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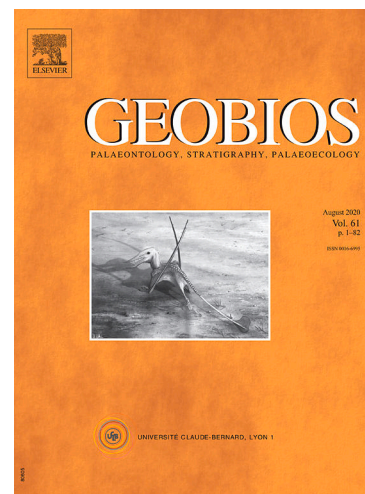
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## **Multiproxy palaeoenvironmental reconstruction of the Bathonian Castelbouc sauropod tracksite (Causses Basin, southern France): insight into a Middle Jurassic insular ecosystem <sup>☆</sup>**

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## Abstract

We report lignitic fossil rich-beds from the Bathonian Castelbouc sauropod tracksite (Castelbouc Cave N°4, Causses Basin, southern France). Showing the co-occurrence of amber with plant, vertebrate and invertebrate remains, they are a precious tool to reconstruct Middle Jurassic dinosaur ecosystems. A multiproxy approach combining sedimentology, petrology, mineralogy and palaeontology led to determine that these fossil rich-beds were deposited in a range of insular coastal palaeoenvironments. They include protected backshore areas such as freshwater/brackish ponds and brackish bay/lagoon showing co-occurrence of terrestrial and marine inputs. The backshore environments were particularly rich in ostracods (*Darwinula* sp., *Fabanella bathonica*) and gyrogonites of charophytes (*Porochara douzensis*). The abundance of conifer remains including leafy axes (*Brachyphyllum*), cones (cf. *Classostrobus*), wood (*Brachyoxylon*) and pollen grains (*Classopollis*) shows that ponds and bay/lagoon were bordered by conifer-dominated forests in which Cheirolepidiaceae were the main component. Such a rich and relatively diverse flora was probably an attractive source of food for megaherbivorous dinosaurs. Vertebrate microremains mostly consist of fish scales (*Ginglymodi* indet.) and crocodylomorph teeth (*Atoposauridae* indet.), two groups that are common components of Middle Jurassic paralic faunas. The palaeobotanical assemblage suggests a warm subtropical climate probably tropophilous with marked alternation between a wet and a dry season.

*Keywords:*

Amber

Conifers

Vertebrate microremains

Ostracods

Palaeoecosystem

## Introduction

Our knowledge of sauropod palaeoecology in Middle Jurassic ecosystems remains extremely limited, particularly in paralic environments. Body fossils of this dinosaur group being very sparse in Europe (Sauvage, 1900; Buffetaut, 1995; Clark et al., 1995; Barrett, 2006; Buffetaut et al., 2011; Manning et al., 2015; Clark and Gavin, 2016) and worldwide (Weishampel et al., 2004), sauropod tracksites yielding fossil rich-beds (with plant, vertebrate and invertebrate remains) are precious tools to reconstruct Middle Jurassic floras and faunas inhabiting dinosaur ecosystems.

In the Causses Basin (southern France), sauropod trackways were recently discovered in the “Calcaires à stipites” Fm. dated from the Bathonian (Moreau et al., 2019). The organic-rich layers from this formation are known since the first half of the 19th century to yield diverse vertebrate microremains (Bleicher, 1872; Saporta, 1873; Seiffert 1969a, 1969b; Fürsich et al., 1995; Kriwet et al., 1997; Knoll et al., 2013, 2014; Knoll and López-Antoñanzas, 2014) and fossil plants (De Serres, 1845; Saporta, 1873, 1891; Nicklès, 1907; Rouire, 1928; Maubeuge, 1949; Doubinger, 1961; Feist and Grambast-Fessard, 1984; Alabouvette, 1988; Philippe et al., 1998). More recently, this formation also yielded diverse archosaur trackways (Sciau et al., 2006; Gand et al., 2007, 2018; Moreau et al., 2012, 2019; Moreau, 2017).

Here, we report new amber-, plant-, vertebrate- and crustacean-bearing beds from the entrance of the Castelbouc Cave N°4 (Lozère; Fig. 1(A)) in which three large sauropod trackways were recently discovered (Moreau et al., 2019). A multiproxy approach is used to characterize Bathonian insular palaeoecosystems of this site (Fig. 1(B)). Sedimentological, petrological and mineralogical analyses are combined to characterize the lithofacies and to understand the evolution of depositional palaeoenvironments. Then, analyses of the palaeontological content are used to reconstruct palaeofaunas and palaeofloras in each depositional palaeoenvironment.

