tetrapod ichnological record of the Triassic, with abundant and diverse (both in morphology and size) ichnotaxa correlated to archosauromorphs (Klein and Lucas, 2021). This success is related with ecological advantages, both in locomotion and feeding, progressively marginalising other groups such as temnospondyls (Fortuny *et al*., 2016). Eventually, between the end of the Middle Triassic and the beginning of the Late Triassic, archosaurs, including the dinosaur lineage, began their domain in the terrestrial ecosystems (Brusatte *et al*., 2011).

## THE LATE PALAEOZOIC-EARLY MESOZOIC IN CATALONIA

The geological and palaeontological record of the Carboniferous, Permian and Triassic periods in Catalonia (NE Iberian Peninsula), and especially in the Catalan Pyrenees, is fairly extensive and complete. Nevertheless, until the last two decades only a few studies had focused on the palaeontological record (see summaries in Fortuny, 2011; Fortuny *et al*., 2011a; Mujal, 2017; see also next section). Geologically, Catalonia is found in the NE of the Iberian microplate, subducting under the European plate due to the Alpine orogeny, leading to the formation of the Pyrenean mountain range.

During the late Palaeozoic and early Mesozoic, the Pyrenean region corresponded to several terrestrial depocentres, together known as the Pyrenean Basin (Gisbert, 1986). It was located in the boundary between the northern and southern landmasses, around the equator of Pangaea, at the southeast of the Variscan or Hercynian range, at the north-eastern margin of the Iberian microplate and with the Tethys sea in the eastern side (Fig. 1). At regional scale, this zone belongs to the Western peri-Tethys realm, which includes the Catalan Basin (Prelitoral Range in the Catalan

Coastal Ranges), the Iberian Basin (Iberian Range), the Balearic Islands, diverse basins from south-eastern France, Sardinia, and diverse regions of the southern Alps (northern Italy), and northern Africa (see Dercourt *et al*., 2000; Bourquin *et al*., 2007, 2011; Cassinis *et al*., 2012, 2013; Gretter *et al*., 2015; Matamales-Andreu *et al*., 2021a, 2022; Matamales-Andreu, 2023). The Pyrenean Basin consisted in a strike-slip rift system divided in several depocentres or sub-basins (Gisbert, 1981, 1986; Gisbert *et al*., 1985; Speksnijder, 1985; Saura and Teixell, 2006; Izquierdo-Llavall *et al*., 2014; Gretter *et al*., 2015; Lloret *et al*., 2018). Generally, this system displayed a semi-graben geometry, with a NW-SE orientation, the active margin (subsiding) in the South and the passive margin in the North (Saura, 2004; Saura and Teixell, 2006). This field trip is within the easternmost of them, the Castellar de n'Hug sub-basin. A recent summary of the sub-basins can be found in Mujal (2017).

The Pyrenean Basin deposits crop out in a narrow belt extended from West to East along the South of the axial Pyrenees (composed by the pre-Variscan basement of igneous and metamorphic origin). Because of the compressive phases during the Alpine orogeny (late Cretaceous-early Miocene), the Palaeozoic-Mesozoic rift system structure was reversed. As a result, the tectonic structure is complex, and strata generally dip southwards and, in some cases, are verticalised or even inverted (Saura and Teixell, 2006).

The Permian and Triassic (and Carboniferous) successions of the Pyrenees are of volcanosedimentary and sedimentary origin. They have been classified in two ways: lithostratigraphic units (LU; Mey *et al*., 1968; Nagtegaal, 1969) and depositional units (DU; Gisbert, 1981). Of note, lithostratigraphic units (formations) were defined in the western area of the Catalan Pyrenees, whereas the depositional units were defined in part in the localities visited in this field trip. As a synthesis, the equivalence between units, from oldest to youngest, is as follows:

- Aguiró Formation and Erill Castell Volcanics, as well as lower part of the Malpàs Formation (LU) = Grey Unit (GU) (DU). Age: late Carboniferous.
- Middle and upper part of the Malpàs Formation (LU) = Transition Unit (TU) (DU). Age: late Carboniferous-early Permian.
- Peranera Formation (LU) = Lower Red Unit (LRU) (DU). Age: early Permian.
- The Upper Red Unit (URU) has no LU equivalence, because this DU does not appear in the western Catalan Pyrenees, where the LU were defined. Age: middle-late Permian.
- Bunter Formation (LU) = Buntsandstein facies unit (DU). Age: Early-Middle Triassic.

This field trip includes stops corresponding to the Permian of the Lower Red Unit (LRU) and Upper Red Unit (URU). As their names indicate, both units consist of red-bed deposits. Nonetheless, they were formed under notably different environmental settings, which constrained the tetrapod faunas, as the ichnoassociations indicate (Voigt and Haubold, 2015; Mujal *et al*., 2016a, 2017a, 2018a; Marchetti *et al*., 2021). The Triassic Buntsandstein facies are also composed of red-beds, again from different terrestrial environments and bearing notoriously different tetrapod (ichno-) fossils (Mujal *et al*., 2016b, 2017b; Ezcurra *et al*., 2017).

## THE PERMIAN AND TRIASSIC VERTEBRATE RECORD OF CATALONIA

Permian and Triassic vertebrate remains are rather scarce in the Iberian Peninsula, but the Catalan record is relatively well known (Fig. 3), mainly thanks to studies conducted in the last decades. The first record of vertebrates from these periods found in Catalonia corresponds to fish scales from the marine upper Ladinian (Middle Triassic) of Camposines-Sant Jeroni (Wurm, 1913). Fishes were reported again from the locality of Gorg Negre (Llopis-Lladó, 1942), followed by the discovery of fishes and marine reptiles in the late Anisian - early Ladinian (Middle Triassic) of Olesa (Schmidt, 1935; Almela and Llopis-Lladó, 1947). However, for the greatest part of the 20th century the main source of Triassic Catalan fossils was the *Konservat-Lagerstätte* of Mont-ral-Alcover, dated as late Ladinian (Middle Triassic) (Calvet *et al*., 1987; Calvet and Tucker, 1995; for non-vertebrate fossil record, see e.g., Via-Boada and Villalta, 1975; Via-Boada *et al*., 1977). This locality records a high diversity of mainly marine organisms, including vertebrates in the form of fishes (with at least 12 actinopterygian families and the sarcopterygian *Alcoveria*; Beltan, 1972, 1975, 1984; Cartanyà, 1999, 2019) as well as reptiles (mostly sauropterygians but also one tanystropheid; Ellenberger and Villalta, 1974; Ellenberger, 1977, 1978; Sanz, 1983; Sanz and López-Martínez, 1984; Alafont and Sanz, 1996; Rieppel and Hagdorn, 1998; Quesada and Aguera-González, 2005; Fig. 4). The data provided by this unusual locality was only complemented by sporadic finds of footprints in terrestrial Permian and Triassic facies (e.g., Casanovas-Cladellas *et al*., 1979; Robles and Llompart, 1987), and Triassic marine fish (Lehman, 1964) and sauropterygians (Sanz, 1983) at the localities of Odèn (Pyrenean Basin) and Can Serra de l'Arca (Catalan Basin), respectively. This situation changed with the discovery of another important locality, La Mora (Montseny, Catalan Basin), this time in the alluvial red-bed facies of the Buntsandstein (early-middle Anisian, Middle Triassic) (Gaete *et al*., 1993, 1994, 1996; Fig. 5). The study of temnospondyl material from this locality (Fortuny and Galobart, 2010; Fortuny *et al*., 2011b) triggered a renewed interest on Triassic (and also Permian) vertebrates from Catalonia by members of the Institut Català de Paleontologia Miquel Crusafont (ICP) and Universitat Autònoma de Barcelona (UAB) (Fortuny *et al*., 2017). Since 2008, dozens of palaeontological campaigns have been performed. They mostly correspond to prospections with the aim of revisiting classical localities and discovering new paleontological sites, but also excavations. The latter have been performed in previously excavated localities (e.g., La Mora, lower Middle Triassic), in classical localities that had never been exploited, such as Odèn or Camposines-Sant Jeroni (Middle-Upper Triassic), and also in new localities discovered by the ICP and UAB team. All the field campaigns were funded by the Department of Culture of the Catalan Government through different granted projects since 2008. Visits to the classical localities, as well as other Permian and Triassic outcrops for which vertebrates had never been reported, led to the recovery of new material and the discovery of a good number of new sites. Fortuny *et al*. (2011a) provided an account of Permian and Triassic vertebrates from the Iberian Peninsula described until that moment and reported new material from Catalonia, like marine reptiles from the localities of Collbató (Catalan

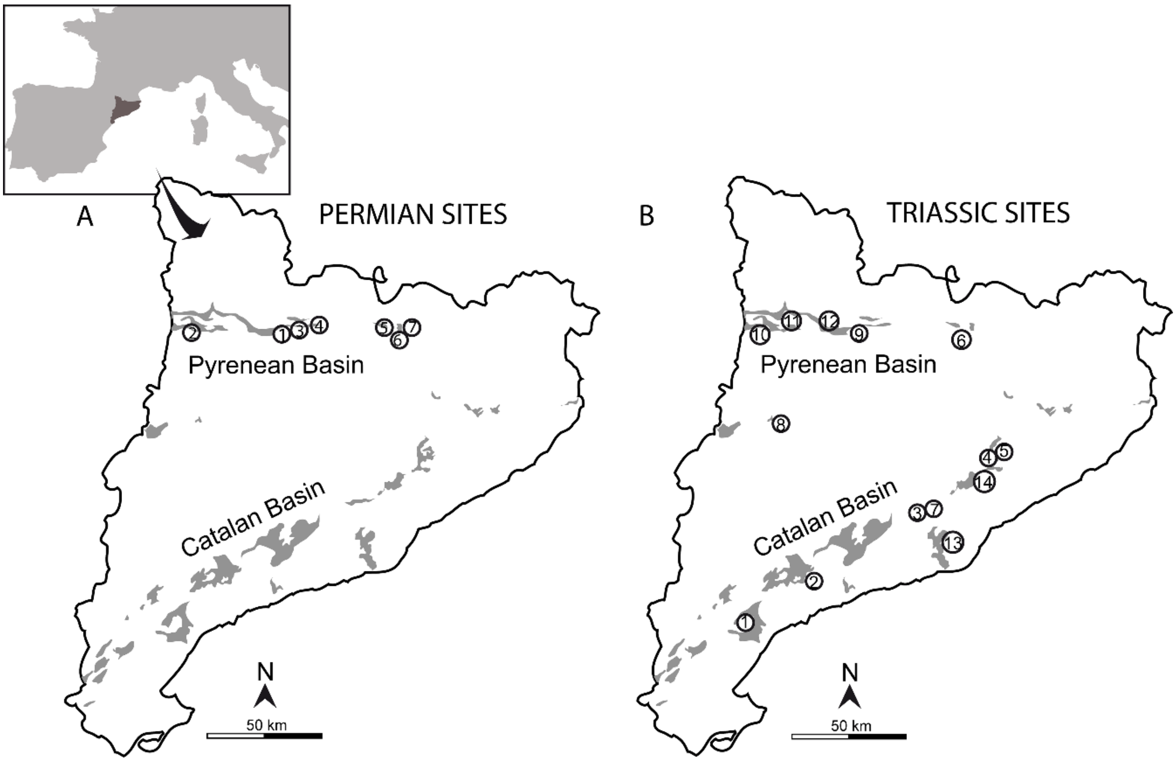


**Figure 3.** Main Permian and Triassic vertebrate fossil sites in Catalonia. A) Permian sites: 1, Palanca de Noves; 2, Coll de Sas and Benés-Avellanos; 3, Coll de Terrers; 4, Coll de Creus and La Trava; 5, Coll Roig; 6, Riera de Monell; 7, Castellar de n'Hug / Cal Ros. B) Triassic sites: 1, Camposines-Sant Jeroni; 2, Mont-ral-Alcover; 3, Olesa and Puigventós; 4, La Mora; 5, Can Serra de l'Arca; 6, Odèn; 7, Collbató; 8, Vilanova de la Sal; 9, Palanca de Noves; 10, Tossal de Pollerini; 11, Buira; 12, Port del Cantó; 13, Penya Rubí; 14, Figaró-Montmany.

Basin) and Vilanova de la Sal (Pyrenean Basin), new fragmentary fish material from Odèn and Vilanova de la Sal, complete and articulated fishes from Camposines-Sant Jeroni, and fragmentary temnospondyl material from Riera de Sant Jaume. Since that review, the known Permian and Triassic record has been expanded through the addition of numerous materials and localities studied by the ICP and UAB team in Catalonia (Fig. 3) as well as in the Balearic Islands. Most of these works were/are part of PhD theses conducted at the ICP and UAB: Fortuny (2011), Mujal (2017), Matamales-Andreu (2023) and De Jaime-Soguero (ongoing), but also multiple Master theses. Vertebrate material coming from the Balearic Islands is dealt with in Matamales-Andreu *et al*. (2021a, b, c, d, 2022, in press) as well as Matamales-Andreu (2023) and references therein. From here on we focus on advances in the study of the Catalan Permian and Triassic record during the last two decades.

The stratigraphically oldest succession studied by the ICP and UAB team is situated at the Erillcastell-Estac sub-basin, in the westernmost part of the Catalan Pyrenees (Mujal, 2017). It contains a diverse assemblage of plants (but no vertebrates) of Gzhelian (late Carboniferous) age in wet environments (Coll de Sas locality, see Mujal *et al*., 2018a; for additional palaeoflora localities see Juncal *et al*., 2019; Tosal *et al*., 2022) that during the early Permian (Cisuralian) evolved into environments under markedly seasonal arid and semi-arid climates with short humid episodes (Mujal

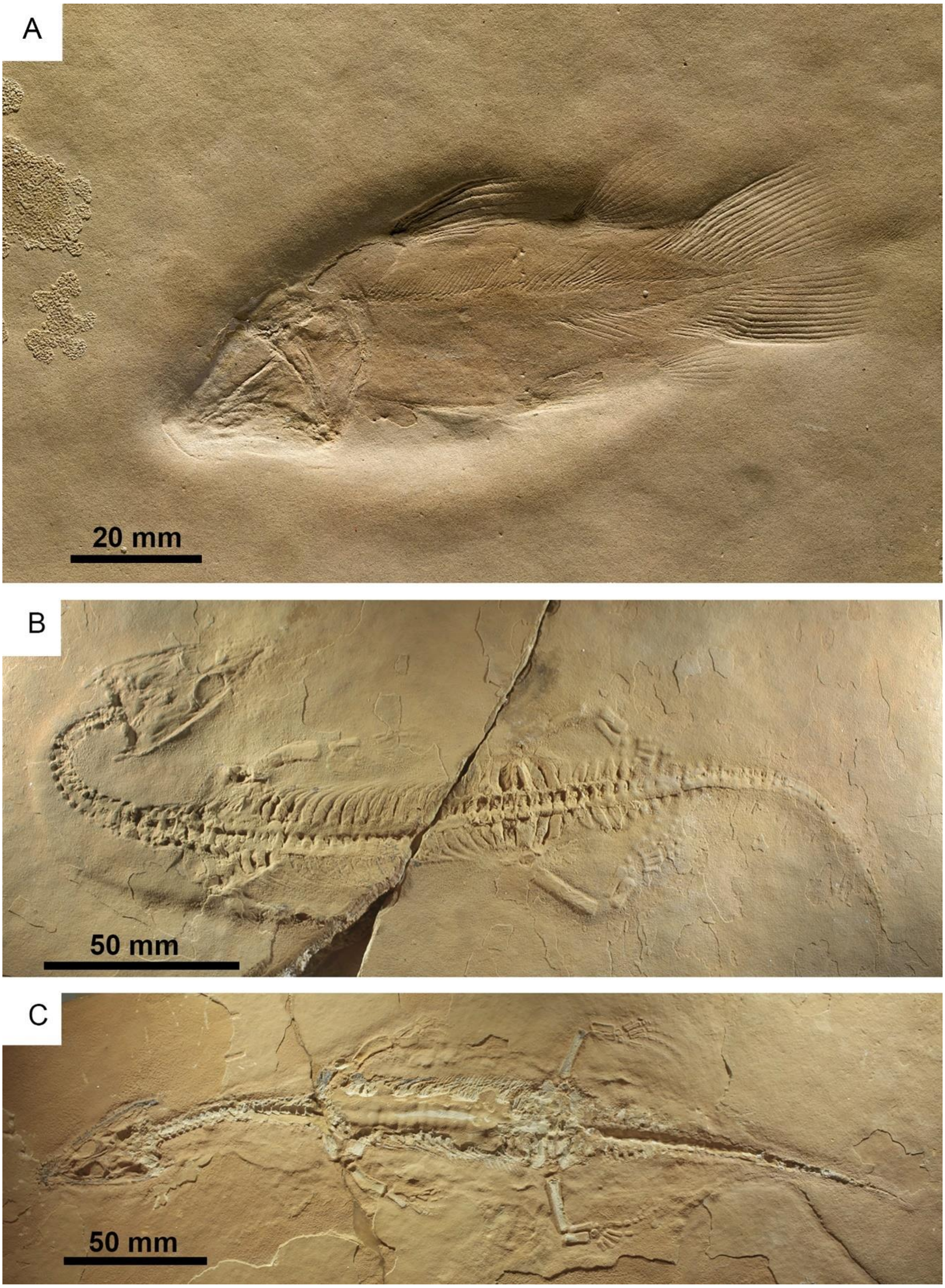


**Figure 4.** Representative vertebrates from the upper Ladinian (Middle Triassic) of Mont-ral-Alcover. A) *Alcoveria brevis*, B and C) *Lariosaurus balsami*. Modified from Cartanyà (2019).

*et al*., 2018a). These Permian successions (Peranera Fm. or Lower Red Unit) contain a diverse tetrapod ichnoassemblage (Voigt and Haubold, 2015; Mujal *et al*., 2016a; Marchetti *et al*., 2021) accompanied with relatively abundant invertebrate traces (Mujal *et al*., 2016a). This Cisuralian tetrapod ichnoassemblage is found in the localities of Avellanos and Benés and includes the following ichnogenera: *Batrachichnus* (correlated to lepospondyls and/or small temnospondyls), *Limnopus* (large temnospondyls), *Pachypes* (pareiasauromorphs), cf. *Ichniotherium* (diadectomorphs), *Dimetropus* (synapsid 'pelycosaurs'), *Varanopus* (and cf. *Varanopus*), *Hyloidichnus* (captorhinomorphs) and *Dromopus* (bolosaurids or araeoscelids), as well as *Characichnos* (swimming traces here correlated to temnospondyls) (Voigt and Lucas, 2018; Mujal *et al*., 2016a; Marchetti *et al*., 2021; Figs. 2, 6, 7). Importantly, this ichnoassemblage is divided in two ichnoassociations, differentiated in ichnotaxonomic composition, diversity and relative abundance of footprints that are linked to different palaeoenvironments (Mujal *et al*., 2016a, 2018a; Fig. 8). Interestingly, a similar scenario can be observed in the Castellar de n'Hug successions (De Jaime-Soguero *et al*., 2022). The same ICP and UAB team studied a second tetrapod ichnoassemblage mostly composed of large footprints from the younger Permian unit, the Upper Red Unit (URU), at the locality of Coll de Terrers (Cadí sub-basin) of purportedly Guadalupian and Lopingian ages (Mujal *et al*., 2017a). This ichnoassemblage, which contains forms similar to *Dolomitipes*, *Pachypes*, *Dromopus-Rhynchosauroides* and a fourth indeterminate morphotype, shows a faunal turnover with respect to the Cisuralian ichnoassemblage and is found in a palaeoenvironmental setting different from those of the Cisuralian ichnoassociations (Mujal *et al*., 2017a). Besides, scarce direct vertebrate remains (a caseid vertebra and indeterminate bone fragments) were discovered at the locality of La Trava (Mujal *et al*., 2016b, c), also in the URU. All in all, these ichnoassemblages allowed for a reconstruction of the tetrapod succession during the Permian (Mujal, 2017). Close to La Trava, the recently discovered locality of Coll de Creus (URU) has yielded an interesting Permian assemblage only preliminarily reported to include charophytes (Pérez-Cano *et al*., 2022) and dipnoi fishes (De Jaime-Soguero *et al*., 2023).