## 2. Geographical and geological context

The Castelbouc Cave N°4 (GPS: 44°20'22.18" N; 3°27'50.05" E) is an 880 m long karstic cave (André, 1992) located in the northern part of the Causses Basin (southern France; Fig. 1(A)), in the Gorges du Tarn (Lozère department, France), 30 km south of Mende. Most active and fossil galleries of this cave are located 500 m under the surface of the Causse Méjean plateau. One of the biggest gallery (the Tunnel gallery) shows spectacular sauropod trackways on its roof (Moreau et al., 2019; Fig. 2).

The cave system develops within the Bathonian limestones and especially within its lower part corresponding to the “Calcaires à stipites” Fm. (*sensu* Charcosset, 2000), having here a thickness of up to 200 m (Charcosset et al., 1996; Cizak et al., 1999). The word “stipites” means “made of trunks” and was formerly proposed by the French palaeontologist Charles Brongniart (Brongniart, 1827; Rouire, 1928). This formation consists of white-gray

mud-supported limestones alternating with dark layers of lignitic marl. Regionally, in the southern part of the Causses Basin, lenticular lignitic beds of the “Calcaires à stipites” Fm. were mined for coal (De Serres, 1859; Rouire, 1946; Galy, 1969). Coaly beds are up to one metre thick in the south of the basin whereas there are very thin or absent in the northern part (Briand et al., 1979).

Based on brachiopods and foraminifera, on regional correlations with sequence stratigraphy (Ciszak et al., 1999, 2000; Charcosset, 1998, 2000) and on  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of a volcanic lava flow (19 km westward of Castelbouc) sealed by the lower part of the “Calcaires à stipites” Fm., it has been established that this formation includes the lower and middle Bathonian stage. However, Castelbouc Cave’s entrance is located at the uppermost part of the “Calcaires à stipites” Fm. (below the “Dolomie II” Fm.), which is considered middle to late Bathonian in age (Charcosset, 1998, 2000).

Fossil plants are abundant in the “Calcaires à stipites” Fm. They mainly include foliar remains, wood, pollen and spores (De Serres, 1845; Saporta, 1873, 1891; Nicklès, 1907; Rouire, 1928; Maubeuge, 1949; Doubinger, 1961; Feist and Grambast-Fessard, 1984; Alabouvette, 1988; Philippe et al., 1998). Whereas dozens of localities yielding plant remains were reported in the “Calcaires à stipites” Fm. (Philippe et al., 1998), palaeontological sites yielding vertebrate microremains are rarer. Vertebrate microremains were reported in Aveyron, at Gardies (Kriwet et al., 1997), Cornhes (Knoll et al., 2014), Les Moulinets (Knoll and López-Antoñanzas, 2014) and La Baume (Knoll and López-Antoñanzas, 2014); in Gard at Saint-Martin (Knoll et al., 2013); as well as in Lozère at Monplaisir (Knoll and López-Antoñanzas, 2014) and inside the Sourguettes Cave (Salveyre, 2007; Gand et al., 2018; Fig. 1(A)). Other vertebrate remains were mentioned by Bleicher (1872) and Saporta (1873) in the area of the “Causse du Larzac”; however, specific geographical origins of sites remain unclear.

### 3. Material and methods

#### 3.1. Sedimentology, petrology and mineralogy

The entrance of the Castelbouc Cave N°4 consists of a narrow and vertical conduit located at the bottom of a cliff. The fossiliferous beds studied here were discovered in the first metres of this conduit as well as in the cliff overhanging the cave entrance (Stratigraphic section 1 in Fig. 3). Inside the karstic network, three other sections (Stratigraphic sections 2 to 4 in Fig. 3) were also established in order to stratigraphically correlate the fossiliferous beds from the entrance with beds of the “Tunnel gallery” hosting sauropod tracks (Fig. 3). The distance between the two areas is ca. 100 m. The walls of the cave galleries being poorly concreted, the correlation between the diverse sections was possible by following the stratigraphy bed by bed all along the karstic network from the entrance of the cave to the “Tunnel gallery”.