As explained in detail below, this field trip takes place in localities from the Castellar de n'Hug sub-basin, at the central-eastern part of the Catalan Pyrenees. It includes three tetrapod track localities (De Jaime-Soguero *et al*., 2022) that complement and expand the tetrapod (ichno-) record so far known (see below). Still in the Pyrenees, the vertebrate record of the terrestrial red-beds of the Buntsandstein facies (late Early-early Middle Triassic) is dominated by footprints of archosauromorphs at Port del Cantó, Tossal de Pollerini, Buira and Palanca de Noves (Fortuny *et al*., 2010; Mujal *et al*., 2016b, 2017b), although scarce direct remains also occur at Port del Cantó and Palanca de Noves (including crocopodan archosauromorph teeth: Ezcurra *et al*., 2017; see also Mujal *et al*., 2016b; Fig. 9). The Buntsandstein Pyrenean ichnoassemblage contains *Rhynchosauroides*, *Prorotodactylus* (with the recently erected species *P. mesaxonichnus*), *Rotodactylus* and large chirotheriid footprints (similar to *Protochirotherium*) and hints at the presence of diverse archosauromorphs distributed throughout the fluvial deposits (Mujal *et al*., 2017b). Even if

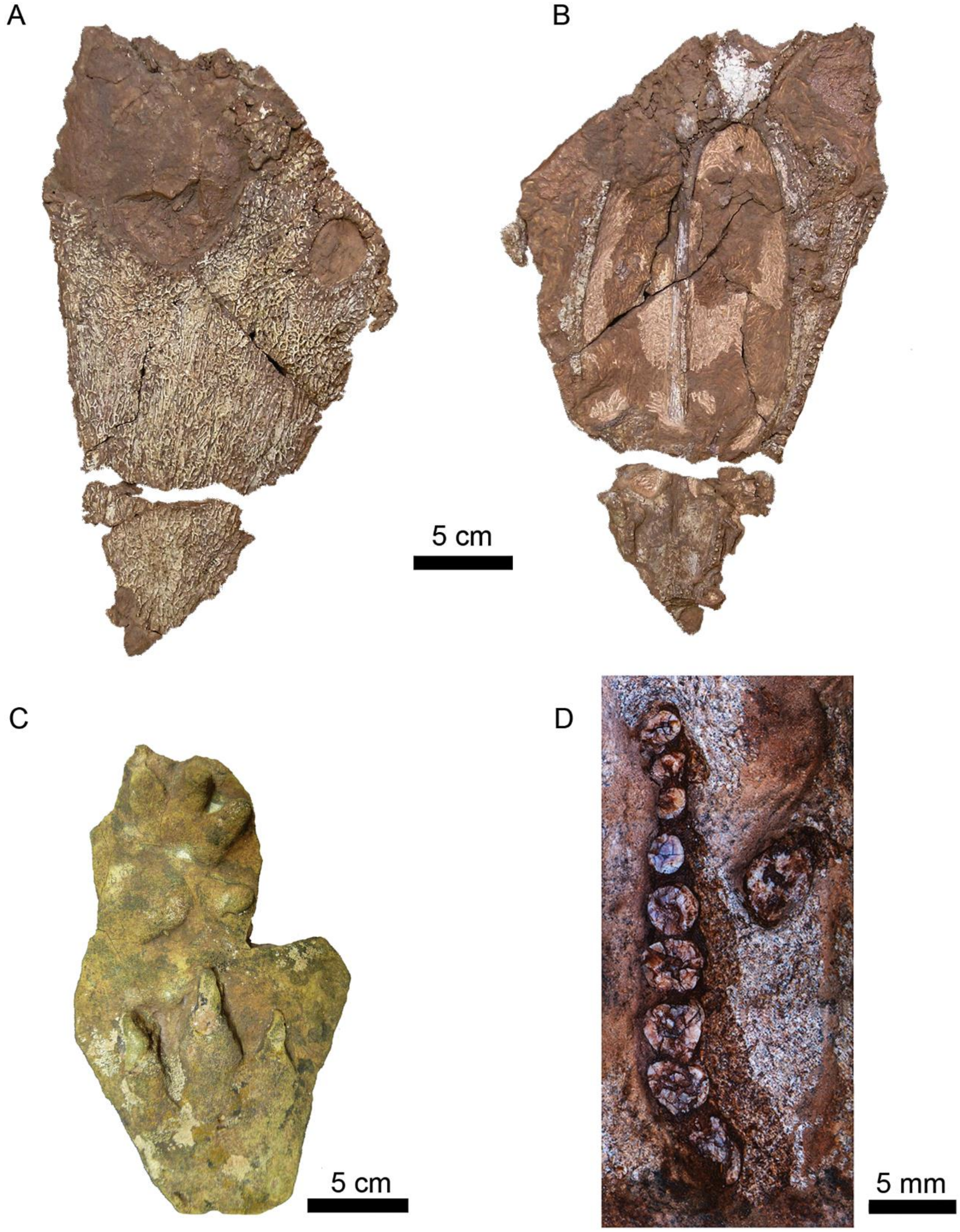


**Figure 5.** Tetrapod groups present in the lower-middle Anisian (Middle Triassic) Buntsandstein facies of the Catalan Basin. A and B) *Calmasuchus acri* skull in dorsal (A) and ventral (B) views. C) Left manus-pes set of *Chirotherium barthi*. D) Procolophonid tooth row. Modified from Fortuny *et al*. (2011a, b, 2014).

the fossil fauna of the terrestrial Triassic of the Catalan Pyrenees is dominated by archosauromorph footprints (Fig. 2), the stratigraphically oldest fossil record there is of horseshoe crab traces found in fluvial deposits overlying the basal conglomerates of the Buntsandstein facies (Mujal *et al*., 2018b). In the Catalan Basin, vertebrate footprints are only found in the Buntsandstain facies (Calzada, 1987;

Valdiserri *et al*., 2009; Fortuny *et al*., 2011a) as well as the terrestrialised portion of the Muschelkalk (M2) (Mujal *et al*., 2015, 2018c; De Jaime-Soguero *et al*., 2021), and there is no Permian vertebrate record. The ichnoassemblage corresponding to Buntsandstein facies (early-middle Anisian) contains *Procolophonichnium*, *Rhynchosauroides*, *Rotodactylus*, *Protochirotherium*, *Synaptichnium*, *Chirotherium* and *Isochirotherium* (Calzada, 1987; Valdiserri *et al*., 2009; Fortuny *et al*., 2011a; Mujal, 2017) (Figs. 2, 5), indicating a predominance of archosauromorphs, although therapsids were likely present too. Direct remains found in Buntsandstein facies of Montseny correspond to capitosaur temnospondyls (*Calmasuchus*, Fortuny *et al*., 2011b), indeterminate procolophonids (Fortuny *et al*., 2014), and crocopodan archosauromorphs (Ezcurra *et al*., 2017; Fig. 5). The youngest Triassic continental deposits containing vertebrates known up to date are those from the middle Muschelkalk (M2; late Anisian-early Ladinian, Middle Triassic), for which remains were virtually unknown until the recent description of ichnites from Penya Rubí, Corbera, Esparreguera, Puigventós, Collcardús, Pedrera de Can Sallent and Figaró/Montmany (Mujal *et al*., 2015, 2018c; De Jaime-Soguero *et al*., 2021; Fig. 10). In these localities, different proportions of ichnotaxa or morphotypes (including swimming traces, *Procolophonichnium*, *Chelonipus*, *Rhynchosauroides*, *Rotodactylus*, *Chirotherium*, *Isochirotherium*, and indeterminate chirotheriids) have been interpreted as reflecting changes in the palaeoenvironment of the different localities (Mujal *et al*., 2018b; De Jaime-Soguero *et al*., 2021). Besides tetrapods, the middle Muschelkalk deposits also contain a trackway assigned to *Kouphichnium*, likely produced by horseshoe crabs (De Jaime-Soguero *et al*., 2020, 2021). Lastly, the youngest Triassic sites bearing vertebrate remains correspond to the marine realm, being the classical *Konservat-Lagerstätte* of Mont-ral-Alcover the most important locality known to date. Even though, new efforts in other localities have yielded less diverse assemblages that, on the other hand, are represented by more informative specimens containing well preserved hard tissues, in contrast to the dolomitised specimens of Mont-ral-Alcover (see Hemleben and Freels, 1977), which barely preserve anatomical details. Among these localities yielding new information are Camposines-Sant Jeroni (late Ladinian) in the Catalan Basin, which has been extensively excavated and partially studied, with the description of the perleidid actinopterygian *Moradebrichthys* (Cartanyà *et al*., 2019; Fig. 11), and Odèn (late Ladinian-middle Carnian) in the Pyrenean Basin, where *Colobodus*, *Peltopleurus*, *Saurichthys*, an indeterminate halecomorph and an indeterminate sauropterygian reptile have been reported (Cartanyà *et al*., 2011, 2015; García-Artigas *et al*., 2022). Finally, Vilanova de la Sal is a locality that has yielded more scarce fish material (possibly including *Eosemionotus* and *Peltopleurus*) but also a partial skeleton of a sauropterygian reptile and is located, again, in the Pyrenean Basin (Fortuny *et al*., 2011a).

## Stop 0. The Permian succession of the Castellar de N'hug sub-basin

The Castellar de n'Hug sub-basin (central-eastern Catalan Pyrenees, Catalonia) is represented by extensive, well-exposed outcrops that help to understand the evolution of the terrestrial Permian

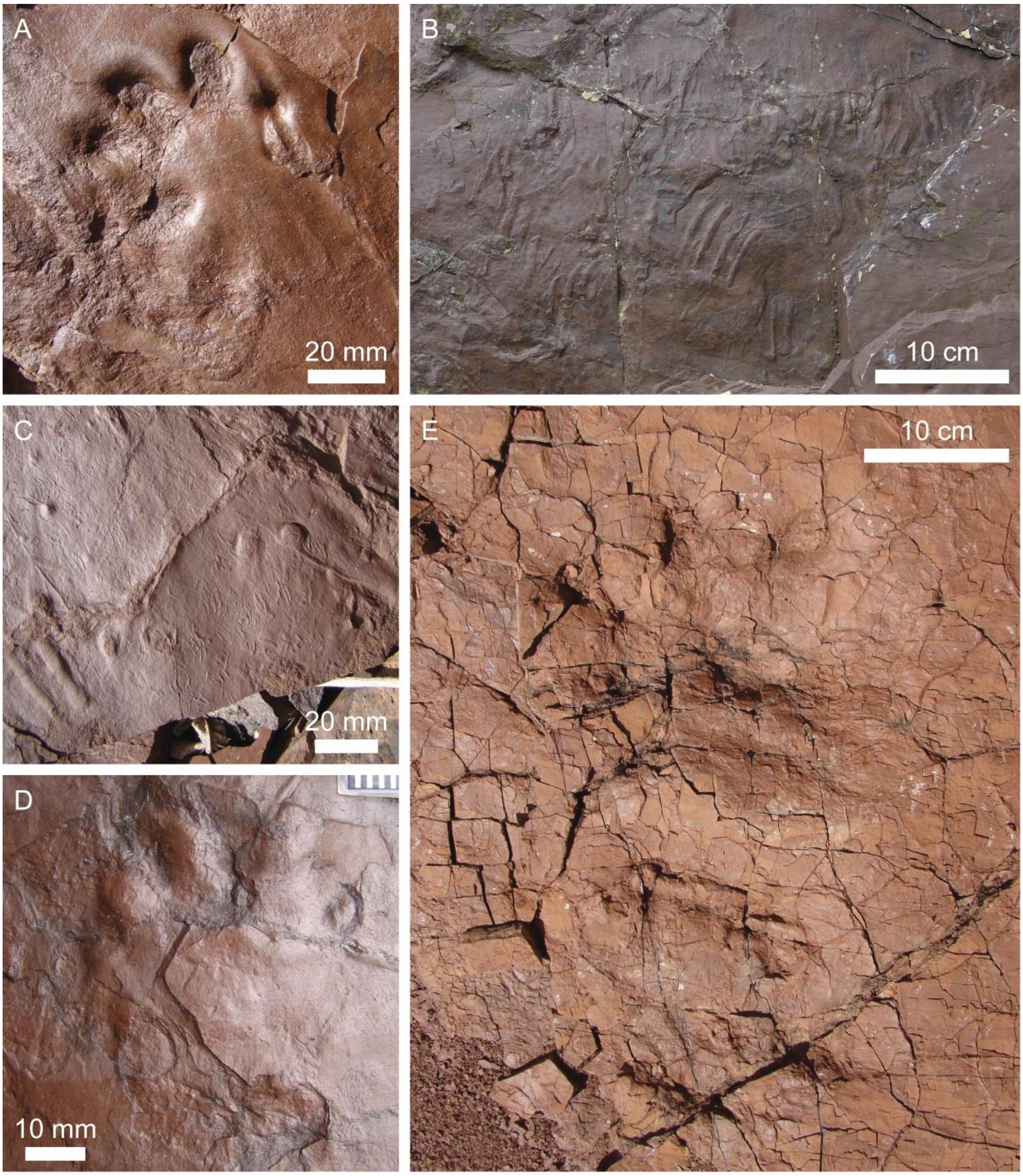
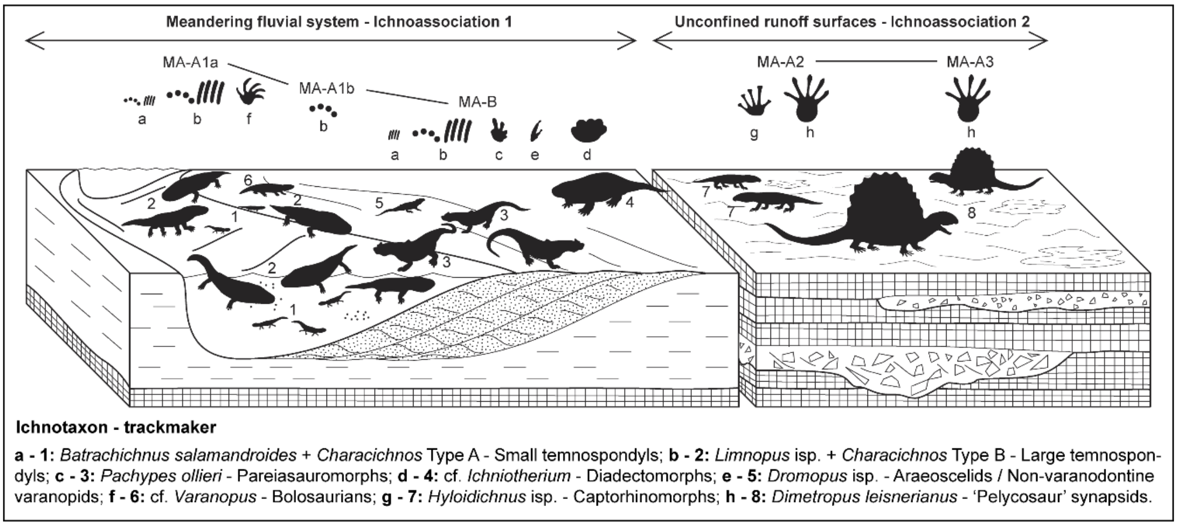


**Figure 6.** Tetrapod footprints present in the Cisuralian Lower Red Unit of Benés and Avellanos sites (A-D) and the ?Guadalupian-Lopingian Upper Red Unit of Coll de Terrers (E). A) Right manus of *Limnopus* isp. B) Large swimming traces (*Characichnos* isp.) associated to *Limnopus* isp. C) Small swimming traces (*Characichnos* isp.) associated to *Batrachichnus salamandroides*, and sparse large *Characichnos* isp. D) Left manus of *Pachypes ollieri*. E) Left manus-pes set of Morphotype I (similar to *Dolomitipes*). Modified from Mujal *et al*. (2016a, 2017a).

environments (and generally ecosystems) in the Iberian Peninsula. The succession includes the longest detritic sequence of the Pyrenean Basin, preserving diverse tetrapod ichnoassociations recognised in three recently discovered localities. In this field trip along the outcrops surrounding the scenic village of Castellar de n'Hug (Fig. 12), we will start visiting the section named after this

**Figure 7.** Palaeoenvironmental and faunal reconstruction of the Lower Red Unit (Cisuralian) ecosystem at the Benés and Avellanos sites. Artwork by Roc Olivé / Institut Català de Paleontologia Miquel Crusafont.

village, a long succession of fluvial deposits interbedded with pyroclastic ignimbrites, and we will finish visiting the ichnofaunas recovered in the lacustrine deposits of the Riera de Monell section. The Castellar de n'Hug sub-basin is located in the easternmost part of the Pyrenean Basin. It is infilled with volcanic, volcanosedimentary and sedimentary deposits from the late Palaeozoic-early Mesozoic (Gisbert *et al*., 1985; Martí, 1996; Barrachina and Martí, 1996; Gretter *et al*., 2015), representing four of the five depositional units described by Gisbert (1981): Transition Unit (TU), Lower Red Unit (LRU, Fig. 13A), Upper Red Unit (URU, Fig. 13B, C) and Buntsandstein facies unit. The deposits of the TU are composed of yellowish and greyish sandstones that occasionally preserve some plant remains. These deposits have been traditionally dated as upper Carboniferous-lower Permian based on the fossil flora (Gisbert, 1981, 1986; Broutin and Gisbert, 1985).



**Ichnotaxon - trackmaker**

**a - 1:** *Batrachichnus salamandroides* + *Characichnos* Type A - Small temnospondyls; **b - 2:** *Limnopus* isp. + *Characichnos* Type B - Large temnospondyls; **c - 3:** *Pachypes ollieri* - Pareiasauromorphs; **d - 4:** cf. *Ichniotherium* - Diadectomorphs; **e - 5:** *Dromopus* isp. - Araeoscelids / Non-varanodontine varanopids; **f - 6:** cf. *Varanopus* - Bolosaurians; **g - 7:** *Hyloidichnus* isp. - Captorhinomorphs; **h - 8:** *Dimetropus leisnerianus* - 'Pelycosaur' synapsids.

**Figure 8.** Palaeoenvironmental reconstruction and distribution of the tetrapod (ichno-) fauna from the Cisuralian of the Erillcastell-Estac sub-basin (Pyrenean Basin). Modified from Mujal *et al*. (2016a) with data from Marchetti *et al*. (2021).

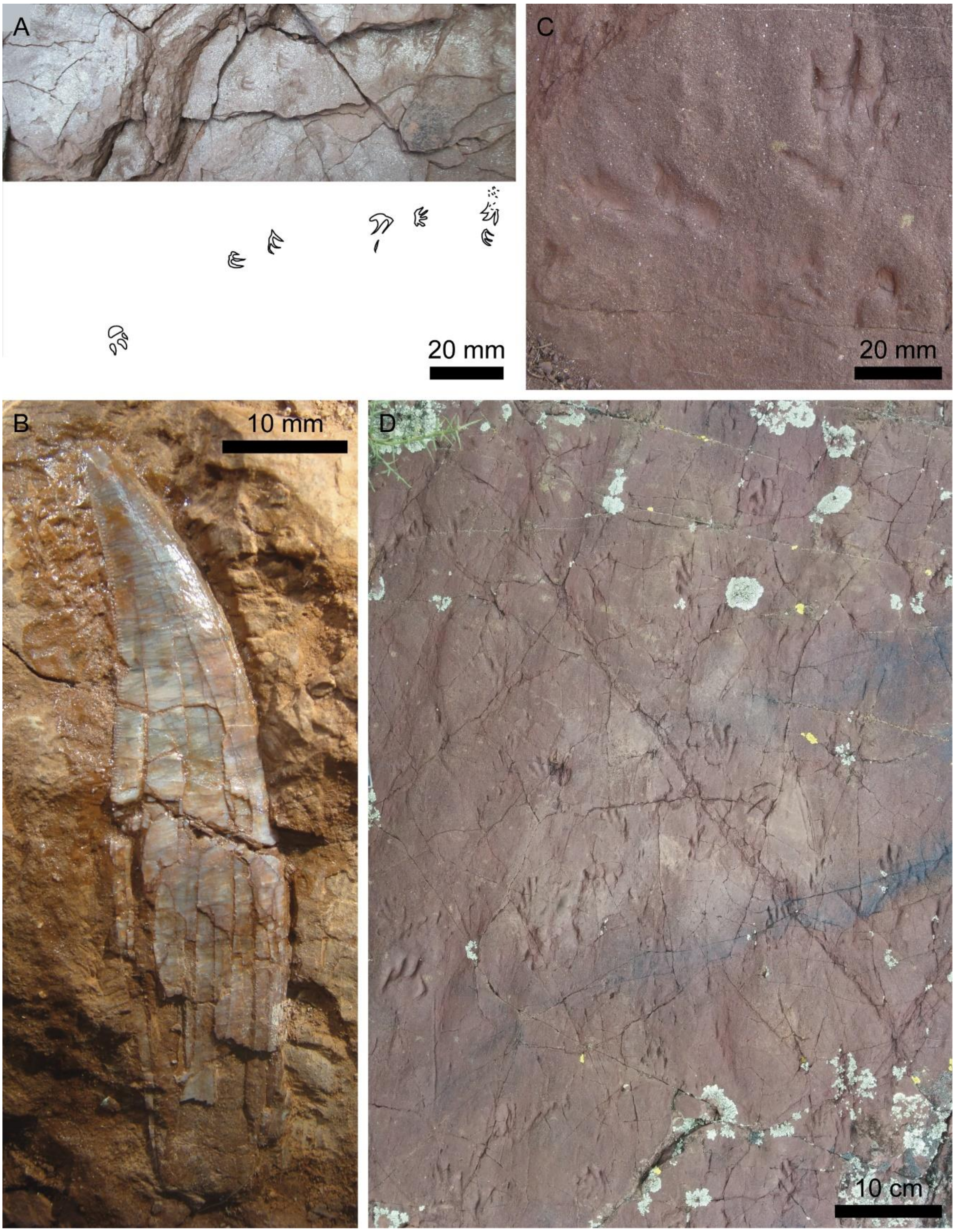


**Figure 9.** Representative tetrapods from the upper Olenekian-lower Anisian (Lower-Middle Triassic) Buntsandstein facies of the Pyrenean Basin. A) Multiple tracks of *Rhynchosauroides* isp. with interpretive outlines. B) Crocopodan archosauromorph tooth. C, D) *Prorotodactylus mesaxonichnus*, including a well-preserved left manus-pes set (C) and multiple tracks on a densely trampled surface (D). Modified from Fortuny *et al*. (2010), Ezcurra *et al*. (2017) and Mujal *et al*. (2017b).

The Castellar de n'Hug sub-basin is located in the easternmost part of the Pyrenean Basin. It is infilled with volcanic, volcanosedimentary and sedimentary deposits from the late Palaeozoic-

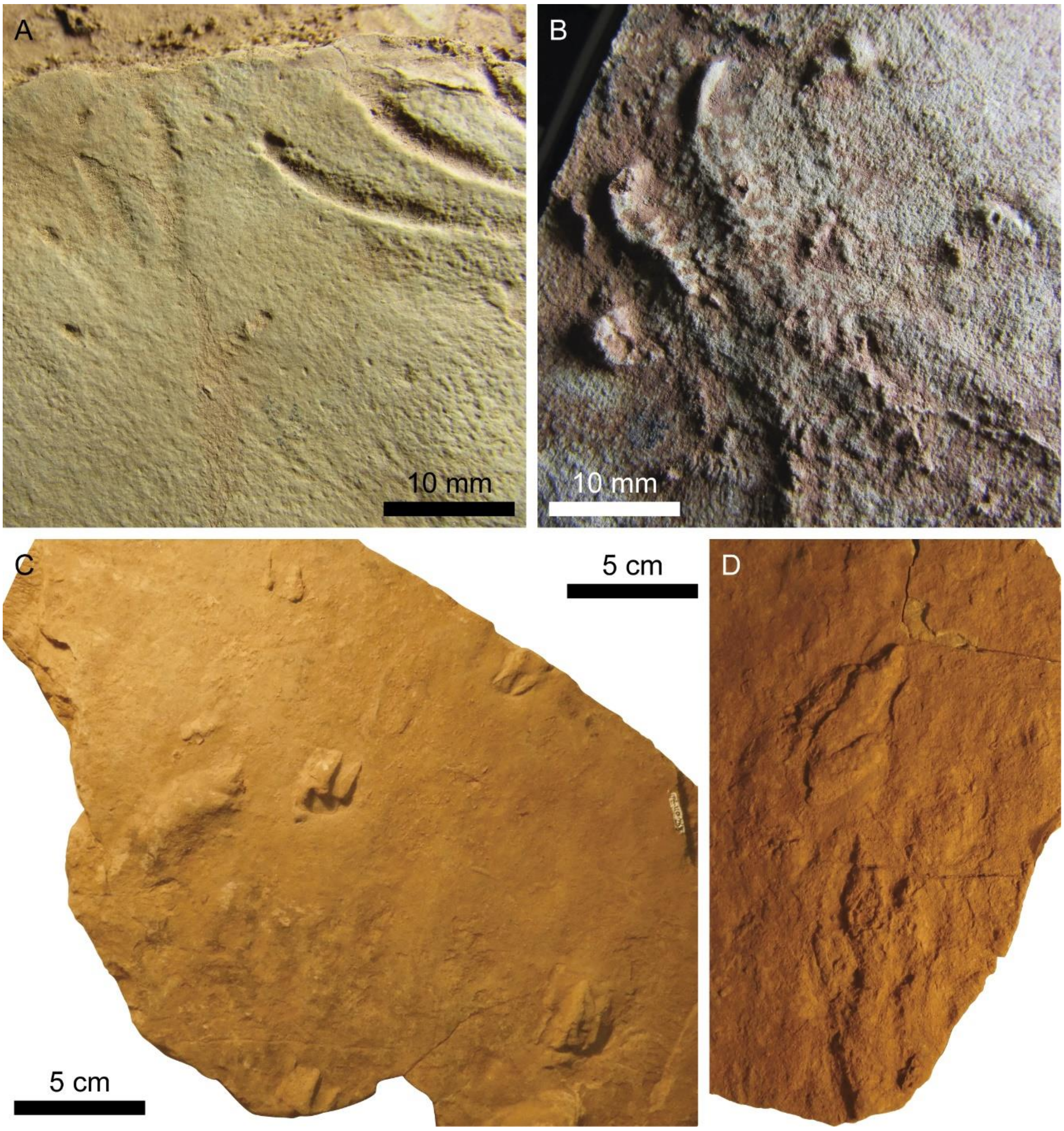


**Figure 10.** Tetrapod footprints from the upper Anisian-lower Ladinian (Middle Triassic) detrital Muschelkalk facies (M2) of the Catalan Basin. A) Right manus of *Rhynchosauroides tirolicus* preserving skin impressions and partial left pes. B) Left imprint of *Procolophonichnium haarmuehlensis* preserving skin impressions. C) Trackway of *Chelonipus* isp. D) Manus-pes sets of *Chirotherium ferox*. Modified from De Jaime-Soguero *et al*. (2021).

early Mesozoic (Gisbert *et al*., 1985; Martí, 1996; Barrachina and Martí, 1996; Gretter *et al*., 2015), representing four of the five depositional units described by Gisbert (1981): Transition Unit (TU), Lower Red Unit (LRU, Fig. 13A), Upper Red Unit (URU, Fig. 13B, C) and Buntsandstein facies unit. The deposits of the TU are composed of yellowish and greyish sandstones that occasionally preserve some plant remains. These deposits have been traditionally dated as upper Carboniferous-lower Permian based on the fossil flora (Gisbert, 1981, 1986; Broutin and Gisbert, 1985). The most characteristic deposits in the area we will visit are red-beds of the LRU and the URU, corresponding to the lower and middle Permian record (Gisbert, 1981; Gretter *et al*., 2015; Fig. 13). The LRU mainly represents an alternation of alluvial deposits (composed of reddish-maroon mudstones, sandstones and conglomerates) as well as volcanic deposits (composed of ignimbrites and cinerites; Figs. 13A, 14). The alluvial deposits correspond to massive mudstones from floodplain settings, combined with sporadic sandstones infilling meandering channels as well as overbank fines. The volcanic rocks, of calcoalcaline composition, are product of explosive eruptions that deposited large amounts of pyroclastic material, some of them reaching several metres of thickness (Martí, 1996; Pereira *et al*., 2014). Volcanic and volcanosedimentary deposits are dominant in the LRU, and the sedimentary intervals mainly result from the reworking of the primary volcanic material. The last stages of the LRU are marked by the disappearance of volcanic deposits, giving path to the URU (Figs. 13B, C, 15), which is dominated by massive mudstones and fine-grained sandstones cyclically deposited. As occurring towards the east (Mujal *et al*., 2017a), the URU is differentiated in two depositional sub-units, lower and upper URU. The first deposits of the lower URU are fine-grained sandstones and mudstones. Sandstones are more common at the lower portion of this sub-unit, while mudstones appear throughout the whole lower URU, denoting a fining-upwards trend. The uppermost interval of the sub-unit is built up of massive mudstones that contain septariform nodules, characterising the end of the lower URU. The uppermost interval of the sub-unit is built up of massive mudstones that contain septariform nodules, characterising the end of the lower URU. These deposits are interpreted as distal floodplain systems, denoting a progressive fining-upwards of the whole Permian succession.

The subsequent upper URU is mainly built up of reddish mudstones with a cyclic alternation between finely laminated silty and sandy mudstones with characteristically mud-cracked surfaces (Fig. 15A, B). The abundant mud-cracks with Y-junctions indicate that the original sediments underwent repeated periods of desiccation, and the cyclic alternation as a whole suggests seasonality in a monsoonal regime. All in all, this sedimentary sequence was probably influenced by the aridification trend and increasing seasonality of the climate observed in western European Permian basins (Roscher *et al*., 2011; De la Horra *et al*., 2012; Gretter *et al*., 2015; Mujal *et al*., 2017a). Finally, the Permian deposits are unconformably overlain by the sedimentary succession of the Triassic Buntsandstein facies. The base of these facies is composed of massive deposits of conglomerates composed of rounded quartz pebbles eroding a so far unknown portion of the Permian succession. These coarse-grained deposits were formed in a fluvial braided system, commonly observed in western Europe (Bourquin *et al*., 2011). Above them, the characteristic micaceous medium-grained sandstones of fluvial origin are observed. However, in the visited areas they are relatively poorly exposed, and their thickness is relatively low, because they are cut by overlaying Cretaceous deposits.

Most of the studies on the extensive Permian terrestrial red-beds in this area were mainly focused on the geological and structural context (Gisbert *et al*., 1985; Martí, 1996; Barrachina and Martí, 1996; Gretter *et al*., 2015), while little attention was paid to the palaeontological content, which remained poorly known until the last decade. Only in the 1980s, a palaeoflora study was carried out,

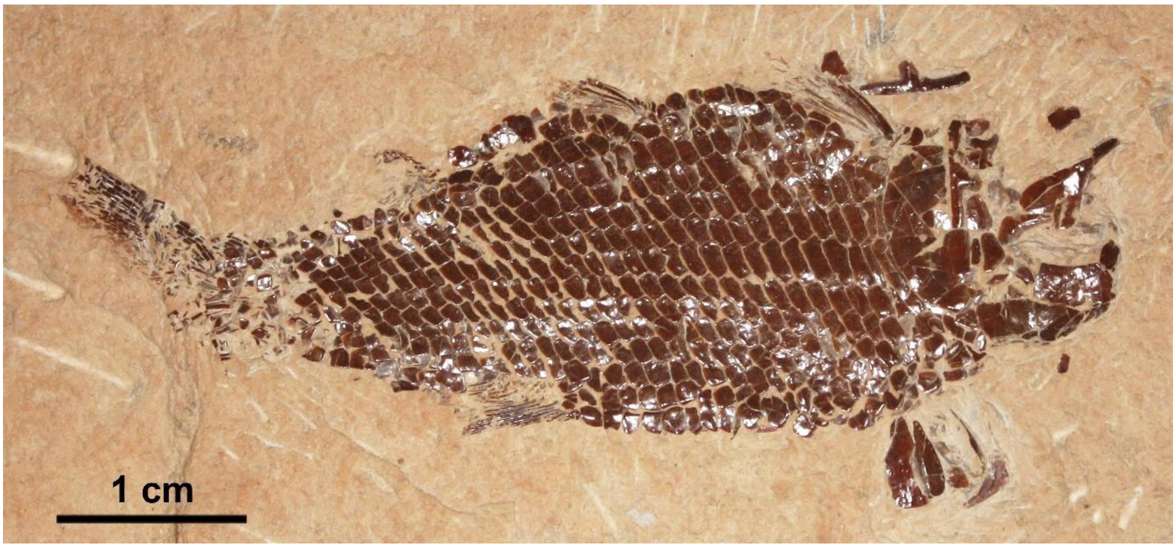


**Figure 11.** *Moradebrichthys vilasecae* specimen recovered in the upper Ladinian (Middle Triassic) site of Camposines-Sant Jeroni. See Cartanyà *et al*. (2019) for further details.

including remains from the LRU in the area of Castellar de n'Hug (Broutin and Gisbert, 1985). The first vertebrate fossils were not discovered until 2015, when a set of prospective palaeontological surveillances led to the discovery of an abundant and diverse record in the form of tracks and trackways, often accompanied with even more abundant invertebrate (arthropod) trace fossils. Despite the absence of skeletal remains, as is usual in the Pyrenean Basin, tetrapod footprints are providing valuable information about faunal composition and age of the succession (e.g., Voigt and Haubold, 2015; Mujal *et al*., 2016a, b, 2017a, 2018a; Marchetti *et al*., 2021; De Jaime-Soguero *et al*., 2022), showing their usefulness as biochronological indicators (Voigt and Lucas, 2018; Schneider *et al*., 2020; Marchetti *et al*., 2022b; Fig. 2).

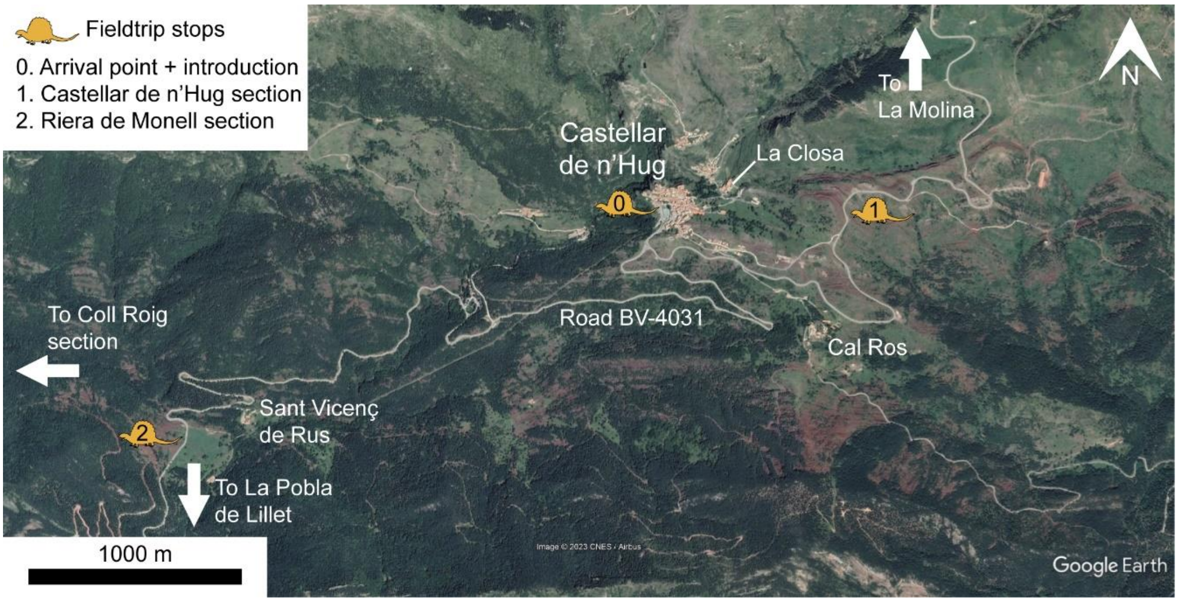


**Figure 12.** Map of the fiel dtrip to the Permian successions of the Castellar de n'Hug sub-basin. Orthophoto from Google Earth.

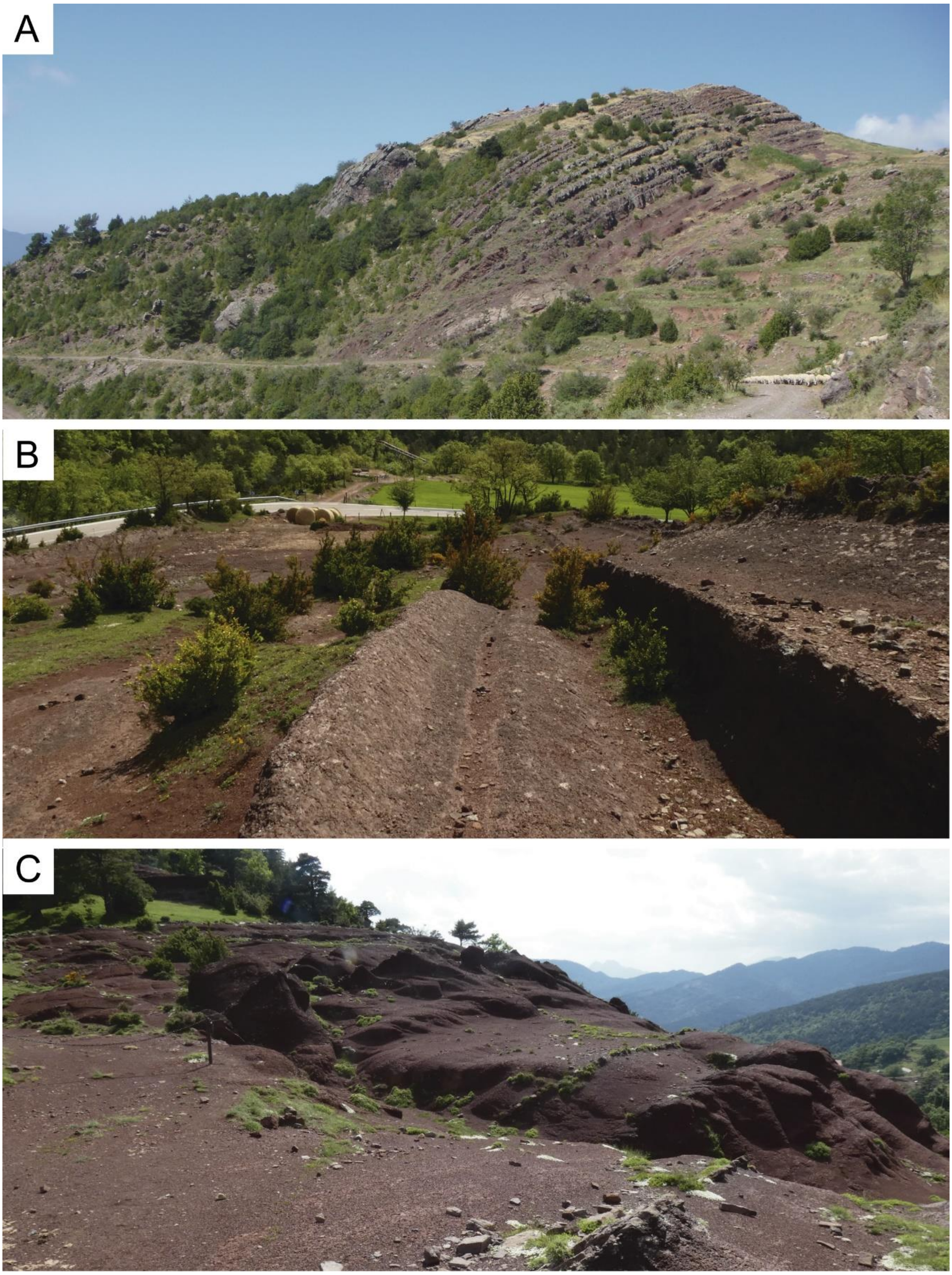


**Figure 13.** Permian red-beds from the Castellar de n'Hug sub-basin. General aspect of the Lower Red Unit volcanosedimentary sequence at the Castellar de n'Hug section (A), and alluvial deposits of the Upper Red Unit at the Riera de Monell (B) and Coll Roig (C) sections.

The tetrapod ichnoassemblage of the Castellar de n'Hug sub-basin is composed of seven ichnogenera (De Jaime-Soguero *et al*., 2022). It indicates the presence of small-sized non-amniote tetrapods (ichnogenera *Batrachichnus* and *Charachichnos*, the latter corresponding to swimming traces), small sized bolosaurid parareptiles and/or non-varanodontine varanopids (ichnogenus *Dromopus*), captorhinomorph eureptiles (ichnogenera *Varanopus* and *Hyloidichnus*), dinocephalian therapsids (ichnogenus *Brontopus*) and pareiasauromorph parareptiles (ichnogenus *Pachypes*) (De Jaime-Soguero *et al*., 2022). In addition, several invertebrate traces, including body imprints as well as plant remains are preserved along the whole the Permian succession. Remarkably, the composition of the entire tetrapod ichnoassemblage is not constant along the sequence: it is divided in two ichnoassociations, stratigraphically and palaeoenvironmentally differentiated. The older one is composed of tracks and trackways of small-medium size correlated to non-amniote and eureptilian trackmakers inhabiting shallow water bodies of fluvial environments; they appear in the LRU and the first layers of the URU. The younger ichnoassociation appears in the cyclic, shallow lacustrine deposits of the upper URU and is dominated by tracks of medium to large size correlated to dinocephalian therapsids, although footprints correlated to eureptiles and parareptiles are also present (Fig. 16). While the first ichnoassociation shows characteristic features of the *Erpetopus* biochron (Artinskian-Capitanian), the second one is restricted to the *Brontopus* sub-biochron (Guadalupian) (Gand and Durand, 2006; Voigt and Lucas, 2018; Schneider *et al*., 2020; Marchetti *et al*., 2022a, b) (Figs. 2, 17). The similarities of this Pyrenean ichnoassemblage with others from the peri-Tethys Permian basins offer a great opportunity to establish further correlations, expanding our knowledge about the evolution of the tetrapod diversity and ecology during the early-middle Permian, shaped by the dramatic events of this time interval. In this stop the participants will be able to examine some representative specimens from Catalan and Permian localities in the form of casts, 3D printed models, and other supports.

## Stop 1. The Castellar de n'Hug section

The Permian section is located to the East of Castellar de n'Hug, along the road that connects this town with the ski resort of La Molina (road BV-4031). In this geological sequence we find deposits from the Lower Red Unit (LRU) to the North and the lower Upper Red Unit (lower URU) to the South (i.e., strata dip and become younger southwards). The sequence starts at kilometre 14 of the BV-4031 road and ends nearby the neighbourhood of Cal Ros, reaching almost 700 m thick. In this stop we will mainly observe the volcanosedimentary deposits of the LRU. One of the most evident features is the great amount of volcaniclastic deposits. They belong to several pulses of explosive volcanism in the form of pyroclastic (Fig. 14B, D) (conglomerate-like) and ash-flow (mudstone/siltstone-like) deposits. Some deposits are several metres thick, and they present a vitreous matrix and antidune structures. Moreover, some ignimbrite deposits have a relevant importance by their richness in zircon crystals, which have been dated as 283.4±1.9 Ma (Pereira *et al*., 2014). These volcanic deposits dominate the LRU of Castellar de n'Hug, and they are also accompanied by well-developed palaeosols, denoting prolonged periods of exposition. Occasionally, the volcanic deposits are

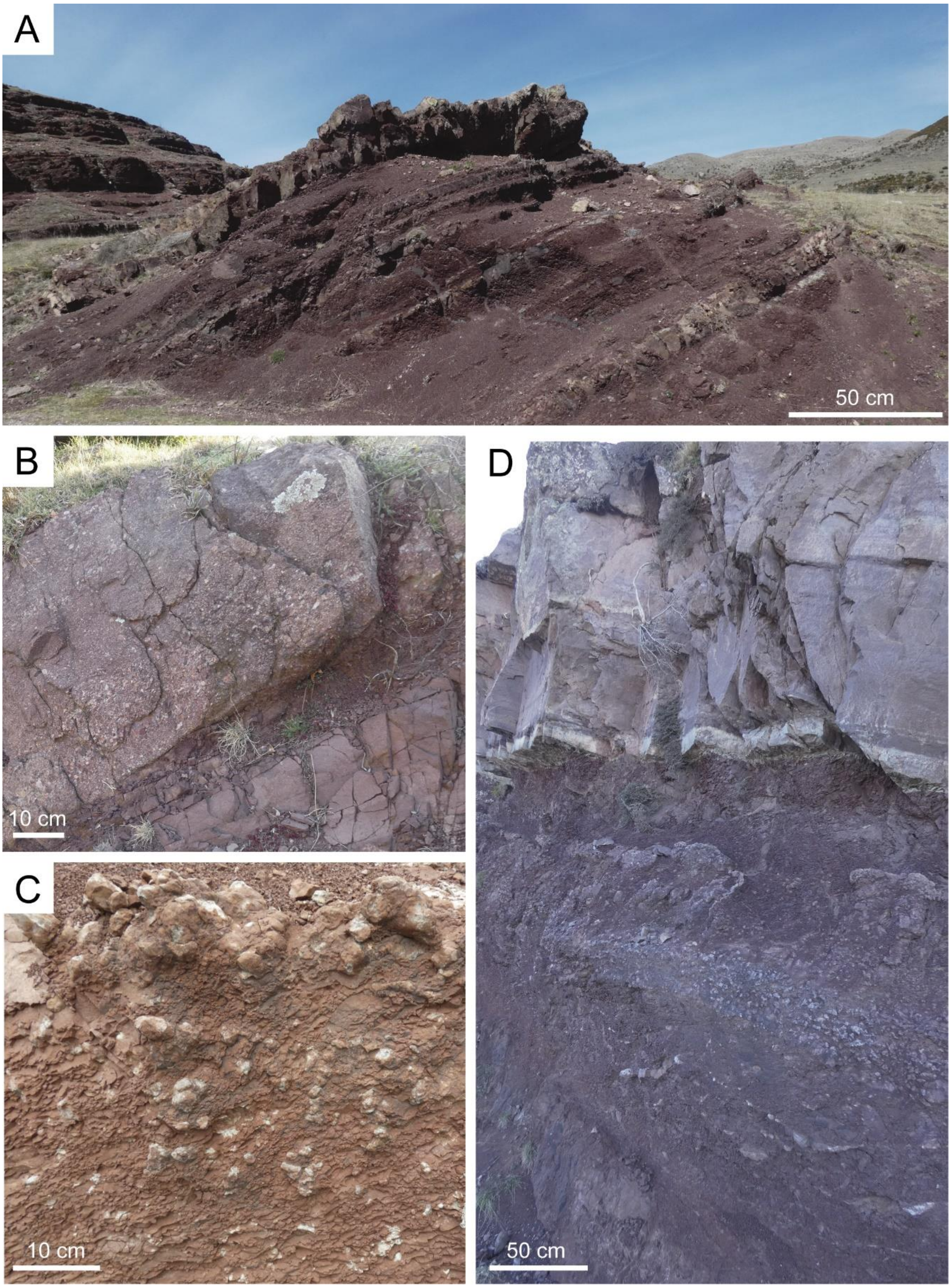


**Figure 14.** Lower Red Unit (LRU) at the Castellar de n'Hug section. A) Sedimentary intercalation of sandstone and mudstone layers, corresponding to fluvial deposits. B) Volcaniclastic breccia with pyroclasts. C) Well developed palaeosols with presence of carbonate nodules. D) Volcaniclastic deposits with well-developed palaeosols overlaid by ash-flow deposits.