In order to characterise the depositional environments of fossiliferous beds from the entrance, detailed sedimentological, petrographic and mineralogical analyses were conducted along the upper part of the stratigraphic section 1 (Fig. 3(B)). Fourteen samples were prepared for standard polished thin sections (Fig. 4) and fifteen samples were prepared for mineralogical analyses (Table 1). Based on field observations as well as microfacies and mineralogical analyses, we have characterized the evolution of depositional environments

along the section. Four layers are particularly fossiliferous (called FS1 to FS4, Fig. 3(B)). Petrographic observation of thin sections, and microphotographs were realized at the GISMO Platform of the Biogéosciences laboratory, University of Bourgogne, using a Nikon AZ100 polarizing microscope equipped with a Luminera Infinity 3 camera.

Mineralogical analyses were carried out at the LMDC laboratory of the University of Toulouse, by X-ray diffraction (XRD) with a Bruker D8 Advance diffractometer. Two protocols were used: the first to quantify the bulk rock minerals; the second for identification of the clay fraction (particles < 2 µm) only. Mineral identification and quantification were performed using the Bruker software Eva v4 and TOPAS and the 2015 ICDD PDF Database. For bulk analyses, samples were powdered by grinding in an agate mortar and pestle, then quantified by Rietveld method (Snyder and Bish, 1989; Bish and Post, 1993). Rietveld used parameters and estimate accuracy (based on Rwp and GOF) were detailed in Taylor and Hinczak (2006), Toby (2006) and Trincal et al. (2014, 2018). Clay mineral extraction was carried out on phyllosilicate rich samples, by sedimentation after weak concentration hydrochloric acid treatment. Then, clay mineral identification was conducted on three XRD runs performed on the oriented mounts following air-drying, ethylene-glycol solvation and heating at 550°C for 2h (Moore and Reynolds, 1997; Thiry et al., 2013).

### 3.2. Extraction of fossil meso- and microremains

Amber-, plant- and vertebrate-bearing beds were firstly observed by one of us (J.-D.M.) in 2018. In order to extract fossil meso- and microremains, a few kg of the sediment from the clayey beds were soaked in a solution of hydrogen peroxide (12%) and water for a few days. The disaggregated sediment was then washed with tap water through a column of sieves (1.0 mm and 0.5 mm meshes). The fossils were picked out by naked eye or under a stereomicroscope. Bulk macerations yielded amber, plant remains, vertebrate microremains, as well as ostracods and fragments of other invertebrate organisms. Plant remains include leafy axes, cones and wood of conifers, indeterminate seeds, fragments of indeterminate ferns, gyrogonites of charophytes as well as diverse pollen grains and spores. Vertebrate remains include osteichthyan scales and reptile teeth. In order to discuss depositional environment, we estimated the proportion of the diverse bioclasts and pointed then into several facies, each one being latter interpreted in terms of depositional environments using a synthetic table with facies associations. Along the upper 18 m of section 1 (Fig. 3(B)) we counted bioclasts in each layer of the section.

SEM micrographs of fossils were taken using a Hitachi TM-1000 scanning electron microscope at GISMO Platform of the Biogéosciences laboratory. Pollen extractions were done using the following procedure: (i) immersion of 7 to 27 g of sediment in HCl (pure, 24h) to remove the carbonates; (ii) immersion in HF (70%, 24h) to remove the silicates; and (iii) immersion in HCl (pure, 4h) to remove the fluorosilicates eventually produced in the previous step. Next, the sample was sieved at 160 µm.

Studied specimens are housed in the palaeontological collections of the University of Bourgogne, Dijon, France (UBGD.294150–UBGD.294182, UBGD.294230–UBGD.294238) and the University Claude Bernard, Lyon, France (MP1972).

### 3.3. Wood analysis

Wood samples are pieces of brown evolved lignite. Whereas externally wood fibres are distinguishable, fractures display black, glossy jet with conchoidal breaks. Such is quite typical for a deep microbial alteration followed by some thermal evolution (Bechtel et al., 2001). Microscopic examination of samples revealed only a few areas where pitting is preserved. We tried first to prepare sections with a razor blade, but these failed to display any preserved pit. Subsequently the samples were investigated by pyroxylin microcasting. Parlodion was dissolved in amylacetate to a thick past-like consistency, and applied in a 1 mm-thick layer on an area selected under the microscope as featuring a well-preserved radial breaking plan. This was allowed to dry for 24h and then carefully lifted up. This translucent peel was mounted on glass and examined under a microscope. This inexpensive, quick and efficient method unfortunately yields peels the surface of which is irregular and we had to use a Keyence VHX-700N digital microscope with a focus stacking function in order to prepare images.