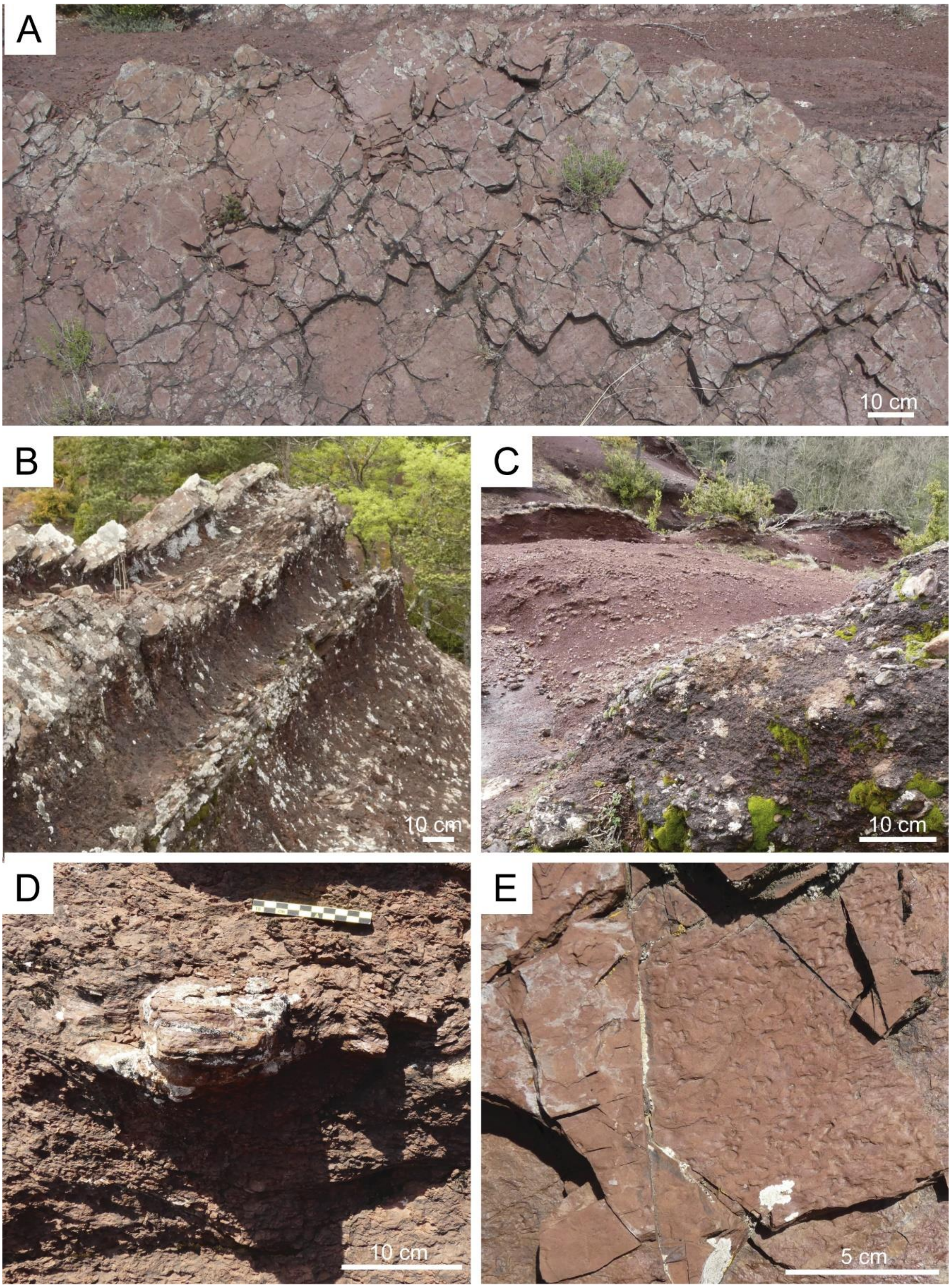


**Figure 15.** Upper Red Unit (URU) at the Riera de Monell section. A) Mud-cracked mudstone surfaces characteristic of the upper URU. B) Cyclic mudstone sequences with mud-cracked surfaces on top. C) Last volcaniclastic breccia of the LRU at the Riera de Monell section separated by carbonate palaeosols. D) Very fine-grained sandstones corresponding to a shallow pond deposit within an ephemeral lacustrine setting. E) Triopsid traces on a mudstone surface.

interrupted by mudstones and sandstones originally deposited in alluvial floodplains and meandering channels that reworked the volcanic material. The floodplain deposits are characterised by massive mudstones eroded by coarser deposits resulting from sporadic and energetic flooding events (Fig. 14A). Prolonged evaporation and desiccation are inferred from the relatively abundant palaeosols represented by carbonate nodules and mud-cracked surfaces (Fig. 14C). Some sandstone channel deposits with lateral accretion associated to overbank deposits highlight the presence of meandering rivers within the floodplains. The lateral accretion channels show the typical morphology of point bars, with lag deposits composed of clast-supported breccia at the erosive base and a fining-upwards sandstone sequence building the main body of the deposit. Besides, related to these channel deposits, cyclic crevasse splay deposits appear, composed of thin laminated mudstones and sandstones (sometimes accompanied with pebbles) and palaeosols. All the tetrapod and invertebrate trace fossils observed in the LRU are preserved on the .surfaces of these floodplain and overbank deposits, and occasionally on smoothed sandstone surfaces related to low energetic streams.

The tetrapod ichnofaunas recorded in this outcrop are restricted to some isolated small-sized tracks attributed to *Batrachichnus*, *Dromopus* and *Hyloidichnus* (Fig. 16). They correspond to the older of the two ichnoassociations previously mentioned in pag. 26. The floodplain beds with biotic remains represent rhythmical overbank deposits, which resulted from seasonal water bodies with suitable conditions to establish small- to medium-sized non-amniote and eureptilian tetrapods. The relatively small size of all the recovered tracks suggests potential environmental and taphonomic (preservational) biases.

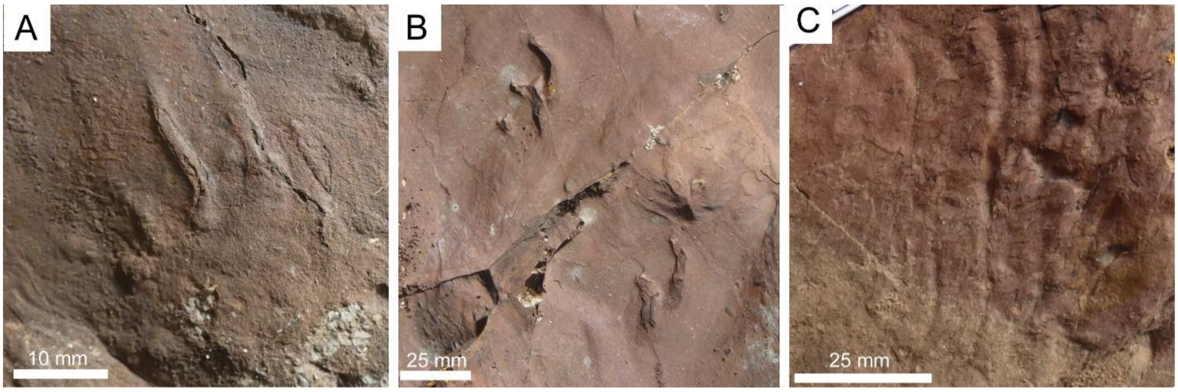


**Figure 16.** Tetrapod footprints from the Lower Red Unit in the Castellar de n'Hug sub-basin. A) Track of *Batrachichnus* with digit drag traces in convex hyporelief. B) Right manus-pes set of *Dromopus* in concave epirelief. C) Partial right track of *Hyloidichnus* with digit drag traces in concave epirelief.

## Stop 2. The Riera de Monell section

The Permian section is located following the road BV-4031 from the town of Castellar de n'Hug to La Pobla de Lillet, near the Romanesque hermitage of Sant Vicent de Rus. The section

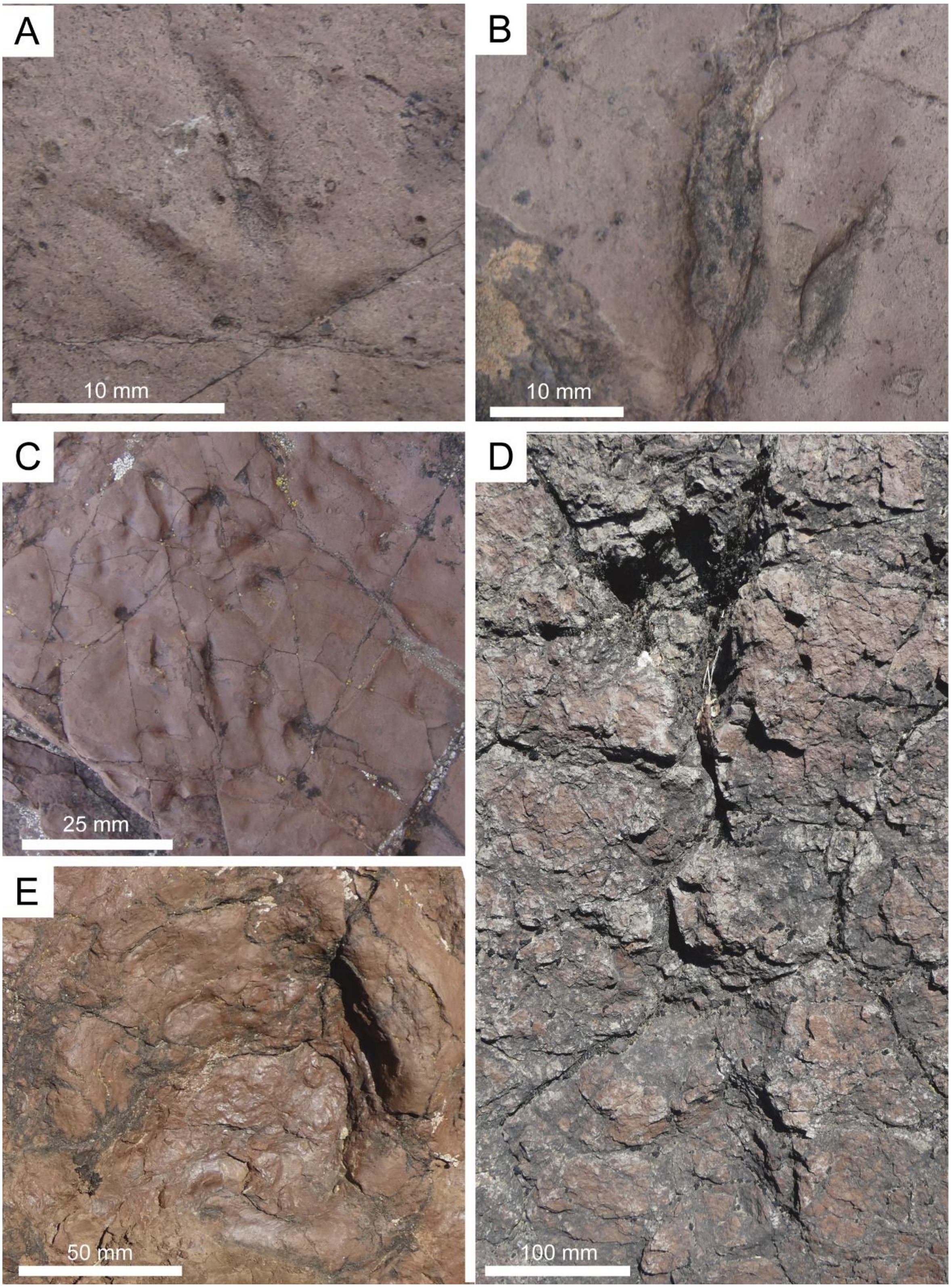


**Figure 17.** Tetrapod footprints from the Upper Red Unit (URU) in the Castellar de n'Hug sub-basin. A) Right track of *Dromopus* in concave epirelief from the lower URU. B) Left track of *Varanopus* in concave epirelief from the lower URU. C) Left manus-pes set of *Hyloidichnus* in concave epirelief from the upper URU. D) Right manus-pes set of *Brontopus* on a mud-cracked surface in concave epirelief from the upper URU. E) Right track of *Pachypes* in concave epirelief from the upper URU.

near the bridge that crosses the creek called Monell (which gives the name to the section) follows the cyclic mudstone succession dipping to the SSW. The section encompasses a >350 m thick sequence of the Upper Red Unit (URU). We can observe the last pyroclastic deposits of the uppermost part of the Lower Red Unit (LRU) at the base (Fig. 15C), and the unconformity of the Buntsandstein facies at the top (i.e., denoting that the succession was even longer). A mudstone interval with abundant septariform nodules marks the boundary between the lower and upper URU. It is in the upper URU where we find all the tetrapod ichnites in this section. The sedimentary rocks of the upper URU are mainly composed of massive mudstones in a cyclic alternation with fine-grained sandstones with characteristic mud-cracked surfaces that correspond to shallow lacustrine settings exposed to strong desiccation rates (Fig. 15A, B, D). The mud-cracks were produced under several wet-dry cycles, and some preserve raindrop impressions, indicating sporadic rainfalls. Other surfaces preserve plant remains similar to ferns, but more characteristic and abundant are the invertebrate traces attributed to notostracans (Fig. 15E), as well as body fossils of triopsids and clam shrimps. Last, but not least, the tetrapod ichno-record, corresponding to the younger ichnoassociation, is particularly relevant on these mud-cracked surfaces. The ichnogenera *Hyloidichnus*, *Dromopus*, and *Pachypes* have been identified, but the most impressive specimen is a trackway composed of six manus-pes sets attributed to *Brontopus* (Fig. 17).

As a whole, the section represents a succession of shallow lacustrine palaeoenvironments including deposits from ephemeral water bodies influenced by a monsoonal pluvial regime, which developed the necessary conditions to record the biotic activity in the wet muddy surfaces. After the impression of the tracks, these soft surfaces underwent a process of dehydration with sporadic rainfalls, manifested by desiccation cracks and raindrop impressions.

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# THE 'DINOSAURS OF THE PYRENEES' ROUTE: A FIELD TRIP TO THE CRETACEOUS ECOSYSTEMS OF THE SOUTHERN PYRENEES

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The field trip "Cretaceous ecosystems of the south-Pyrenean basins" scheduled within the 20th EAVP Conference (2023) aims to briefly introduce the richness and fossil diversity of the continental Cretaceous deposits of the southern Pyrenees. By following a route of the existing dissemination project entitled 'Dinosaurs of the Pyrenees', the field trip is conceived to a) explore the Cretaceous ecosystems of the region, and b) learn how results of primary research can be employed to boost the economic development of rural areas. By visiting exhibitions at museums and localities, participants will know the fossil record, diversity, and biology of Maastrichtian dinosaurs, and part of the extensive collection of fossils recovered for more than a century in the Lower Cretaceous lagerstätten site of La Pedrera de Meià. In addition, the novel and immersive experiences of the VIGEOCULT project transport the participants into the continental environments of the latest Cretaceous, alongside herds of hadrosaurids and titanosaurs.

## INTRODUCTION

The main goal of this field trip is to approach the attendees of the 20th EAVP Conference to the richness and fossil diversity of the continental Cretaceous outcrops of the southern Pyrenees. An excellent way to show the importance of these outcrops and the associated fossil record is to run through the cultural route known as the '**Dinosaurs of the Pyrenees**' (www.dinosauresdelspirineus.cat). This route has been an instrumental vehicle in disseminating the scientific results of the primary research leaded by the Dinosaur Ecosystems Research Group at the Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA) and thus promoting literacy on the Earth, Life, and other STEM sciences in the local communities (Galobart and Figuerola, 2020). It also aims at using this initiative as a tool to boost the economic development of the rural areas of the southern Pyrenees, where vertebrate fossil localities are found. The project includes visits to the following museums and dissemination centres in Catalonia: Dinosfera (Coll de Nargó municipality,

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Alt Urgell county), the Museu de la Conca Dellà, and Epicentre (Isona i Conca Dellà and Tremp municipalities, Pallars Jussà county), the Centre d'Interpretació del Montsec de Meià and the Centre de Dinamització de Tartareu (Vilanova de Meià and Les Avellanes i Santa Linya municipalities, La Noguera county), and the Centre d'Interpretació dels Dinosaures de Fumanya (Fígols municipality, Berguedà county). In addition, most of these centers are integrated within of the Orígens UNESCO Global Geopark (https://www.geoparcorigens.cat/en/).

The essential premise of the project 'Dinosaurs of the Pyrenees' is that fossils must be as close as possible to the original fossil localities where they were collected and therefore in all these centers the paleontological heritage serves as a significant asset in the development of the economy of the Pyrenean counties harboring the Cretaceous fossil localities. Each new scientific discovery, such as the recent new species *Abditosaurus*, *Ogresuchus*, *Tamarro*, or *Leviathanochelys* (Sellés *et al.*, 2020, 2021; Castillo-Visa *et al.*, 2022; Vila *et al.*, 2022) among others, are included in the museographic discourse after their scientific publication, and sparks and boosts the interest of the public in visiting these institutions, increasing the influx of visitors and enhancing tourism in the entire region. Thus, paleontology becomes a sort of socioeconomic engine as a way to complement agriculture and livestock, still the preeminent industry in this area.

The field trip scheduled for the 1st of July of 2023 within the 20th EAVP Conference visits three of the centers encompassed in the project 'Dinosaurs of the Pyrenees' (Fig. 1), as well as a fossil track locality, and uses the paleontological heritage exhibit in these museums and in the field to introduce the visitors to the Cretaceous ecosystems of the region. The participants will visit exhibitions and localities and get into 3-D virtual reality reconstructions depicting Early and Late Cretaceous (Barremian and Maastrichtian ages, respectively) ecosystems. They will know the fossil record, diversity, and biology of Maastrichtian dinosaurs, and part of the extensive collection of plants, arthropods, and vertebrate fossils collected at the Lower Cretaceous lagerstätten site of La Pedrera de Meià.

## 1. THE LATE CRETACEOUS CONTINENTAL ECOSYSTEMS

The first part of the field trip explores the Late Cretaceous continental ecosystems in the southern Pyrenees. Much of what we know about these ancient ecosystems comes from the fossil record of the geologic formations exposed along several synclines and areas of the south-central and eastern Pyrenees. In Catalonia, from east to west, the main areas are the Vallcebre syncline (Berguedà County, Barcelona province), the Coll de Nargó syncline, the Tremp syncline, and the Àger syncline (Alt Urgell, Pallars Jussà, and La Noguera counties, respectively). In all of them, the main geologic formation yielding fossils of organisms from ancient ecosystems is the Tremp Formation (upper Cretaceous-lower Paleocene), a unit classically known as “Garumnian” facies (Leymerie, 1868). It is

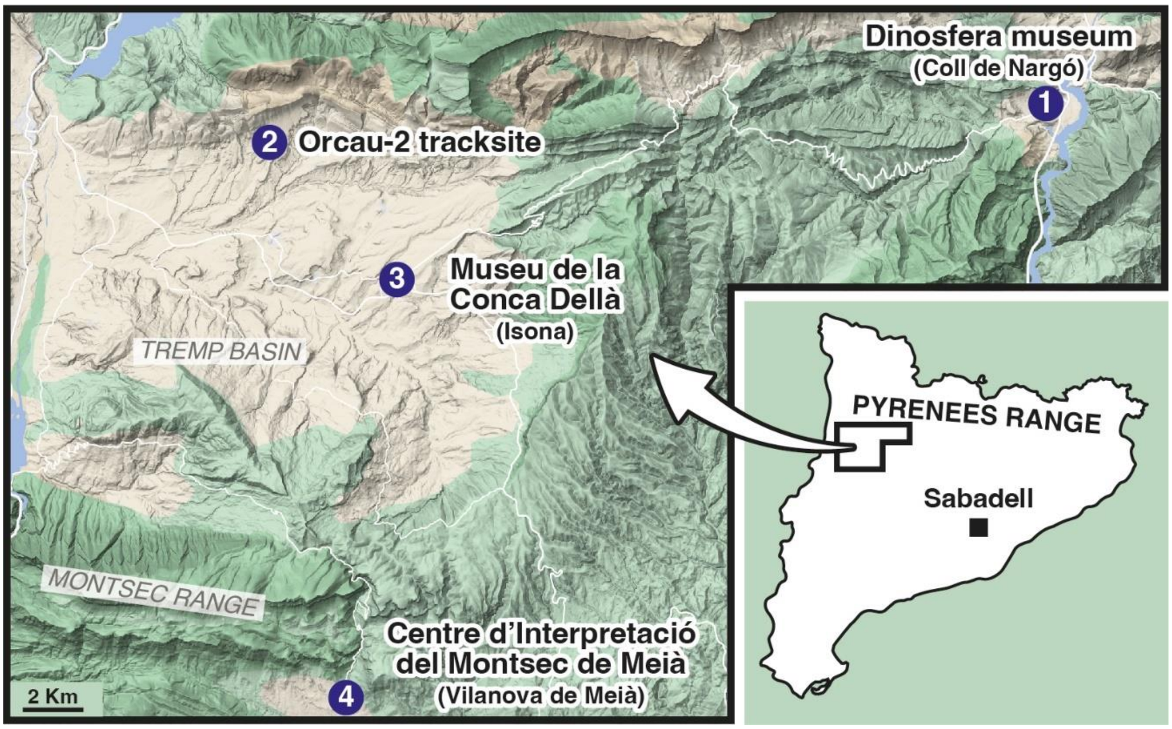

**Figure 1.** Geographic location of the main stops and museums (numbers 1 to 4) visited during the field trip within Catalonia (Spain). Map from GoogleMaps (accessed on the 28th of May 2023).

divided into various subunits that during the very end of the Cretaceous (late Campanian and Maastrichtian ages) recorded the transition from coastal to entirely continental environments.

## 1.1 The Coll de Nargó dinosaur nesting area

The first area to be visited by the participants in the field trip is the Coll de Nargó Syncline (Alt Urgell County, Lleida province, Catalonia). It comprises the Coll de Nargó dinosaur nesting site, an extensive area including several continental outcrops with abundant egg localities along the drainage of the Sallent River. These localities mainly occur in the reddish mudstones of the basal units of the Tremp Formation and represent ancient floodplain environments (Sander *et al.*, 2008; Sellés *et al.*, 2013).

The first reports of dinosaur eggshells in the region date back to the second half of the XX century (Baudrimount, 1961; Erben *et al.*, 1979, among others). Later, a large number of German paleontologists (Ashraf and Erben, 1989; Peitz, 2000; Mueller-Töwe *et al.*, 2002; Sander *et al.*, 1998, 2008) and researchers from the Universidad Complutense de Madrid conducted paleontological studies in the area (López-Martínez, 2000). Subsequent projects led by the Institut Català de Paleontologia Miquel Crusafont and the Museu de la Conca Dellà reported new outcrops and described a unique record of oologic species through time (Vila *et al.*, 2006, 2010; Sellés *et al.*, 2013).

*A diverse oological record*

The most striking characteristic of the Tremp Formation outcrops in Coll de Nargó is the abundance and diversity of eggshell types, whose study has generated important controversies regarding their parataxonomic affinity. Initially, Sander *et al.* (1998) and Peitz (2000) identified the eggshells from Coll de Nargó as cf. *Megaloolithus mammilare*, while López-Martínez (2000) emphasized that *M. siruguei* was the most abundant egg type in the area, among other oospecies. Escuer *et al.* (2006) mentioned the occurrence of up to four different oospecies, adding to the previously named oospecies *M. aff. aureliensis* and *Cairanoolithus* sp. Later on, Sellés *et al.* (2013) reevaluated the dinosaur oological diversity of the area, concluding that four different oospecies occurred in the region - *M. aureliensis*, *M. siruguei*, *Fusioolithus baghensis* (after Fernández and Koshla, 2015), and *Cairanoolithus* cf. *roussetensis* - and proving the significant oological diversity of the area (Fig. 2A-D). Finally, megaloolithid eggs are generally attributed to titanosaur sauropods based on the discovery of in-ovo embryonic remains (Chiappe *et al.*, 1998, among others, but see Grigorescu *et al.*, 2010), whereas the endemic European egg-type *Cairanoolithus* is tentatively attributed to a non-ornithopod ornithischian, most likely to a nodosaurid ankylosaur (Sellés and Galobart, 2016), albeit no embryonic remains can unambiguously confirm such affinity.

*Eggs, clutches, and nesting behavior*

Aside from the parataxonomic controversy, the Coll de Nargó area is a critical location to understand the nesting strategies of Late Cretaceous titanosaurs and offers a unique opportunity to assess many paleobiological issues such as the mode of nesting and incubation of European sauropods. The first attempts to interpret the titanosaur reproductive behavior in the Coll de Nargó nesting area were provided by Sander and colleagues in 1998 (with conclusions reviewed in Sander *et al.*, 2008), who briefly described megaloolithid egg clutches containing three to six eggs organized in a bowl-like arrangement and deposited in ancient paleosols. Between 2005 and 2007 a series of excavations produced key information about the sedimentology of the nesting horizons, the egg types, and the taphonomy of eggs and clutches (i.e., 3D arrangement and distribution). Thus, Vila *et al.* (2010) underscored that eggs in the Pinyes locality - and by extension all the eggs in the area - exhibit an ellipsoidal shape due to tectonic stress that influenced egg size and shape (Fig. 2E) and could potentially lead to misinterpretation of reproductive biology. The authors also contributed to a better understanding of the nesting behavior of titanosaurs by demonstrating that the eggs arranged in large clutches of 25 or more eggs (Fig. 2G-H) in a shallow bowl-shaped pit (Vila *et al.*, 2010), corroborating previous inferences on clutch morphology. Eggs revealed a predominance of concave down eggshell orientation “floating” within the sedimentary matrix that infilled the eggs, a distribution that is consistent with the burial condition of the hatched eggs, which is also in agreement with the conductance values for these eggs (Jackson *et al.*, 2008) and supports the idea that they were incubated underground.

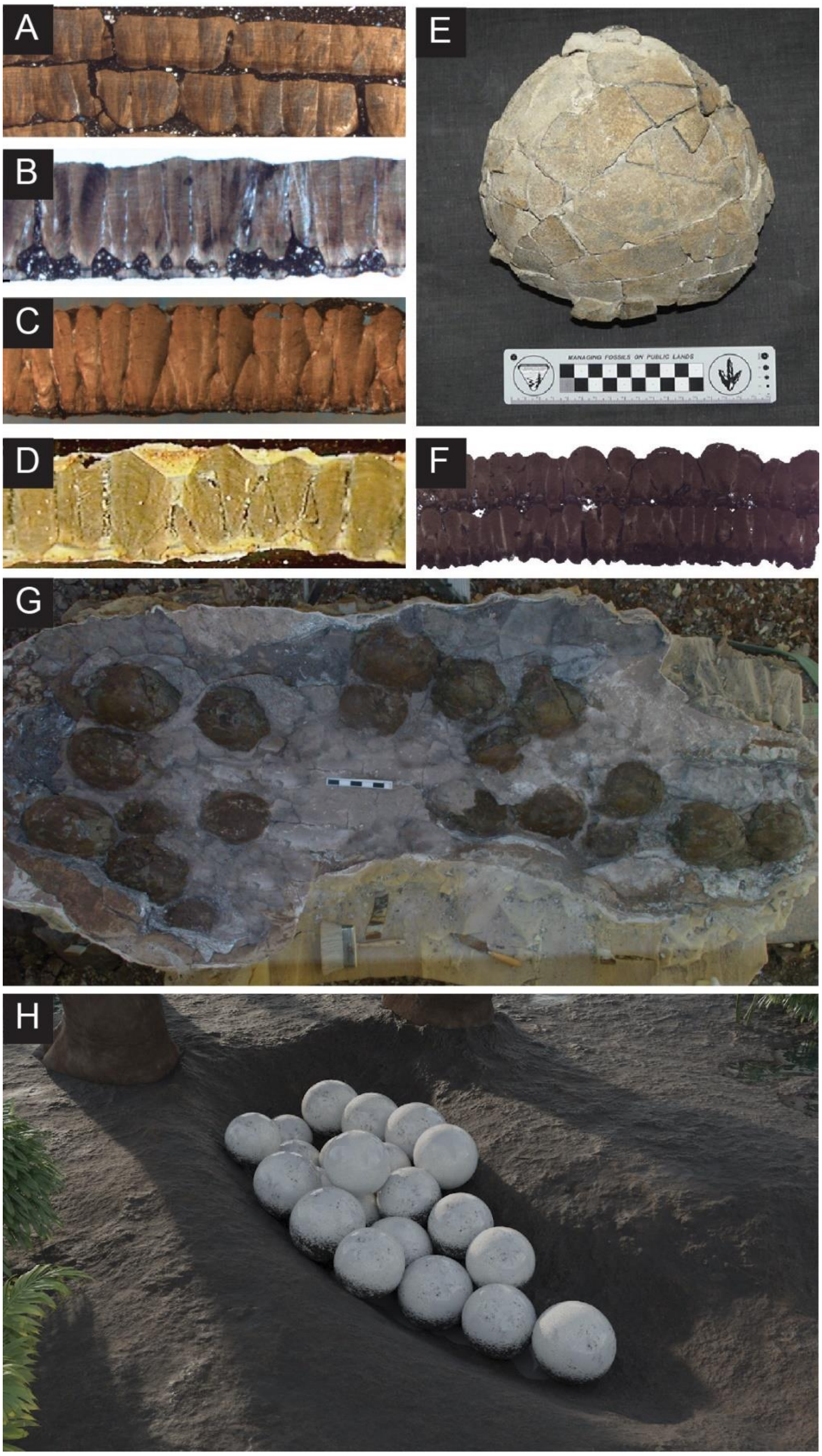

**Figure 2.** The dinosaur oological record from the Coll de Nargó nesting area. Examples of the different oospecies discovered in the fossil locality in radial thin section: A, *Cairanoolithus* cf. *roussetensis;* B, *Megaloolithus aureliensis*; C, *Megaloolithus siruguei*; D, *Fusioolithus baghensis. Megaloolithus siruguei* is the most common egg type in Coll de Nargó, being represented by complete but tectonically distorted eggs (E), pathological eggshells (F), and complete clutches with up to 25 eggs (G). Digital illustration of a titanosaur female laying its eggs in a bowl-shaped pit (H).

Those who visit the Coll de Nargó outcrops will realize the multiple layers yielding eggs and eggshells. This extraordinary egg succession (occurrence of eggshells, eggs, and clutches along 41 consecutive stratigraphic levels; Sellés *et al.*, 2013) points to a nesting area used for a very long time (at least 4 Ma). Furthermore, some of the egg-bearing levels contain up to three different egg types, suggesting that the nesting area was shared by different dinosaur species, although not necessarily at the same time (Sellés *et al.*, 2013).

### *An enigmatic small predator*

In April 2013, small skeletal remains were discovered in the vicinity of a sauropod nest in a site known as the El Mirador (western Coll de Nargó; Fig. 3A). A few days later, members of the ICP started digging the skeleton, confirming the singularity of the discovery but, sadly, the specimen was stolen. When the specimen was recovered a month later it had been damaged, with several fragmented bones and many others missing (Fig. 3B). After a long preparation process the fossil was finally exhibited at the Dinosfera Museum in Coll de Nargó. The specimen includes the anterior part of the snout (Fig. 3C and D), reminiscences of the forelimbs and hindlimbs, and most of the dorsal and sacral axial skeleton of a small-sized sebecid notosuchian (Sellés *et al.*, 2020). The unique combination of anatomical characters of the specimen, coupled with a series of autapomorphies, allowed the erection of *Ogresuchus furatus* ("the ogre crocodile that was stolen"; Fig. 4E). The "ogre" condition of the new sebecid lies in the fact that it was discovered suspiciously close to hatched titanosaur eggs and even though there is no evidence of predatory activity in any of the eggs neither stomach contains in the skeleton, Sellés *et al.* (2020) postulated that the 1-m-long crocodile could easily predate hatchling titanosaurs, given that they were less than 40 cm long at hatch.

*Ogresuchus* is another striking piece of the puzzling Late Cretaceous terrestrial ecosystems from the southern Pyrenees. The new crocodylomorph was recovered in phylogenetic analyses as a sebecid more closely related to Paleocene South American taxa than to the European ones from the Eocene. Despite the paleogeographic history of the clade remains obscure, by considering the paleogeographic configuration of the continent at the end of the Cretaceous, it seems that *Ogresuchus* was related to an African immigration wave of an unrecorded sebecid lineage. Though speculative, this hypothesis fits well with the current paleontological data that prove some kind of faunal connection between Southern Europe and Northern Africa during the Late Cretaceous (Csiki-Sava *et al.*, 2015; Vila *et al.*, 2022).

## Stop 1: The Dinosfera museum

The Dinosfera museum, built in 2010, is located close to the Coll de Nargó nesting area and is conceived as a window to dinosaur reproduction by exhibiting dozens of dinosaur eggs, clutches, and nests. Visitors start the visit by watching an introductory video that explains how the land was

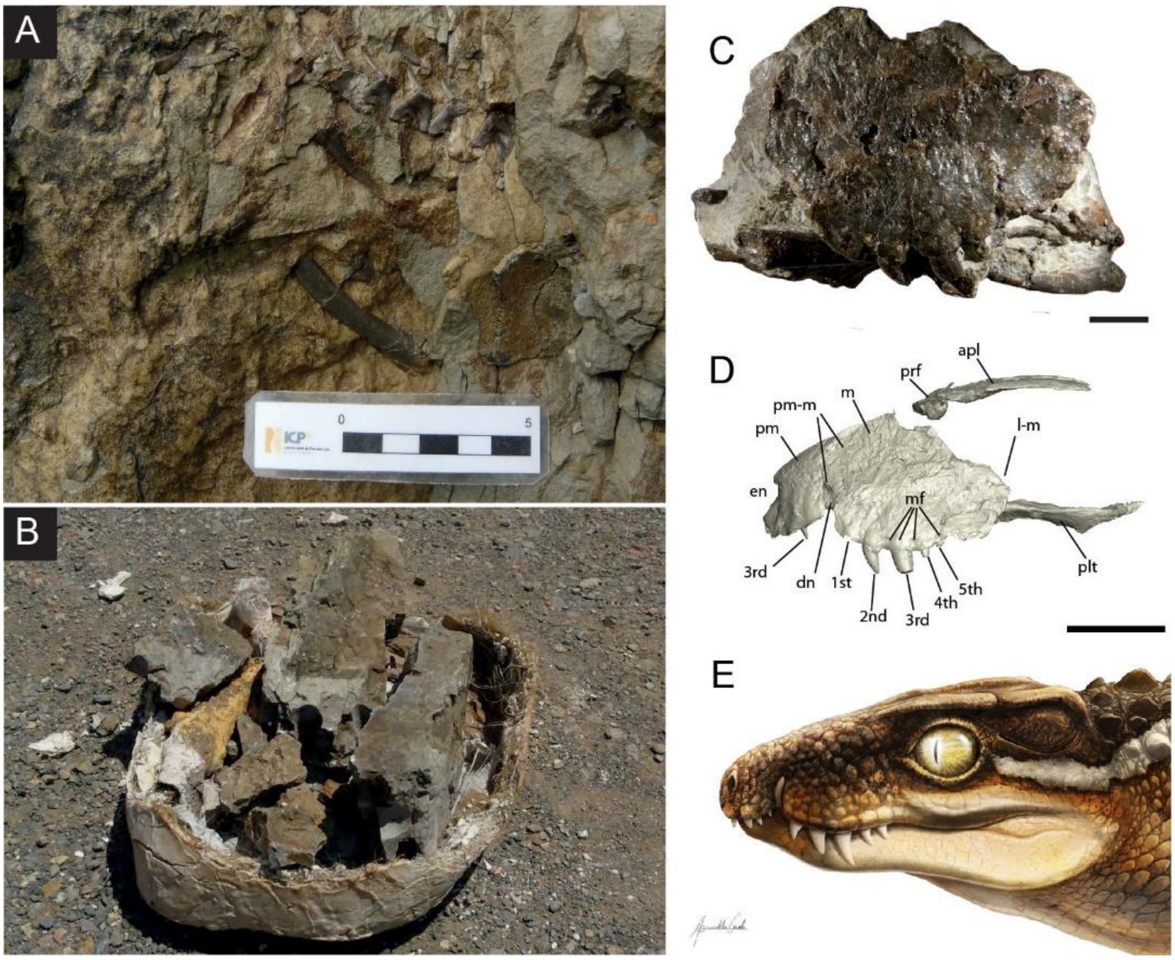

**Figure 3.** *Ogresuchus furatus*, the small sebecid from the Upper Cretaceous of southern Pyrenees. The fossil remains as discovered (A), and as recovered after its theft (B). Cranial elements after preparation (C), 3-D digital reconstruction (D), and an artistic reconstruction (E) by paleoartist ICRA-art. Abbreviations: apl; anterior palpebral; dn, dentary notch; en, external nares; m, maxilla; mf, maxillary foramina; plt, palatal; pm, premaxilla; pm-m, premaxilla-maxilla contact; prf, prefrontal. Scale bars equal 2 cm.

configured during the Late Cretaceous, and what landscapes and ecosystems held the dinosaur species. It follows with a model depicting how a titanosaur female made the nest, under the stalking presence of the crocodile *Ogresuchus*. Sections of the museum deal with the geology and discoveries in the region but also include a close approach of what an amniote egg is, its evolution, structure, and morphology. The next section is focused on the importance of the Coll de Nargó nesting area, the diversity of eggshell oospecies and their possible layers, and the excavation and preparation of the largest dinosaur nest found in Europe. An interactive screen allows the visitor to play the role of a field paleontologist, trying to excavate a virtual egg clutch using the appropriate tools. Finally, brief information is provided on the paleontological use of CT scans, how to reconstruct the 3D morphology of a clutch or the focus of ongoing research. A brand new section tells the striking history of the discovery of the crocodile *Ogresuchus*.

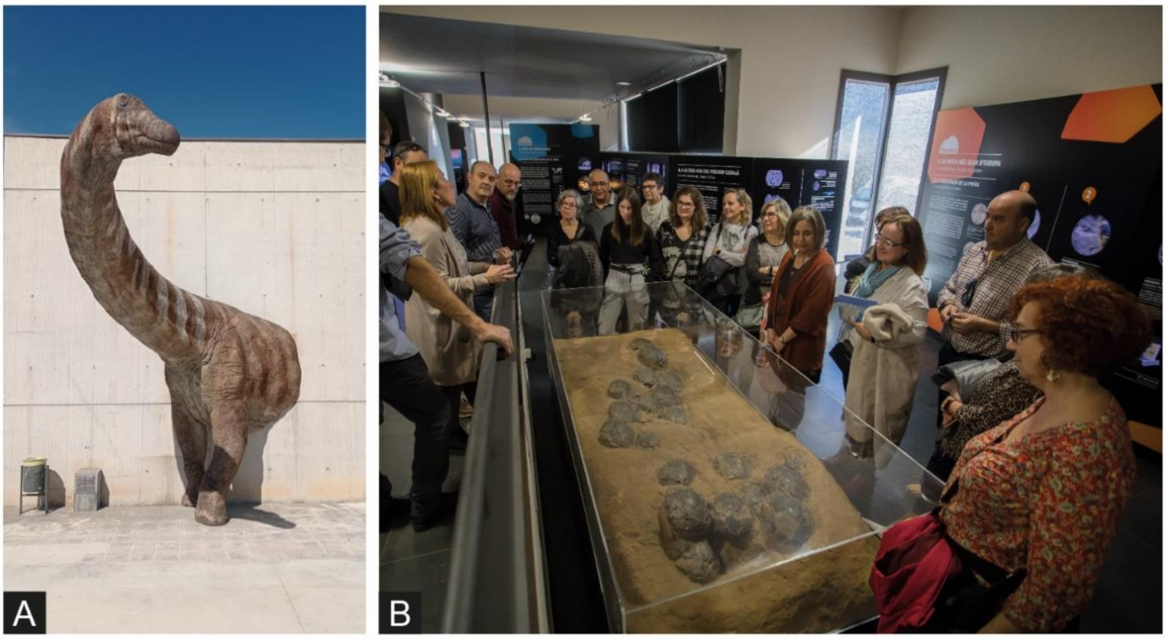

**Figure 4.** Dinosaur exhibition at the Dinosfera museum. A, real-sized model of the titanosaur *Abditosaurus kuehnei*, at the museum entrance; B, visitors around the largest sauropod egg clutch found in Europe.

## 1.2 The Tremp Basin

The second area to be visited by the participants in the field trip is the eastern Tremp Basin, the largest one with deposits of the Tremp formation in the southern Pyrenees. That is why historically most of the stratigraphic and paleontological studies have been concentrated there, producing most of the findings and advances in the characterization of continental environments and ecosystems from the end of the Cretaceous (Maastrichtian age) in the Pyrenees. First discoveries in this basin date back to the beginning of the 20th century, and for almost sixty years only isolated finds of bones and eggs report the occurrence of dinosaur fossils (Marín and Bataller, 1929; Lapparent and Aguirre, 1956; Lapparent, 1958; Bataller, 1958) although they do not represent systematic research in the study of dinosaurs. It is worth highlighting, however, the excavations made in the mid-1950s by the paleontologist Walter Georg Kühne (Talens, 1955), who excavated the first semi-articulated titanosaurian sauropod found in Europe (Vila, 2022). In the late 70s and middle 80s, Spanish researchers concentrated their efforts on half a dozen sites with bones and footprints, such as Els Nerets (or Vilamitjana), Sant Romà d'Abella, and Orcau-2 (Llompart *et al.*, 1984; Casanovas *et al.*, 1987, 1993, 1995), and in the 90s egg localities were reported and/or reanalyzed (Sanz *et al.*, 1996; Sander *et al.*, 1998; Vianey-Liaud and López-Martínez, 1997).