## 4. Results

### 4.1. Facies and facies analysis

The stratigraphic column displays limestone and dolomite beds alternating with fossiliferous marly layers (Fig. 3(B)). Detailed sedimentological analyses allowed to distinguish six facies, F1 to F6 (Table 2; Fig. 4):

- F1 consists of grey cryptalgal limestone (mudstone) forming 0.4 to 1.2 m-thick beds showing abundant and thin wavy to planar laminites corresponding to the alternation of micrite and microsparitic layers (Fig. 4(A)). Surfaces of laminites bear mud cracks sometimes filled by ooids. Rare ostracods and some foraminifera are dispersed in the rock. F1 is mainly composed by calcite (96 to 99 wt%);
- F2 consists of limestone (mudstone to micro-wackestone) forming 0.5 to 5.0 m-thick beds yielding ostracods and displaying abundant bioturbation interpreted as possible root casts (Fig. 4(B)). Locally, F2 shows tiny fragments of highly altered wood fragments, charophyte gyrogonites and peloids. F2 yields rare isolated foraminifera and fragments of brachiopod shells. This facies is mainly composed by calcite (95 to 100 wt%);
- F3 consists of grey to green marl (biomicrite) forming 0.4 to 0.6 m-thick beds with abundant ostracods, charophyte remains (gyrogonites and thalli), cuticles of conifers, wood remains and peloids (Fig. 4(C)). Some lithoclasts and gastropods as well as rare vertebrate teeth, bivalves and foraminifera are present. Locally, F3 shows cracks probably induced by pedogenetic activity. This facies is mainly made up of a mixture of carbonates (69 to 70 wt% of calcite) and clay (27 to 28 wt%);
- F4 consists of grey to black lignitic to oolitic marl forming 0.3 to 1.0 m-thick beds yielding abundant plant remains including wood (up to 30 cm wide compressed trunks), cuticles, palynomorphs and rare tiny amber grains. F4 shows some bivalves, gastropods, echinoid spines, corals, charophyte gyrogonites and vertebrate remains dispersed in the matrix. Locally, marl alternates with pluricentimetre-thick lenses of oolitic limestone

(oosparite) containing intraclasts and rare micritised bioclasts (foraminifera, bivalves and gastropods; Fig. 4(D)). Marls are mainly composed of clay (49 to 52 wt%) and calcite (36 to 46 wt%) whereas oosparite lenses are almost exclusively composed by carbonates (99 wt% of calcite and 1 wt% of dolomite). This facies is close to those of the layer bearing sauropod tracks in the Tunnel gallery (Moreau et al., 2019). We tentatively correlate this track-bearing surface (stratigraphic section 4 in Fig. 3(A)) with the higher vertebrate-yielding beds from the entrance of the cave (FS4; stratigraphic section 1 in Fig. 3(B)). In both areas, it consists in the single black lignitic to oolitic marl bed showing large trunks. This layer constitutes a benchmark bed in the stratigraphy of the Castelbouc Cave N°4;

- F5 consists of a grey to yellowish peloidic to oobioclastic limestone (pelbiomicrite to oobiomicrite) forming 0.7 to 1.2 m-thick beds yielding abundant fragments and micritised bioclasts including bivalves, brachiopods, bryozoans, benthic foraminifera (miliolids), corals, echinoderms (including some spines of echinoids) as well as some ooids and intraclasts (Fig. 4(E)). This facies is almost exclusively composed of carbonates (97 to 100 wt% of calcite);
- F6 consists of a grey to yellowish dolomite (wackestone) forming plurimetre-thick beds bearing fully dolomitized ooids. This facies is almost exclusively composed of carbonates (53 to 97 wt% of dolomite and 1 to 47 wt% of calcite; Fig. 4(F)). The dolomite is clearly secondary, with small dirty crystals (planar-S type) replacing the micritic matrix and coarser subhedral crystals (planar C-type) replacing bioclasts and ooids.

In terms of facies associations, two groupings can be highlighted (Table 1). The first one groups F2 and F3 which contain relatively similar allochems, but in distinctive matrixes (micrite vs. marls). Moreover, these two facies clearly alternate in the stratigraphic succession, sometimes with vertical progressive transitions between them. Another association groups the F5 and F6 facies. In fact, F6 resulted from a partial to full dolomitization of F5, leaving ghosts of allochems and sedimentary structures looking those of the F5 facies.