In the last two decades the number of studies exclusively focused on the Maastrichtian vertebrates in the Tremp Basin has grown exponentially and include advances in the faunal succession, systematics, paleobiology, paleobotany, palynology, paleoenvironmental reconstructions, and chronostratigraphy from dozens of new bone, egg and track localities (Riera *et al.*, 2009; Torices *et al.*, 2012, 2015; López-Martínez *et al.*, 2000; Vila *et al.*, 2013, 2016, 2022; Prieto-

Márquez *et al.*, 2013, 2019; Fondevilla *et al.*, 2018, 2019; Dalla Vecchia *et al.*, 2013, 2014; Blanco *et al.*, 2016, 2020; Marmi *et al.*, 2012a, 2014, 2015; Sellés *et al.*, 2014a, b, 2021, among many others).

*Components of the continental Late Cretaceous ecosystems*

Data gathered in the last century in the southern Pyrenees has led to substantial progress in our understanding of the diversity, phylogenetic systematics, evolution and paleobiology of organisms that compose the Maastrichtian ecosystems in southwest Europe. The main groups of organisms recognized in the eastern Catalonian part of the Tremp Basin are presented below.

- Vertebrates: among the micro- and macro-vertebrates composing the Maastrichtian ecosystems are the small-sized herpetofauna, comprising lissamphibians and squamates. The former are represented by the widespread Albanerpetontidae and the diverse Anura (Fig. 5A-D; Blanco *et al.*, 2016). Anurans include discoglossines, alytines, paleobatrachids, and probably pelobatid or gobiatid. Four groups of squamates have been identified: anguids, “scincomorphs” (Fig. 5F-G), iguanids, and, possibly, the oldest European gekkotans (Fig. 5E). According to the most recent data, the Maastrichtian herpetofauna from the Pyrenees is mainly represented by Laurasian groups, while taxa with Gondwanan affinity are absent from the fossil record (Blanco *et al.*, 2016). Such absence is unlikely to be caused by environmental bias because the studies considered a large variety of paleoenvironments, including lacustrine, lagoons, floodplains, and meandering rivers depositional settings. Thus, it is postulated that the absence of Gondwanan taxa might correspond to a regional extinction event during the early Maastrichtian (Blanco *et al.*, 2016). Testudines mainly consist of isolated shell plates (Marmi *et al.*, 2012b; Blanco *et al.*, 2015), which remain largely unstudied. Exceptions are the partial carapace of the fresh-water bothremydid *Polysternon isonae* (Fig. 5H; Marmi *et al.*, 2012a). Maastrichtian ecosystems were composed by a diverse set of crocodilians which includes the gavialoid cf. *Thoracosaurus*, the “atoposaurid” cf. *Theriosuchus* (Fig. 5J-L), the hylaeochampsid *Acynodon* (Fig. 5N), the notosuchid *Doratodon*, but notably several species of the European endemic family Allodaposuchidae (*A. subjuniperus*, Blanco *et al.*, 2020; *A. palustris*, Blanco *et al.*, 2020; *A. hulki*, Blanco *et al.*, 2015, 2020; Fig. 5O). The occurrence of such diversity in a relatively reduced geographic area is explained by a niche partitioning process, promoted by a specific feeding behavior and a particular environmental distribution of the taxa. In this scenario, cf. *Thoracosaurus* could inhabit coastal environments; cf. *Theriosuchus* and *Acynodon* mainly prowled swamps and marshes, sharing those environments with *A. palustris* and cf. *Theriosuchus*. This latter taxon also could have occupied the fluvial floodplains, cohabiting with *A. hulki*, and *A. subjuniperus* (Blanco *et al.*, 2020). The pterosaur remains are extremely elusive (Fig. 5I) and are limited to a single locality (Torrebilles-2; Dalla Vecchia *et al.*, 2013), which represent the youngest pterosaurian remains ever discovered in Europe.

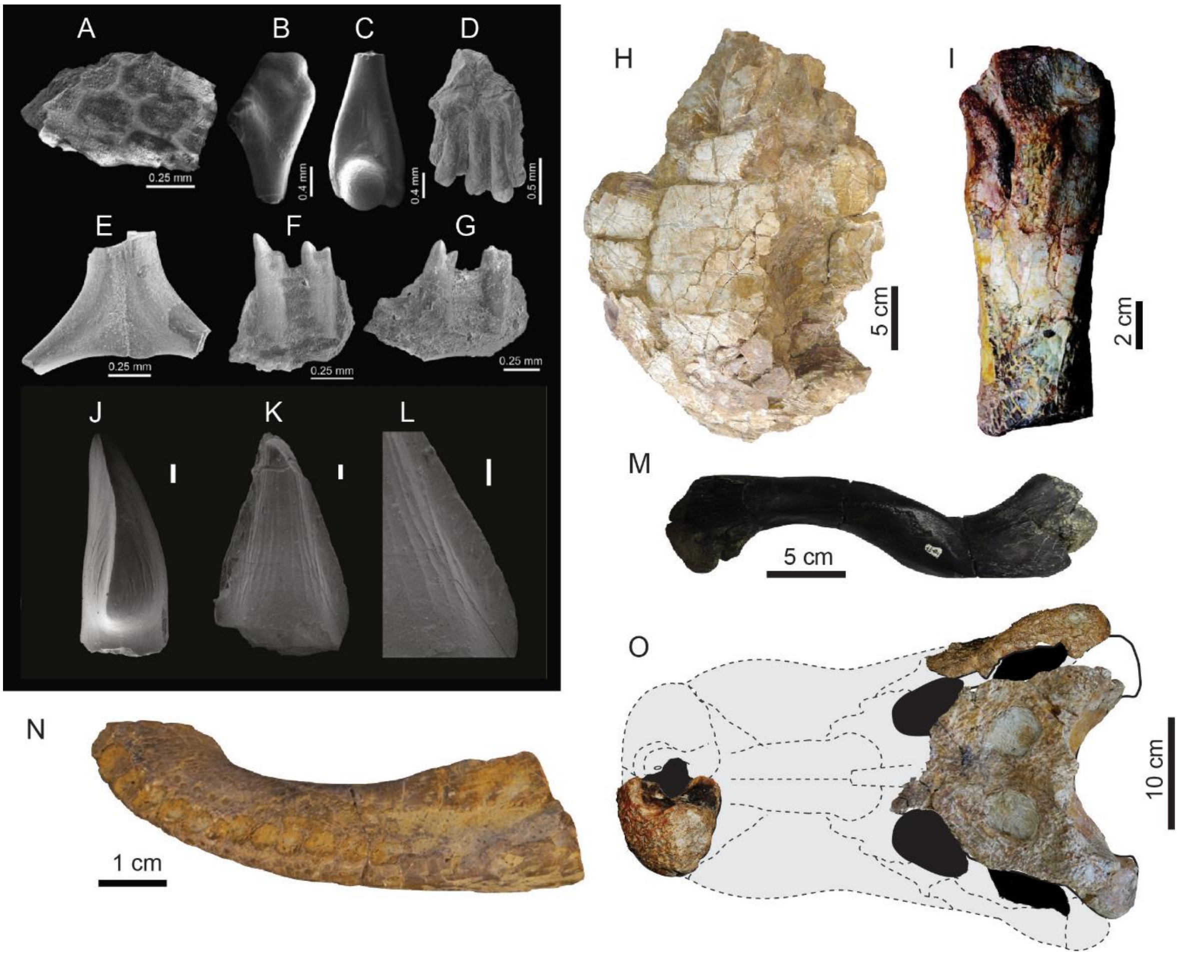

**Figure 5**. Non-dinosaurian fossil record from Late Maastrichtian of the Tremp Basin (southern Pyrenees). Albanerpetontid amphibians: A, Frontal (IPS85004) in dorsal view. B, Proximal (IPS85010b) and C, distal (IPS85010a) epiphyses of humeri in ventral view. D, Left premaxilla (IPS85020) in lingual view. Squamates: E, Frontal (IPS84998) of an indeterminate Gekkota in ventral view. F-G, Tooth-bearing bones (IPS84999, IPS85000) of an indeterminate 'scincomorph' lizard in lingual view (modified from Blanco et al., 2016). Testudo: *Polysternon isonae* (MCD-5095) in dorsal view (modified from Marmi et al., 2016a). Pterosauria: I, right femur (MCD-5036) in lateral view (modified from Dalla Vecchia et al., 2013). Crocodilia: J-L, cf. *Theriosuchus* teeth (IPS96647 and MCD-7008). M, Femur of an indeterminate crocodylomorph (MCD-5544) in lateral views. N, lower jaw of cf. *Acynodon* (IPS13360) in occlusal view. O, Cranial elements of *Allodaposuchus hulki* (MCD-5139) in dorsal view (modified from Blanco et al., 2015, 2020).

Dinosaurs played a major role in the Late Cretaceous (Maastrichtian) ecosystems and, consequently, their fossil record shows great taxonomic diversity and abundance in the Tremp Basin (Fig. 6). Among herbivores, nodosaurid ankylosaurians have an extremely scarce and fragmentary record in the basin, being limited to a single humerus, two armor plates, and one isolated tooth (Santafé *et al.*, 1997; López-Martínez *et al.*, 1999, 2001; Martín Jiménez *et al.*, 2017). Little can be said about these components of the ecosystem, beyond their phytophagous diet and their small size. Another group of herbivorous dinosaurs were iguanodontian ornithopods. The more basally-branching representatives of this clade so far recorded in the basin are rhabdodontids. However, unlike other European regions, the current rhabdodontid record in the southern Pyrenees is extremely scarce. The only evidence of these animals in the Tremp Basin is the holotype scapula of

*Pareisactus evrostos* (Párraga and Prieto-Márquez, 2019) from the lower Maastrichtian Basturs Poble bonebed. Despite the fragmentary nature of these remains, they represent the youngest occurrence of the group in the entire Ibero-Armorican region (Fondevilla *et al.*, 2019), placing the last occurrence of the clade around the early-late Maastrichtian boundary (ca. middle-upper part of chron C31r). In contrast, and as in most other regions of the Globe, the 'duck-billed' hadrosaurids were the most common, diverse, and abundant group of dinosaurs that once roamed the southern Pyrenees. Undoubtedly, they were the most prominent components of herbivorous dinosaurs in the ecosystem. Two species have been described in the eastern Catalan part of the Tremp Basin: *Pararhabdodon isonensis* (Casanovas-Cladellas *et al.*, 1993; Serrano *et al.*, 2021) and *Adynomosaurus arcanus* (Prieto-Márquez *et al.*, 2019), both belonging to the subclade Lambeosaurinae. These two taxa were relatively large hadrosaurids, with lenghs in excess of 7-8 m. The phylogenetic hypotheses point to a close relationship with the Chinese species *Tsintasaurus spinorhinus*, as outgroups to the major speciose clade of lambeosaurines that includes the better-known forms from North America and Asia. Recently, a puzzling new styracosternan (clade that includes hadrosaurids), *Calvarius rapidus,* has been described from the Tremp Basin (Masia de Ramon locality, within the last 100,000 years of the Cretaceous; Prieto-Márquez and Sellés, in press). All that is known from *C. rapidus* is a small elongate left metatarsal IV, indicating an animal of no more than 2 m in length. By analogy with the similarly gracile metatarsals of lightly built, small-bodied cursorial ornithopods and early ornithischians, it is likely that *C. rapidus* was also capable of rapid locomotion. This new species also represents an exception to the larger and more massively-built styracosternan body type, as well as yet another case of endemism in an insular terrestrial environment. In addition to the skeletal material, dozens of sites with footprints and trackways have been identified and assigned to the ichnogenus *Hadrosauropodus* (Vila *et al.*, 2013), and eggshells of the oogenus *Stromatoolithus europaeus* (Sellés *et al.*, 2014b after Xufeng *et al.*, 2021) have been also reported.

In terms of fossil abundance, the second largest group of herbivorous dinosaurs in the continental ecosystems are the sauropods, represented solely by members of Titanosauria. To date, only one species has been described in the Tremp Basin, *Abditosaurus kuehnei* (Vila *et al.*, 2022), belonging to the saltasaurine titanosaur clade, although there is evidence of the presence of more taxa yet to be described (Vila *et al.*, 2012; Vázquez and Castillo-Visa, 2021). A very distinctive feature of the titanosaurians in the Tremp Basin, and by extension in the southern Pyrenees, is their disparity in size; there are small forms and others that would reach 20 meters in length (yet to be described). In this regard, *A. kuehnei* is larger than other titanosaurian species from south-western Europe; this points the idea that it belongs to an immigrant lineage of titanosaurians that reached Ibero–Armorica during the early Maastrichtian. This bone record is complemented by a very extensive record of footprints and trackways (see more in the 'Stop 2: The dinosaur tracksite of Orcau-2' section), and eggs and clutches assigned to this group (see more in the 'Coll de Nargó nesting area' section).

Finally, the predators in the ecosystem were represented by the theropod dinosaurs. Its presence is attested although its fossil record is very elusive in the Tremp Basin. Apart from the

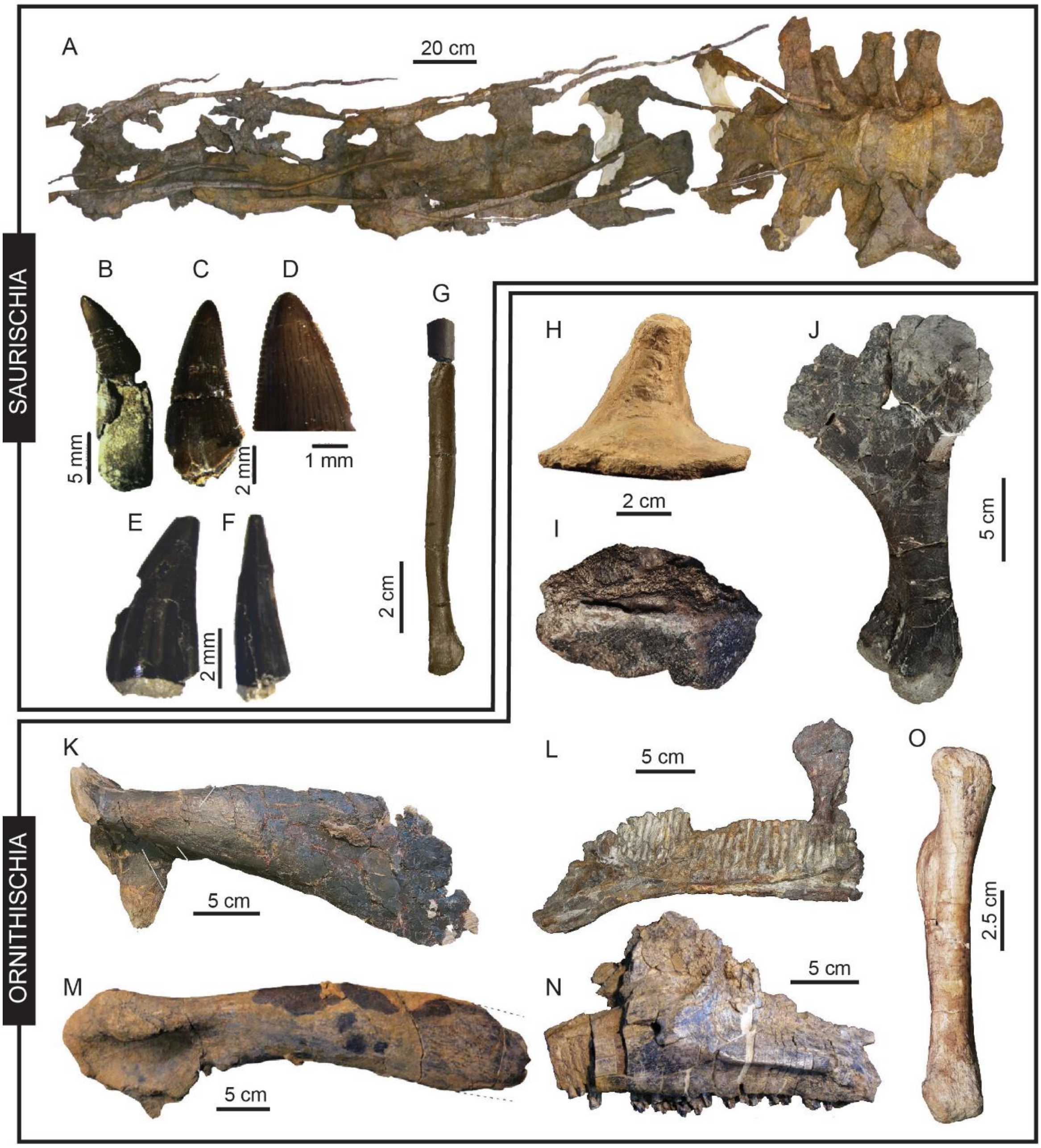

**Figure 6.** Non-avian dinosaur fossil record from the Maastrichtian of the Tremp Basin (southern Pyrenees). Saurischia (A-G): A, *Abditosaurus kuehnei*, holotype, nearly complete articulated neck (MCD-9882) in ventral view (modified from Vila et al., 2022). B-D, cf. Dromaeosauridae isolated tooth (MCD-5033), complete specimen (B), detail of the crown (C), detail of denticles (D). E-F, aff. *Paronychodon* tooth (MCD-5582) in labial (E) and caudal (F) views (modified from Marmi et al., 2016a). G, *Tamarro insperatus*, holotype, a partial right metatarsal II (MCD-7073) in dorsal view (modified from Sellés et al., 2021). Ornithischia (H-O): H-O, Nodosauria indet., sacral spike (MCD-0074) in lateral view (H), dorsal osteoderm (MCD-5035) in dorsal view (I), and right humerus (MNCN 59304) in anteromedial view (J). K, *Pareisactus evrostos*, holotype left scapula (MCD 5371) in lateral view (modified from Párraga and Prieto-Márquez, 2019). L, Dentaries from Basturs Poble bonebed (MCD-5007) in lingual view (modified from Prieto-Márquez et al., 2019). M, *Adynomosaurus arcanus*, holotype left scapula (MCD-7125) in lateral view. N, *Pararhabdodon isonensis*, left maxilla (MCD-4919) in lateral view (modified from Prieto-Márquez et al., 2013). O, *Calvarius rapidus*, holotype left metatarsal IV (MCD-8734) in dorsal view (modified from Prieto-Márquez and Sellés, in press).

metatarsal bone of the basally-branching troodontid *Tamarro insperatus* from the Sant Romà d'Abella site (Sellés *et al.*, 2021), the vast majority of non-avian theropod remains from the basin correspond to isolated teeth (some of them attributed to medium-size ceratosaurs, and others to a wide variety of small dromaeosaurids; Prieto-Márquez *et al.*, 2000; Torices *et al.*, 2015; Marmi *et al.*, 2016a; Castillo-Visa et al, 2022) and to eggshells (*Prismatoolithus trempii* and *Pseudogeckoolithus*; Vianey-Liaud and López-Martínez, 1997; Sellés *et al.*, 2014a).

- Plants: The palaeobotanical record of the transitional and continental environments of the Tremp Basin is featured by a wide diversity of plant fossils, including freshwater algae, mosses, clubmosses, horsetails, ferns, cycads, conifers, monocot and eudicot angiosperms (Villalba-Breva *et al.*, 2015; Marmi *et al.*, 2015; Marmi *et al.*, 2016b). All these taxa are reported from spores, pollen, seeds as well as vegetative remains (i.e., leaves and stems). Reconstructed plant communities by means of these palaeobotanical evidences and taphonomical analyses provide the basis of the primary production of the Maastrichtian continental ecosystems from the Pyrenean Basin and are distributed in various environments (Marmi *et al.*, 2016b; Fig. 7). Thus, mudflats, marshes, and coastal lakes ('Grey unit' of the Tremp Formation) exhibited hydrophytic vegetation consisting of meadows of brackish porocharacean (*Feistiella malladae*) as well as e freshwater characean (*Peckichara* and *Microchara* species) and clavatoracean (*Clavator brachycerus*) algae. Emerged areas surrounding freshwater swamps and lakes were dominated by the cheirolepidiacean conifer *Frenelopsis*, palms (*Sabalites longirhachis*), and a diversity of ferns including members of Schizaeaceae, Cyatheaceae, and Polypodiaceae. In the estuarine to fluviatile floodplains ('Lower red unit' of Tremp Formation), evidence for hydrophytic vegetation was poorer and mainly represented by a low diversity of charophyte assemblages mostly composed of few species of the genus *Microchara* growing in ponds. The floodplains, with abundant Betulaceae-like eudicot taxa, were much richer in angiosperms than the coastal areas. The riparian environments were largely dominated by *Saliciphyllum gaetei*, an eudicot displaying willow-like leaves, along with the palm *Sabalites longirhachis*, as well as abundant cattails (Typhaceae indet.) (Marmi *et al.*, 2015, 2016a).

## Stop 2: The dinosaur tracksite of Orcau-2

The track locality of Orcau-2 is found 600m east of the village of Orcau (municipality of Isona i Conca Dellà, Pallars Jussà County), at the northern margin of the Tremp Basin. Stratigraphically, the tracksite, dated as to the early Maastrichtian (Fondevilla *et al.*, 2019), belongs to the basalmost portion of the Tremp Fm, in the 'grey unit' or 'La Posa member'. This unit is typically represented by alternations of grey marls and sandstones, limestones and coals, and interpreted as a marine-to-continental transitional environment (Rosell *et al.*, 2001; Riera *et al.*, 2009), and particularly, as a shallow lagoon or estuary (Liebau, 1973) protected by barrier island systems of the Arén Sandstone Fm (Díaz-Molina *et al.*, 2007). The stratigraphic section in the site is mainly represented by six sub-

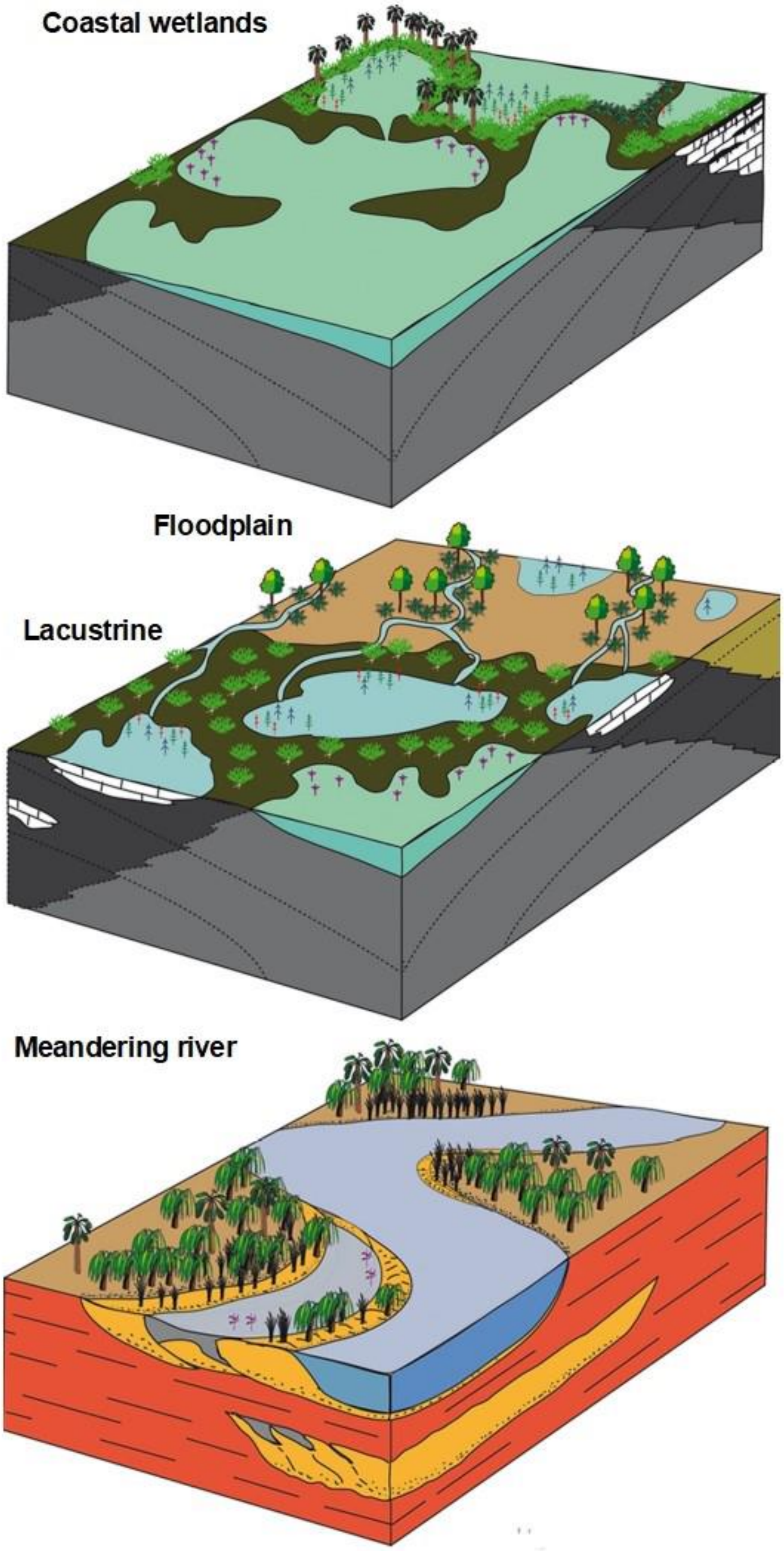

**Figure 7.** Paleoenvironmental reconstructions of vegetation growing in different environments of the southern Pyrenees basins based on data from the 'grey' and 'lower red' units of the Tremp Formation (modified from Marmi et al., 2016b).

vertical and decimetric levels of moderately to intensively bioturbated limestones with tracks and trackways exposed along 200m (Fig. 8). The section is capped by a rudist level referred to as the *Hippuritella castroi* horizon (Vicens *et al.*, 2004) and a tractive level of reworked oncoids with embedded dinosaur bone fragments (including a fragmentary hadrosauroid tibia). The tracksite was originally reported by Carme Llompart, Lourdes Casanovas, and Jose Vicente Santafe (Llompart et al., 1984) who described two distinct ichnogenera, *Orcauichnites garumniensis* and *Ornithopodichnites magna*, both attributed to ornithopods. The third and most abundant morphotype was assigned to sauropods. In 2004, a reassessment of the tracksite (Vila *et al.*, 2011) confirmed the presence of sauropod tracks, although the state of preservation and the intense dinoturbation observed in all the locations prevented the reliable identification of the previously named ornithopod ichnogenera. In this regard, the trampling index ("dinoturbation index" after Lockley and Conrad, 1989) ranges from moderate to intensive, with tracks typically overlapping one another and only a few trackways discernible.

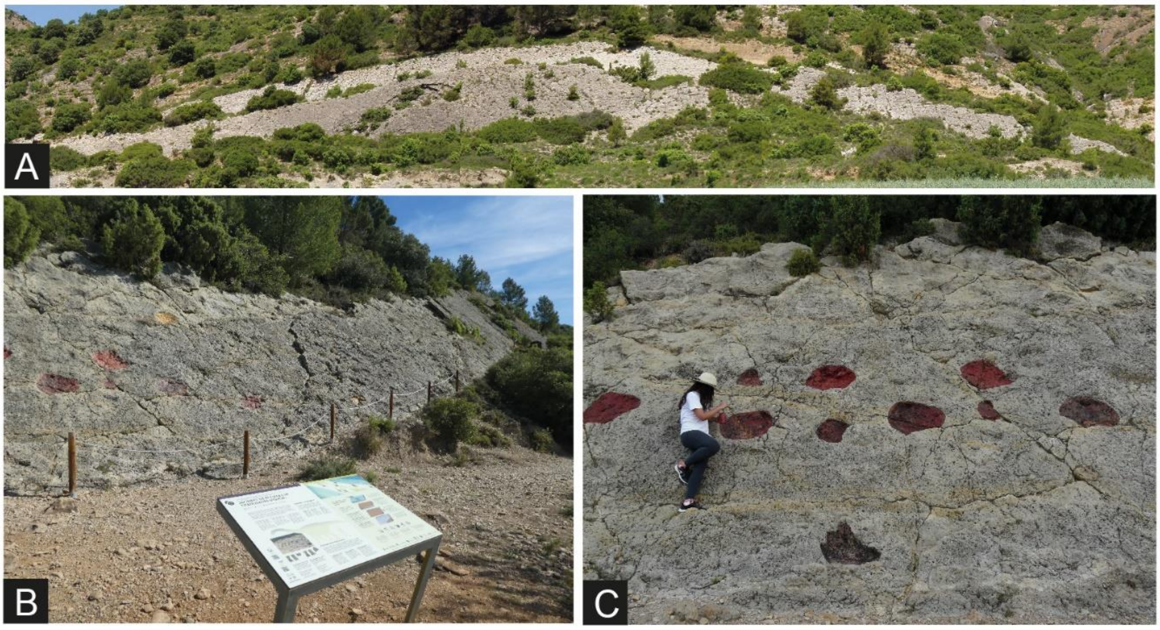

**Figure 8.** Orcau-2 tracksite. A, General view of the site with exposure of the track-bearing levels. B, Partial view of the site with dissemination panels for visitors. C, Partial exposure of a titanosaur trackway, color-highlighted for the sake of interpretation.

Some of the best-preserved isolated tracks correspond to pes and manus footprints. Pes tracks are entaxonic and subtriangular to oval with a posterior narrow area and an anterior wide area, some of them depicting four claw marks. Manus tracks present a U-shaped with anteriorly convex and posteriorly concave outlines, and lack the digit I impression in the inner margin. Alongside the multiple isolated footprints in the trampled surfaces, at least three sauropod trackways are present. The trackways exhibit an alternating sequence of outward rotated tracks: small and rounded to crescent-like manus tracks and large, oval-shaped pes tracks. Heteropody is about 1:3 and Pes trackway ratio (PTR, after Romano *et al.*, 2007) is about 33%, thus indicating a clear wide-gauge pattern. All these characters, together with track morphology, support a titanosaur attribution. Trackways represent single individuals and two of them present the same walking direction, suggesting social behavior.

## Stop 3: The Museu de la Conca Dellà

Located in the old town of the Isona i Conca Dellà village (Pallars Jussà, Lleida), the Museu de la Conca Dellà was founded on April 1995 and, for more than 25 years, the three floors of the museum were organized in such a way that visitors could take a trip to the pastimes of the region (including the exhibition of elements from the Roman and medieval times). After a recent rehabilitation and updating, the museum re-opened on 3rd of March 2023 and, at present, the collection is the repository of about 13,035 ethnological, archaeological, and palaeontological elements, 30% of which belong to Cretaceous fossils. In the first floor exhibition, the visitor will find mainly dinosaur fossils unearthed in the Tremp Basin (Figure 9), including the 5-m-long articulated neck of the titanosaurian *Abditosaurus*, the 2-m-high hindlimb of the lambeosaurine *Adynomosaurus*, the tiny metatarsal of the theropod *Tamarro*, the skeleton of the crocodylian *Allodaposuchus hulki*, and the 3-m-high forelimb and a skull reconstruction of two yet unnamed titanosaurs of the region.

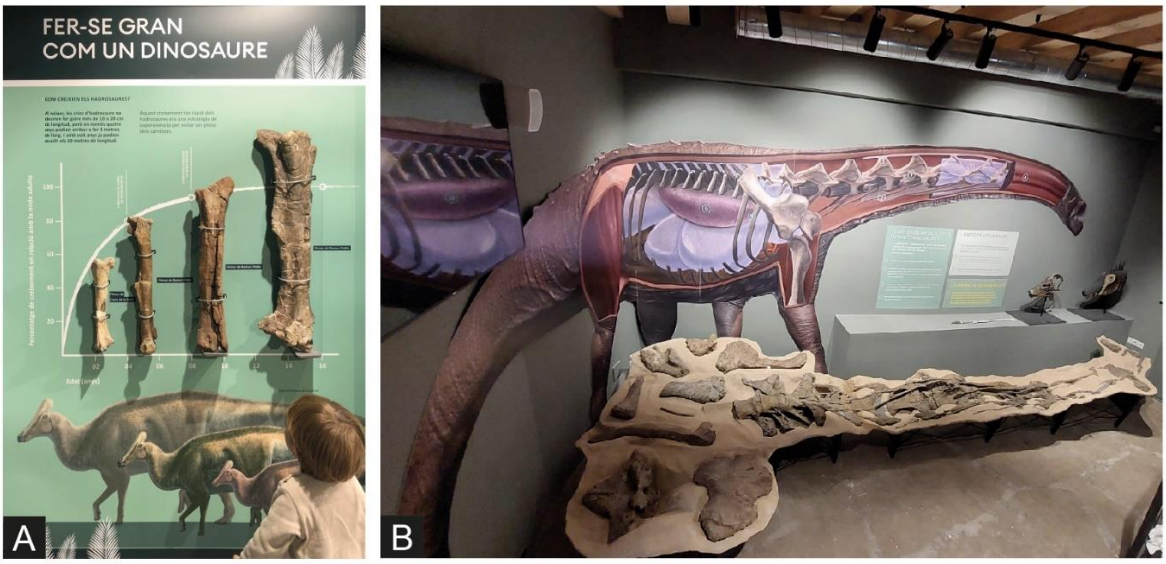

**Figure 9.** Dinosaur exhibition at the Museu de la Conca Dellà. A, panel explaining how hadrosaurid dinosaurs grew, with real specimens; B, exhibition room with holotypic material of *Abditosaurus kuehnei*.

## The VIGEOCULT project: 3D reconstructions of ancient landscapes and faunas

Since very recently, the 'Dinosaurs of the Pyrenees' project benefits from VIGEOCULT, a novel and multidisciplinary research project that aims at creating a unique open natural museum by developing high-quality virtual and augmented reality experiences. By doing so, the visitors will be able to understand how our planet and its inhabitants have evolved and changed over time. To achieve this goal, the project currently focuses on creating audio-visual materials with the highest scientific rigor by using the most advanced technological support. As a result, VIGEOCULT points to the elaboration of outstanding immersive experiences that will attract visitors interested in understanding Earth's evolution and its preservation. Beyond being visually spectacular, the elaborated contents and experiences have indisputable educational values with a clear dissemination purpose, and are expected to impact the public and help to promote a sustainability consciousness in Earth Sciences.

### *Immersive experience: titanosaurian sauropods walking in a coastal mudflat*

The virtual reconstruction of the sauropods walking on the Orcau-2 mudflat aims at illustrating the roaming behavior of titanosaurs described by Marmi *et al.* (2014) (Fig. 10A-B). Since no skeletal remains have been found at Orcau-2, we used the size of the footprints and the trackway parameters measured on the site and the body size and proportions of the titanosaurian *Abditosaurus kuehnei* (Vila *et al.*, 2022) to estimate the size of the sauropods. For the body skin texture, we base most of the model on the studies of Fondevilla *et al.* (2016) and Pittman *et al.* (2022), and as for the biomechanics and locomotion, the virtual model of the titanosaur was animated following the studies of Sellers *et al.* (2013) and Vidal Calés (2019). The coastal mudflat was based on a modified photogrammetric model of ria Partial Natural Reserve of Ría de Villaviciosa (Asturias, Spain), a current area with very similar sedimentological characteristics to those interpreted for the Orcau-2 site (Fig. 10A). The reconstructed plant community was based on the studies of Villalba-Breva *et al.* (2012) and Marmi et al (2016b), which described a coastal landscape dominated by angiosperms (about 75% of the plant diversity), charophytes abundantly proliferating along the shores of the lagoons and forming extensive greenish rims, ferns and cheirolepidiacean conifers (e.g., *Frenelopsis*) occupying the margins of the swamps, and the palm-like trees (*Sabalites longirhachis*) forming extensive forests (Fig. 10B).

### *Immersive experience: the herds of roaming lambeosaurine hadrosaurids*

The virtual reconstruction of the herds of roaming lambeosaurine hadrosaurids (Fig. 10C-D) is primarily based on the geological and paleontological information of the dinosaur bone-bed of Basturs Poble, 5 km northwest of the Museu de la Conca Dellà. Anatomic reconstructions of lambeosaurine hadrosaurids are primarily based on body size proportions documented at the site (Fondevilla *et al.*, 2018). Missing skeletal elements were reconstructed following the skeletons of the most closely related species *Pararhabdodon isonensis* and *Tsintaosaurus spinorhinus* (Fig. 10C), according to current phylogenetic hypotheses. Although in life hadrosaurids may have been bulkier than usually depicted (Manning, 2008), the volumetric reconstruction of our individuals is based on classic illustrations (Paul, 1997), which are commonly used in biomechanical studies (e.g., Henderson, 2014; Maidment *et al.*, 2014). Given the absence of hadrosaurid skin impressions in the southern Pyrenees, we sculptured the skin texture of our virtual models following integumentary impressions of other hadrosaurid taxa (Bell, 2014) (Fig. 10D). Finally, the models were animated according to the biomechanic locomotion approach of Sellers *et al.* (2009). The landscape was reconstructed to represent a floodplain adjacent to a meandering fluvial system, according to the sedimentological research by Riera (2010). Types and distribution of vegetation were reconstructed according to the paleoenvironmental models postulated by Marmi *et al.* (2015, 2016b) for the Maastrichtian continental environments of the Tremp Formation (Fig. 10D).

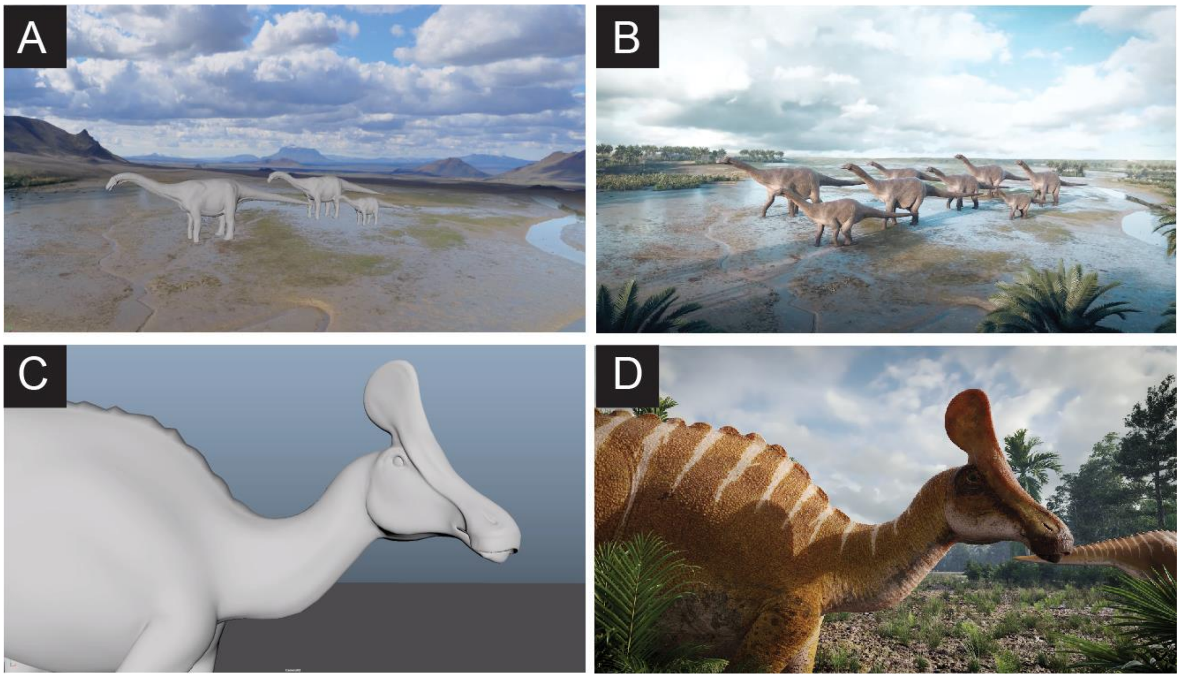

**Figure 10.** Digital reconstruction process of Late Cretaceous dinosaur environments. Digital model (A) and renderization (B) of the lambeosaurine herd from the Basturs Poble site. Preliminary digital model (C) and renderization (D) of the mudflat and the titanosaur herd of the Orcau-2 site.

## 2. THE EARLY CRETACEOUS ECOSYSTEMS IN THE SOUTHERN PYRENEES

The second part of the route proposed in the 'Dinosaurs of the Pyrenees' project explores the continental ecosystems during the Early Cretaceous, a time when the current region of the southern Pyrenees remained submerged under the waters of the ancient Tethys Ocean. However, due to eustatic oscillations and tectonic activities, a short period of emersion took place during the Early Cretaceous (Tugend *et al.*, 2014). This event is recorded on the lithographic limestones outcropping on the southern side of the Montsec range (Fig. 11) and yields a rich fossil record from the Konservat-Lagerstätte of La Pedrera de Meià and the nearby sites (i.e., La Cabroa, or El Reguer sites) (Barale *et al.*, 1984; Mercadé, 1991; Gil-Delgado *et al.*, 2023). These sites, formed in a lacustrine environment, are a unique window to the evolution of terrestrial life, as they capture the dawn of the modern continental ecosystems, including one of the first flowering plants, *Montsechia vidalii*, the first eusocial insects *Meiatermes bertrani*, fishes such as *Ocloedus subdiscus* or the fresh-water shark *Lissodus palustris*, the primitive frog *Eodiscoglossus santonjae*, the enigmatic atoposaurid *Montsecosuchus depereti,* and the oldest Enantiornithes *Noguerornis gonzalezi* (Gómez-Alba, 1991; Martínez-Delclòs and Martinell, 1995; Gomez *et al.*, 2015; Gil-Delgado *et al.*, 2023).