## 4.2. Systematic palaeontology

### 4.2.1. Invertebrates

Phylum Arthropoda Gravenhorst, 1843

Class Ostracoda Latreille, 1802

Order Podocopida Sars, 1866

Family Darwinulidae Bardy and Robertson, 1885

Genus *Darwinula* Jones, 1885

*Darwinula* sp.

Fig. 5(A)

**Material:** One specimen, UBGD.294177.

**Description:** This ostracod is characterized by oblong to elongated valves that display an almost straight ventral margin, a gently curved dorsal margin, a narrowly rounded anterior border located very low and a larger posterior margin with maximum curvature located around mid-height (Fig. 5(A)).

**Remarks:** Ostracods were found in the facies F1 to F4. They are abundant in F1 in which they are the main component of the palaeontological assemblage (particularly in FS2). Bulk macerations of marl yielded disarticulated valves in FS1 (facies F3). In the “Calcaires à stipites” Fm., Andreu et al. (1999) reported *Darwinula* cf. *leguminella*, *Darwinula leguminella* recently being re-attributed to *Alicenula*, 1998 by Martens et al. (2003), and *Darwinula* sp. in several localities from Lozère and Aveyron whereas Knoll et al. (2013) reported *Darwinula magna* from Gard. The valves of *Darwinula magna* are much larger and sub-rectangular posteriorly. The species from the “Calcaires à stipites” were not illustrated making any comparison impossible so that we chose to keep this species is open nomenclature.

Family Cytheridae Baird, 1850

Genus *Fabanella* Martin, 1961

*Fabanella* cf. *bathonica* Oertli in Bernard et al., 1959

Fig. 5(B, C)

**Material:** Three specimens, UBGD.294178–UBGD.294180.

**Description:** The specimens are characterized by sub-rectangular lateral outline with nearly straight ventral margin, straight and horizontal dorsal border and sub-triangular posterior border (Fig. 5(B, C)). The anterior margin is largely rounded and bordered by a laterally compressed flange. The lateral surface is partially covered with sediment but appears mostly smooth with relatively large depressions regularly distributed that may correspond to normal pores.

**Remarks:** These ostracods share similarities with *Cyprideis? bathonica* from the Bathonian of Western France (Bernard et al., 1956), which was reattributed later to *Fabanella* by Oertli (1963). *Fabanella bathonica* is characterized by parallel and sub-straight ventral and dorsal margins, smooth surface except 5 to 6 longitudinal ridges ventrally, posterior border with about seven small teeth at right valve and a weak peripheral “sulcus” anteriorly. Similarities between the two species are strong but the absence of a series of posterior teeth and the weaker oral concavity at the present specimens lead us to identify it as *Fabanella* cf. *bathonica*.

Class Malacostraca Latreille, 1802

Order Decapoda Latreille, 1802

Infraorder Astacidea Latreille, 1802

Astacidea indet.

Fig. 5(D, E)

**Material:** One specimen, UBGD.294182.

**Description:** The specimen consists of a 8.5 mm long and 5.5 mm wide fragment of chela (Fig. 5(D, E)). Only the fixed finger is preserved and shows granulated inner and outer surfaces, while the occlusal margin bears at least three molariform teeth.

**Remarks:** UBGD.294182 was collected from FS4 (facies F4). The size of the chela is important and could correspond to an indeterminate astacidean lobster.

#### 4.2.2. Vertebrates

Class Actinopterygii Cope, 1887

Infraclass Holostei Müller, 1846

Division Ginglymodi Cope, 1872

Ginglymodi indet.

Fig. 6(A)

**Material:** Ten specimens, UBGD.294176, UBGD.294230–UBGD.294238.

**Description:** The best preserved ganoid fish scale (UBGD.294176) is complete and displays a smooth surface (Fig. 6(A)). The scale is 3 mm long and 2 mm wide. It bears a pair of anteriorly oriented pegs (Fig. 6(A)).

**Remarks:** These ganoid fish scales were collected in FS4 (Facies F4). They are similar to those observed in several callipurbeckiid (Ginglymodi: Semionotiformes) and lepidotid (Ginglymodi: Lepisosteiformes) taxa (Lopez-Arbarello and Sferco, 2018); however, we assign them to an indeterminate ginglymodian fish due to the scarcity of the material available. Such scales were also reported in bioclastic and lignitic marl exposed in the Tunnel gallery of the Castelbouc Cave N°4 (Moreau et al., 2019). Ginglymodian scales and/or teeth were also previously reported (as *Lepidotes* sp.) from several outcrops from Aveyron (Gardies: Kriwet et al., 1997; Cornhes: Knoll et al., 2014; Les Moulinets and La Baume: Knoll and López-Antoñanzas, 2014) and Gard (Saint-Martin: Knoll et al., 2013; Table 3).