## 2.1 The La Pedrera de Meià locality and the nearby sites

*Historical background*

Like the famous lithographic limestone outcrops from Solnhofen in Baviera, the discoveries of the Montsec Konservat-Lagerstätte fossil sites are linked to the 19th-century industrial extraction of lithographic rocks for the printing industry (Vidal, 1875, 1898; Aragonès, 2018). The skyrocketing price of lithographic limestone at the end of the 19th century forced Catalan industrials to find any possible way to cheapen the costs, like discovering their own quarries close to the industries. Taking advantage of his geological knowledge, the mining engineer Luis Marià Vidal discovered the lithographic limestone quarry of La Pedrera de Meià (La Pedrera de Rúbies syn.) around 1875 (Lacasa, 2016; Aragonès, 2018; Galobart *et al.*, 2018), its exploitation starting soon after. Although there are no records of the date of the first discoveries, it seems that the first fossils from La Pedrera de Meià were recovered by the miners during the initial years of the quarry activity, in the late 1890s. Vidal was immediately aware of the importance of the discoveries, publishing some first results in 1902, which included the report of the by then oldest frogs (Vidal, 1902; Bataller, 1956). Since then, the exceptional fossil record from La Pedrera de Meià has attracted the attention of experts all over Europe. Consequently, Vidal was in close contact with H.E. Sauvage of the Muséum d'Histoire Naturelle in Boulogne-sur-Mer (France), F. Meunier of the Antwerpene Tiergartens (Belgium), and C.R. Zeiller of the French Académie des Sciences, among other specialists (Meunier, 1902; Sauvage, 1903; Zeiller, 1902). As a result of those collaborations, about 50 new species were described until the early 1930s. However, the irruption of the Spanish Civil War in 1936 and the consequent post-war stage truncated any attempt to continue the studies (Gil-Delgado *et al.*, 2023). It was not until the early 1950s that the La Pedrera de Meià fossil record was re-discovered by Dr. Lluís Ferrer i Condal, revitalizing the interest in the site, which provided exceptional specimens such as the second fossil frog recorded since the times of Vidal (Ferrer Condal, 1955; Lacasa, 1979; Galobart *et al.*, 2022). Ferrer i Condal not only collected fossils for his collection but also was the host and the guide for the field expeditions of paleobotanist F.M. Wonacott in 1954 and 1955. By the late 1960s, the site again attracted the attention of international experts, such as Dr. Sylvie Wenz from the Muséum National d'Histoire Naturelle de Paris, who studied the ichthyofauna during the 1960s (Wenz, 1964; 1968) and Dr. Georg Krusat from the Freie Universität Berlin who performed a detailed geological study of the Montsec range (Krusat, 1966). During the 1970s, the site was especially visited by researchers from the Universidade de Lisboa and the British Museum of Natural History. At the end of the 70s, the Institut d'Estudis Ilerdencs (IEI; Lleida) initiated a series of annual excavations under the supervision of Dr. G. Barale from the University of Lyon. These excavations lasted until the end of the 1980s, being later continued by Dr. X. Delclòs from the Universitat de Barcelona until 1996. All these excavations were supported by the IEI members under the guidance of Antoni Lacasa (Galobart *et al.*, 2018; 2022; Martínez-Delclòs, 1991a). Aside of some sporadic visits, since 2019 the excavations have annually resumed with the participation of Institut Català de Paleontologia (ICP), Universitat Autònoma de Barcelona (UAB), Museu de la Conca Dellà and Centre d'Interpretació del Montsec de Meià (Gil-Delgado *et al.* 2023). A century and a half after their discovery, the lithographic outcrops from el Montsec have provided more than 4,380 specimens and 112 new species. However, this outstanding fossil record is scattered throughout several European institutions, such as the Natural History Museum of London, the Muséum National d'Histoire Naturelle Paris or the Paläontologische Museum of Humboldt University Berlin, among many others (Galobart *et al.*, 2022; Gil-Delgado *et al.* 2023).

### *Geological setting and paleoenvironmental interpretation*

La Pedrera de Meià site is located on the southern side of the Montsec range (NW Iberian Peninsula), one of the many mountain chains associated with the orogeny of the Pyrenees (Fig. 11), although the origins of the site is even previous to the uplift of those mountains. The Montsec range consists of 3,000-m-thick of sediments from the Late Triassic to the Late Cretaceous (Garrido-Mejías and Ríos, 1972), recording most of the Mesozoic tecto-sedimentary evolution of the northeastern margin of the tectonic Iberian plate. During the Jurassic, this region was subjected to the western opening of the Tethys Ocean and, because of that, this period is entirely represented by deep marine deposits. Changes in tectonic dynamics at the end of the Jurassic, however, favored the partial closure of the space that set apart the northern margin of the Iberian plate and the southwestern region of the European plate (Jammes *et al.*, 2009). Eventually, the latest Jurassic deposits became subaerially exposed. As a consequence of such exposure, a significant sedimentary gap is recorded between the uppermost stages of the Jurassic and the lower Cretaceous in the Montsec range, exemplified by the occurrence of karsts and ferruginized surfaces. Later on, an important Early Cretaceous lacustrine carbonate sequence, known as "La Serra del Montsec Charophyte Limestones" (Barale *et al.*, 1984; Fregenal-Martínez and Meléndez, 1995; Peybernès, 1976), was discordantly deposited above the Jurassic karstic breccias (locally named "boundary breccias"). This unit includes the 50-m-thick "La Pedrera de Rúbies Lithographic Limestones" subunit and the fossil-bearing strata of La Pedreda de Meià, which are dated as Barremian, according to stratigraphical and biochronological data (Martín-Closas and López-Morón, 1995).

Overall, the lithographic limestones were deposited in a lake context (Barale *et al.*, 1984), but the local stratigraphic sequence of La Pedrera de Meià can be divided into three distinctive

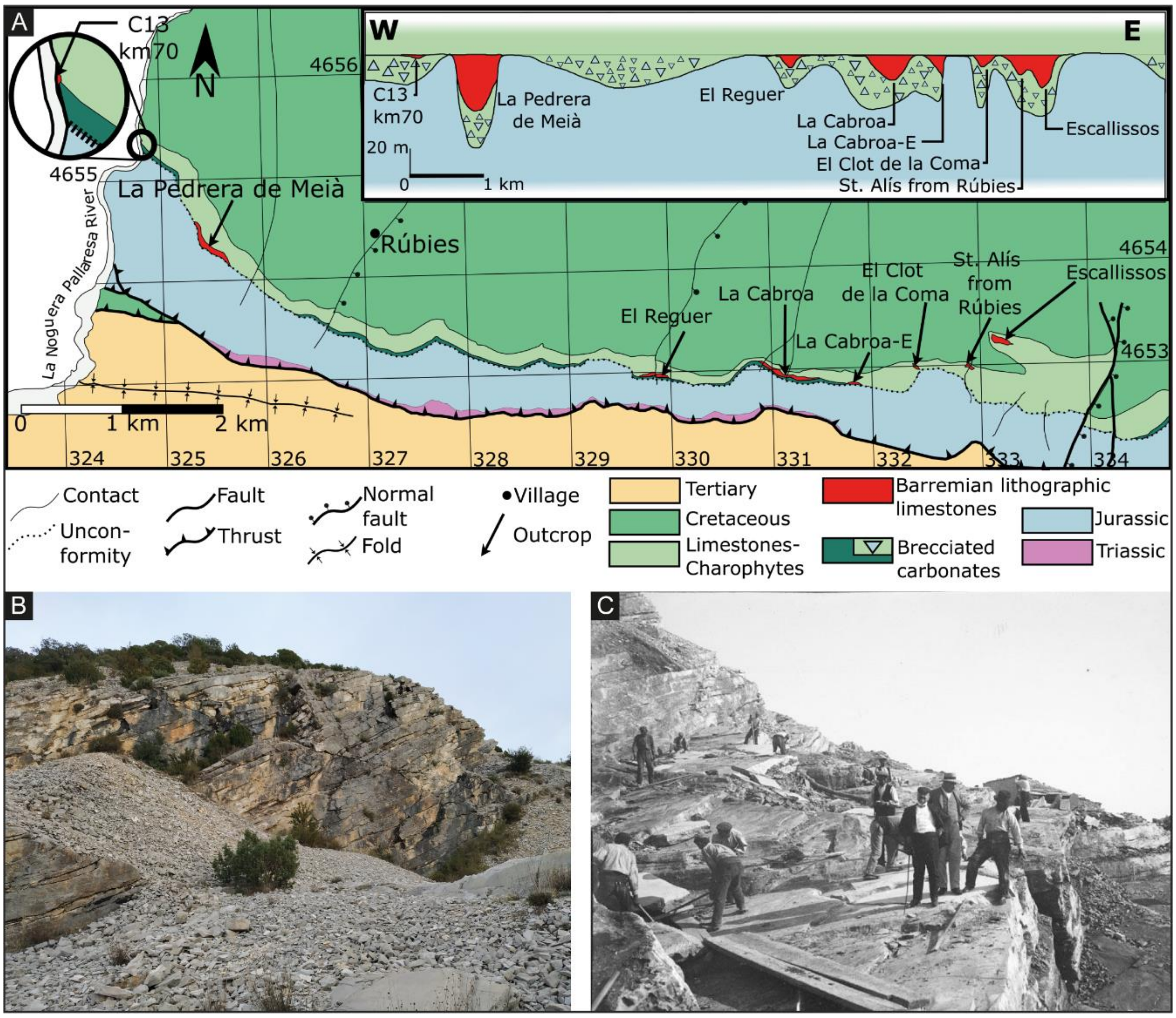

**Figure 11.** Location map, current and old outcrops views from the La Pedrera de Meià site. A) Geological map of the Montsec range within the lithographic limestone sites and outcrops in red, the lithographic limestones model section (modified from Gil-Delgado *et al.*, 2023). B) The La Pedrera de Meià site (2021 photo). D) Miners in La Pedrera de Meià (1900 photo by Lluís Marià Vidal, Arxiu Fotogràfic Centre Excursionista de Catalunya, AFCEC VIDAL A0402). More information at https://pedrerademeia.geoparcorigens.cat/es/

stages. The lower and upper thirds of the sequence represent a gradual transition from the enclosing charophyte limestone. The occurrence of foraminifera and charophytes in these parts of the section indicates a marine/transitional context, suggesting a coastal-lake genesis of the Montsec lithographic limestones (Barale *et al.*, 1984; Fregenal-Martínez and Meléndez, 1995; Mercadé, 1991; Pi *et al.*, 2003). By contrast, the sedimentological characteristics of the middle part of the stratigraphic section suggest it was deposited in a deep palustrine environment (Gil-Delgado *et al.*, 2023). This middle part also records important anoxia events, suggesting significant stratification of the water column at the center of the lake. The semi-permanent anoxia at the bottom of the lake created the ideal conditions for the exquisite preservation of the fossil remains discovered at the La Pedrera de Meià site, hence the consideration of the locality as a Konservat-Lagerstätte (Martínez-Delclòs, 1991a). New geological data suggest that this lake system could have had a permanence of about 40 ky (Gil-Delgado *et al.*, 2023).

*Components of the continental Early Cretaceous ecosystem*

The lithographic limestones from the Montsec range were formed in a semi-permanent anoxic coastal lakes system related to the western margin of the Tethys Ocean during the Barremian, including other sites such as La Cabroa, El Reguer, and five smaller outcrops (Krusat, 1966; Gil-Delgado *et al.*, 2023). The lake ecosystem was composed of dozens of species of insects and crustaceans, several groups of fishes, amphibians, reptiles, and birds, all of them surrounded by a diverse flora (Fig. 12). Even though there is no specific study dealing with the ecological relationships between the species that inhabited the “La Pedrera de Meià Lake” yet, a general picture can be sketched by gathering available information (Fig. 13).

The ichthyofauna was notably diverse, with several species occupying different ecological niches. For example, *Rubiesichthys gregali* -distally related to modern milkfish- could feed on algae, zooplankton, and small invertebrates (Wenz, 1984, 1991a; Poyato-Ariza, 1996). *Ichthyemidion vidali* or *Anaethalion* of the Elopiformes family (ladyfishes) probably feed on smaller fishes and crustaceans (Wenz, 1991a; Poyato-Ariza, 1995), such as the small shrimp *Delclosia roselli* (Via, 1971; Rabadà, 1990). The small amiiformes (bowfin) *Amiopsis woodwardi* could also have similar feeding preferences. *Propterus vidali* and *Notagogus ferreri* were slow but precise swimmers, capable of maneuvering around the algae and plants that grew in the lake (Sauvage, 1903; Wenz, 1964; Wenz, 1991a). Like modern carp, *Lepidotes hergotis* had a modified mandible capable of sucking its prey at long distances (Whalley and Jarzembowski, 1985), mainly aquatic insects like *Mesopalingea leridae*. *Ocleodus subdiscus* showed a durophagous dentition (Wenz, 1991a; Poyato-Ariza and Wenz, 2002), being able to feed on the ampullarii gastropods and crustaceans. With up to 25 cm in length - though even larger specimens have been discovered in recent years -, *Caturus tarraconensis* (Sauvage, 1903; Wenz, 1991a) was likely one of the top predators of the trophic chain, capable to prey any of the aforementioned fishes, as well as crawfish (i.e., *Austrapotamobius llopisi*), mollusks, and aquatic insects. Fresh-water sharks like *Hybodus woodwardi* likely laid their eggs (*Paleoxyris* sp.) at the oxygenated margins of the lake, hanging on the branches of the algae and the basal angiosperm plants (i.e., *Montsechia vidalii* and *Ranunculus ferreri*) (Gomez-Pallerola, 1988; Wenz, 1991a). The ichthyofauna assemblage also includes *Ascalabos vidali*, *Leptolepis* sp., *Ophiopsis montsechensis*, *Pleuropholis* sp., and *Vidalamia catalaunica* (Wenz, 1991a).

Odonat insects like *Ilerdaegomphus pallerolae* flew close to the water's surface, while their nymphs (*Palaeaeschna vidali*) pullulated on the littoral zone of the lake, alongside Ephemeroptera larvae (i.e. *Mesopalingea leridae*) (Martínez-Delclòs, 1991a). The gerrid-like *Chresmoda aquatica,* with its long and thin legs, moved above the water (Martínez-Delclòs, 1991a), and several species of anurans (i.e., *Eudiscoglossus, Montsechobatrachus, Neusibatrachus* (Wenz, 1991b) jumped

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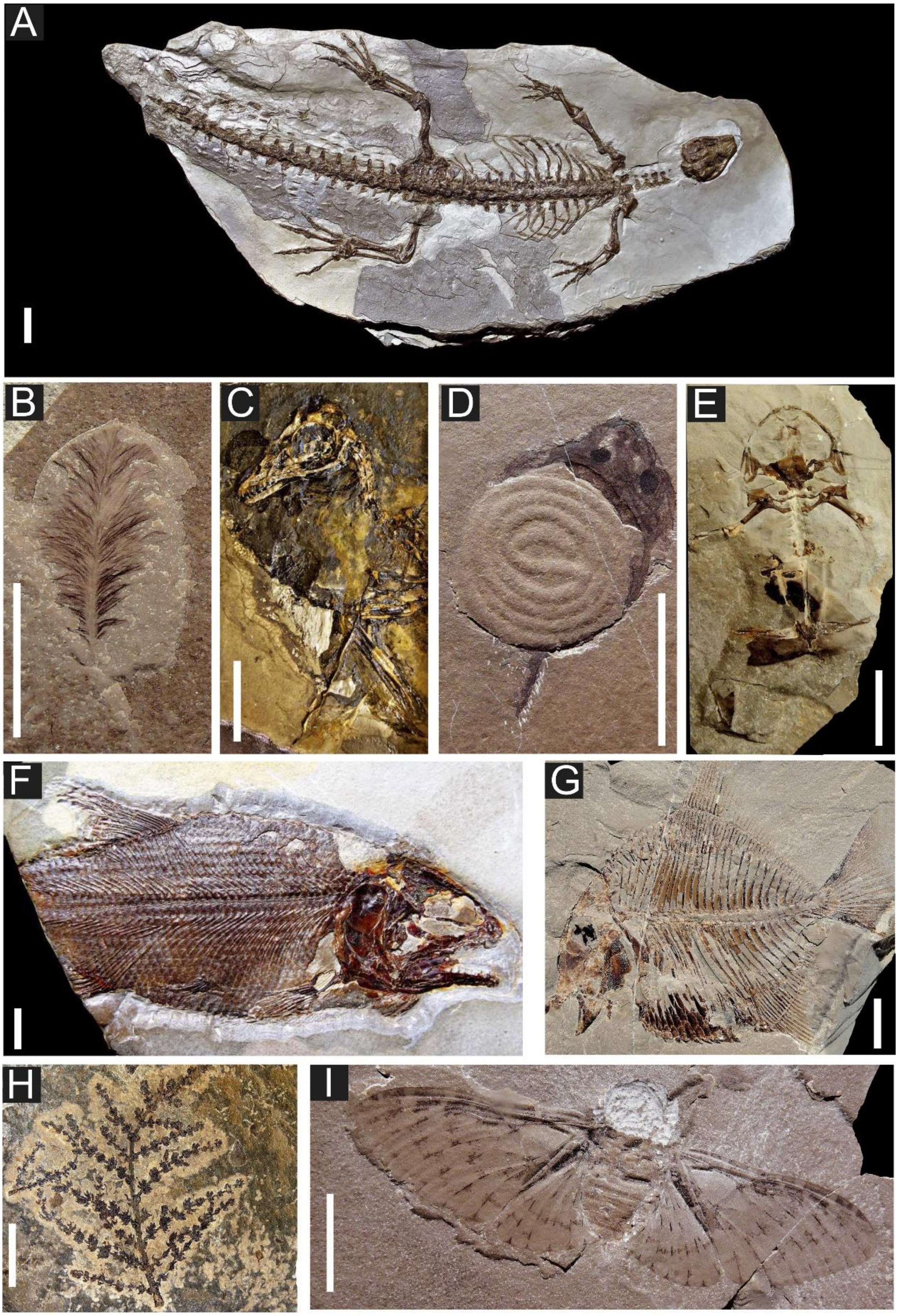

**Figure 12.** A, *Montsecosuchus depereti*; B, *Ilerdopteryx viai* feather; C, Enantiornithes indet.; D, tadpole, Anura indet.; E, *Eodiscoglossus santonjae*; F, *Caturus tarraconensis*; G, *Ocloedus subdiscus*; H, *Montsechia vidalii*; I, *Pachypsyche vidali*. Scale bar equals 1 cm. Images modified from Galobart *et al.* (2018).

around the edge of the lake, while tadpoles developed within the warm waters. The lizard *Meyasaurus faurai* was adapted to an amphibian lifestyle, feeding on fish according to the discovered stomach contents (Buscalioni and Sanz, 1991). A second lizard, *Pedrerasaurus latifrontalis,* shows some similarities to *Meyasaurus*, although it is unclear if they were closely related (Bolet and Evans, 2010). By contrast, *Eichstaettisaurus* is a lizard characterised by a long torso and shorter limbs, suggesting it was a ground-dwelling with low running speed (Evans *et al*., 1999). Finally, with up to 50-cm-long, and a body covered with osteoderms, the atoposaurid *Montsecosuchus depereti* was the top predator of the ancient lakes (Buscalioni and Sanz, 1991).

Out of the water, hundreds of insects fluttered in the air and ran across the ground. The robust, four-winged paleontinids, such as *Pachypsyche vidali*, had a sucking beak folded under their thorax, which they used to suck sap from trees. *Meiatermes bertrani* is one of the oldest termites ever discovered. This eusocial insect, of which winged adults and workers have been recovered, probably nested in the trunks of the trees (Martínez-Delclòs, 1991b). Despite their scarcity, orthopters (grasshoppers) were also present in the surroundings of "La Pedrera de Meià Lake". By contrast, several species of coleoptera (i.e., *Bolbonectus lithographicus, Brochocoleus indibili, Cionocoleus longicapitis, Montsecanomalus zherikhini, Zygadenia martinclosa*s, among many other species) populated the continental environments close to the lake (Ponomarenko and Martínez-Delclòs, 2000; Soriano and Delclòs, 2006). Blattids like *Mesoblattina colominasi*, *Nogueroblatta fontllongae*, or *Orbablattula infrequens* were also common in these environments (Martínez-Delclòs, 1993). There is evidence of the presence of mycetophilid dipters like *Palaeodocosia cabruae* and *Synapha rubiesensis*, whose occurrence suggests the presence of fungi close to the lake (Blagoderov and Martínez-Delclòs, 2001). Finally, there are also notable examples of arachnids, such as *Montsecharachne amicorum, Macryphantes (Palaeouloborus) cowdeni,* and *Cretaraneus vilaltae*. The particular morphology of the legs of *Cretaraneus* suggests that it could spin flat webs (Selden, 1990; 1991). Despite the absence of direct evidence, most of the above-mentioned insects were likely preyed upon by the basal enantiornithine *Noguerornis gonzalezi* and other birds (i.e. LP-4450-IEI; Lacasa Ruiz, 1989).

According to the evidence, certain plant elements (leaves and branches) from the nearby forest were eventually incorporated into the lake system. This forest had a canopy structure primarily composed of araucariacean trees (*i.e., Araucarites pedreranus, Brachyphyllum* sp*., Dammarites coriacea, Nagieopsisi hispanica, Pagiophyllum pereranum*)*,* though gimnosperms (*Ginkgo* sp. and *Eretmoglossa lacasai*)*,* bennettitales (*Zamites* sp.), cycads (*Deltolepis* sp.), taxodiaceas (*Sphenolepis*), and the caytoniacea *Sagenopteris* complete the arboreal stratum. On the other hand, the understory contained ferns (i.e., *Weichselia, Ruffordia,* and *Onychiopsis),* conifers like *Podozamites,* as well as *Equisetum* (Barale, 1991)*.* In addition to that, there is a great diversity of palynological remains associated with conifers and ferns, while angiosperm pollen (cf. *Clavatipollenites* sp.) is almost nonexistent. Such plant association informs of a warm, even arid, environment where plants mainly grew at the edge of the lake (Barale, 1991; Courtinat, 1984).

**Figure 13**. Idealized reconstruction of the La Pedrera de Meià lake. Artwork by ICRA_Arts.

## Stop 4: The Centre d'Interpretació del Montsec de Meià

Opened in April 2021, the Centre d'Interpretació del Montsec de Meià is found in the Vilanova de Meià village (La Noguera county, Lleida) and exhibits a selection of the outstanding fossil record unearthed from La Pedrera de Meià and the nearby site of La Cabroa. Most of the elements shown in the current exhibition are inherited from the temporal exposition "Paleontologia a les terres de Lleida. La Pedrera de Meià i l'inici d'un món modern" (Paleontology of Lleida. La Pedrera de Meià site and the beginning of the modern world), which was produced by the IEI and loaned to the local museum.

The paleontological exhibition introduces visitors to the rich fossil record from the Montsec and the different types of fossilization employing specimens from private collections. After that, the visitors can appreciate a carefully selected collection of fossils including insects, crustaceans, plants, fishes, amphibians, reptiles, and other taxa from the lithographic limestones sites of the Montsec range, all of them originally collected by the Geo-paleontology section of the Institut d'Estudis Ilerdencs. For those who are interested, the museum has equipment for scholars and offers educational workshops for children and adults.

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