Class Reptilia Laurenti, 1768

Order Crocodylomorpha Hay, 1930

Family Atoposauridae Gervais, 1871

Atoposauridae indet.

**Remarks:** Atoposaurid crocodylomorphs are mainly represented by a few small teeth. Three tooth morphotypes (A to C) can be distinguished.

Atoposauridae indet. – Morphotype A

Fig. 6(B–D)

**Material:** Three specimens, UBGD.294168–UBGD.294170.

**Description:** The morphotype A (Fig. 6(B–D)) is 1.9–3.1 mm in length and shows a lanceolate-shaped crown, slightly compressed labiolingually and faintly recurved lingually. The base of the crown is constricted. The labial and lingual faces are weakly ornamented, with a few slight vertical folds. The mesial and distal carinae are sharp and bear pseudodenticles (pseudoziphodont condition).

Atoposauridae indet. – Morphotype B

Fig. 6(E, F)

**Material:** Two specimens, UBGD.294171, UBGD.294172.

**Description:** The morphotype B (Fig. 6(E, F)) is 1.7–3.1 mm in length and consists of a slender subconical crown, slightly recurved and with no labiolingual compression (i.e., circular cross section). The crown shows no basal constriction. The well-marked ornamentation consists of numerous longitudinal ridges.

Atoposauridae indet. – Morphotype C

Fig. 6(G)

**Material:** One specimen, UBGD.294173.

**Description:** This broken tooth lacking the apex is 2.6 mm long and subconical in shape (Fig. 6(G)). The lingual and labial faces are separated by two smooth mesial and distal carinae. The crown shows nine longitudinal facets. These facets are flat to shallowly concave in apical view, giving to the crown a polygonal cross section.

**Remarks:** These crocodylomorph teeth were collected from two beds, FS4 (Facies F4) and FS1 (Facies F3). The presence of three dental morphotypes ranging from more or less slender caniniform teeth to lanceolate-shaped teeth is consistent with the heterodont dentition known in various atoposaurid crocodylomorphs from the Jurassic of Western Europe (e.g., *Knoetschkesuchus*, *Theriosuchus*; Schwarz et al., 2017). Therefore, we refer all the tooth material from Castelbouc to a single, indeterminate atoposaurid taxon. Reptile teeth were mentioned in “Calcaires à stipites” Fm. since the second half of the 19<sup>th</sup> century (Bleicher,

1872). More recently, isolated teeth tentatively assigned to atoposaurids were reported at Gardies (Kriwet et al., 1997) and Saint-Martin (Knoll et al., 2013; Table 3); teeth of indeterminate crocodylomorphs were also reported at Les Moulinets (Knoll and López-Antoñanzas, 2014).

Crocodylomorpha indet.

Fig. 6(H)

**Material:** One specimen, UBGD.294174.

**Description:** UBGD.294174 consists of a small, 3.0 mm long, 1.7 mm wide and 1 mm thick fragment of crocodylomorph osteoderm (Fig. 6(H)). In dorsal view, the superficial surface is ornamented with deep subcircular pits. In ventral view, the surface of the fragment is smooth. Margins are not preserved.

**Remarks:** The specimen was collected from FS4 (Facies F4). Similarly, Kriwet et al. (1997) reported fragments of crocodylomorph bony armour plates associated with teeth from Gardies. It is worth noting that Salveyre (2007) and Gand et al. (2018) mentioned a partial skeleton of an indeterminate crocodylomorph from the Sourguettes Cave, 20 km south of the Castelbouc Cave N°4 (in the “Calcaires à stipites” Fm. which is Bathonian in age and not Bajocian as mentioned in Salveyre, 2007).

#### 4.2.3. Plants

Class Charophyceae Rabenhorst, 1863

Order Charales Dumortier, 1829

Family Porocharaceae Grambast, 1962

Genus *Porochara* Mädler, 1955

*Porochara douzensis* Feist-Castel et Grambast-Fessard, 1984

Fig. 7

**Material:** Six specimens, UBGD.294158–UBGD.294163.

**Description:** Specimens consist of medium-sized, 660–850 µm long, 520–580 µm wide, porochacean gyrogonites with an ovoidal subprolate shape (length/width ratio = 1.1 to 1.3; Fig. 7). In lateral view, the number of convolutions varies from 8 to 13. The spiral cells are concave. The apex is truncated. The base is round and shows a small basal pore. The basal plate has not been observed but is known to be multipartite in this species.

**Remarks:** These specimens were isolated after bulk macerations of marl from FS1 (facies F3) and FS4 (facies F4). Gyrogonites of charophytes are also abundant in facies F2. Gyrogonites were mentioned in the “Calcaires à stipites” Fm. since the 19<sup>th</sup> century (Bleicher, 1872).

*Porochara douzensis* was first named *Musacchiella douzensis* by Feist and Grambast-Fessard (1984). This species was erected based on material from Les Douzes, 30 km South West of the Castelbouc Cave N°4. Regionally in the Causses Basin, *P. douzensis* was also reported from the Bathonian of Aveyron and Gard (Knoll et al., 2013, 2014). In the Middle Jurassic, this species was also reported from the Callovian of Tunisia (Tiss et al., 2019).

Class Polypodiopsida Cronquist, Takht et W. Zimm, 1966

Polypodiosida indet.

Fig. 8(A, B)

**Material:** One specimen, UBGD.294157.

**Description:** Foliar remains of ferns are represented by a single and small distal portion of a circinate pinna (Fig. 8(A, B)). The specimen is 1.5 mm long, 1.0 mm wide and displays a charcoalfied aspect.

**Remarks:** This specimen was collected in FS4 (Facies 4).

Class Pinopsida Burnett, 1835

Order Coniferales Engler, 1897

Family Cheirolepidiaceae Turutanova-Ketova, 1963

Genus *Classostrobus* Alvin, Spicer et J. Watson, 1978

*Classostrobus* sp.

Fig. 8(C, D)

**Material:** One specimen, UBGD.294154.

**Description:** Cone is small, spherical to ovoid, 2.6 mm long and 3.0 mm wide, bearing helically arranged microsporophylls (Fig. 8(C, D)). The microsporophyll heads are greatly convex, triangular in shape, longer than wide. They show a large base and an acuminate apex. Abaxial surface is slightly keeled along the total length of the microsporophylls. Microsporophylls are up to 2 mm long and up to 2 mm wide. Microsporophylls show papillae similar to those observed on the isolated leaves we ascribed to *Brachyphyllum* sp.

**Remarks:** This specimen was recovered from FS4 (facies F4). *Classostrobus* is a common Mesozoic male cone, typically bearing *Classopollis* pollen grains. Although we did not observe pollen grains in this cone, *Classopollis classoides* constitutes the most abundant palynomorph in FS4 (54%; Table 4).

Genus *Brachyoxylon* Hollick et Jeffrey, 1909

*Brachyoxylon cf. trautii* (Barale, 1981) Philippe, 1995

**Material:** One specimen, MP1972.

**Description:** The wood is a tracheidoxyl, with marked growth rings and narrow latewood limited to a few cell layers. No resin channel, nor axial parenchyma were observed. Tracheids cross-sections could not be observed. Tracheid pitting was noticed on radial walls only, with pits mostly in long uniseriate rows of contiguous slightly deformed pits. In some places distant and round pits were observed, distributed randomly through the rings. Only a few biseriate pits were observed, all opposite and contiguous. As estimated from the limited observations that were possible, the radial pitting is of the mixed type, largely dominated by the araucarian type. Rays are low, 2 to 6 cells high (N = 24; mean = 3.2), homogenous. It was not possible to decipher if they were all homocellular. Ray cell walls appeared thin and unpitted, except for cross-fields. These have 4 to 10 cupressoid oculipores each, disposed in an araucarioid way.

**Remarks:** Wood was identified in three facies (F2, F3 and F4). It is particularly abundant in FS4 (facies F4) where it consists of up to 30 cm wide trunks, which are strongly compacted. Although there is no reluctance to assign this specimen to *Brachyoxylon* Hollick et Jeffrey (Philippe and Bamford, 2008), the limited nature of the observations, in particular of the radial pitting of the tracheids, leads to some caution with regard to identification as *Brachyoxylon trautii*. *B. liebermannii* has a more abietinean radial pitting of tracheids and less pits per cross-field, while *B. voisinii* has a less araucarian radial pitting of tracheid, with abietinean pits being almost limited to late wood, and less pits per cross-field too (Thévenard et al., 1995). After its first description (Barale and Contini, 1973), based on material from the Bajocian of Franche-Comté (Northeastern France), *B. trautii* was found abundantly in the Bathonian and Oxfordian of the same area (Philippe, 1995) and in various parts of France (Meuse, Vaucluse) and Switzerland (Philippe et al., 2010) as well. Despite extensive research on the Bathonian palaeoflora of the Causses (Philippe et al., 1998), *B. trautii* has not yet been well-identified in the Bathonian deposits from the Causses, although the genus *Brachyoxylon* is well represented there (Thévenard et al., 2022).

Family incertae sedis

*Brachyphyllum* sp.

Fig. 8(E–K)

**Material:** Three specimens, UBGD.294151–UBGD.294153.

**Description:** Leafy axes are straight to slightly curved (Fig. 8(E, F)). The longest specimen is 22 cm long. Shoots are narrow, up to 5 mm in diameter. Leaves are persistent, helically arranged, and highly appressed and imbricated. Leaves are scale-like, triangular to rhomboidal, as long as wide, and keeled on the abaxial side (Fig. 8(G–J)). Apically, they display a short free part. Abaxial surface of leaves is convex, whereas adaxial surface is concave. The leaf margin is entire. Shape of the leaf apex is pointed to round. Leaves show short papillae on the cuticle of both the abaxial and adaxial surfaces (Fig. 8(K)). Leaves are amphistomatic. Subsidiary cells of stomatal apparatuses form a thick and well-marked rim around the pit apertures.

**Remarks:** Such leafy axes are preserved as compressions with cuticles. They are particularly abundant in fossiliferous layers FS3 (Facies 3) and FS4 (Facies 4). Based on the gross morphology of leafy axes and leaves we ascribe these remains to *Brachyphyllum* sp. However, in absence of more information of the arrangement and the structure of stomatal apparatuses and epidermal cells we refrain from assigning this material to a species.

## Amber

Fig. 8(L)

**Material:** One specimen, UBGD.294150.

**Description:** A single and small piece of fossil resin was collected from FS4 (facies 4). It consists of a more or less transparent, orange-brown, droplet-shaped, 5.0 mm long and 3.5 mm wide grain, with a resinous brilliance (Fig. 8(L)).

**Remarks:** Jurassic ambers have been mentioned only in a few palaeontological sites throughout the world (Langenheim, 1969; Philippe et al., 2005; Azar et al., 2010; Nohra et al., 2013; Neri et al., 2017), Middle Jurassic amber remaining exceptional, only reported from rare localities in China (Nohra et al., 2013), Jordan (Abu Hamad and Uhl, 2015) and Thailand (Philippe et al., 2005). In France, Jurassic amber (scleretinite) was mentioned in the literature in deposits near Le Vigan (Gard, southern France; Dufrénoy, 1859; Leymerie, 1859; De Brun, 1902). Although the stratigraphic origin of this latter amber seems unknown (Dufrénoy, 1859), Lacroix (1910) tentatively proposed a Bathonian age. Jurassic amber was also mentioned in Charente (western France; Coquand, 1858; Lacroix, 1910) that seems to be Toarcian in age according to Nel et al. (2004). However, the geological age of these historical Jurassic amber localities, observed at the end of the 19<sup>th</sup> or the beginning of the 20<sup>th</sup> century, is unverifiable because none amber grains have been collected and studied recently from these outcrops. The more reliable ages of French Jurassic ambers correspond to palaeontological investigations made during the last 15 years and often unpublished. Thus, tiny amber grains were found in Hettangian deposits from Le Veillon, in the Vendée department (F. Thévenard and M. Fix, pers. com.). In the Causses Basin, Knoll et al. (2014) briefly mentioned (but did not describe nor figure) a single grain of amber from the Bathonian of Cornhes (Aveyron), 30 km South West of the Castelbouc Cave N°4.

Class indet.

Seed indet.

Fig. 8(M)

**Material:** One specimen, UBGD.294156.

**Description:** This coalified seed is ovoid in shape, 2.3 mm long, 2.0 mm in diameter and flattened in the longitudinal axis (Fig. 8(M)). The surface of the seed shows numerous thin furrows running from the base of the seed to its apex. Base of the seed bears a circular scar corresponding to the hilum.

**Remarks:** This specimen was collected in FS4 (Facies 4).

## 5. Discussion

### 5.1. Depositional environments

Analyses of microfacies and palaeontological content allowed to identify a relatively wide range of coastal palaeoenvironments with freshwater, brackish to euhaline conditions (Table 1; Fig. 9). The abundance of mud cracks in facies F1 indicates that sediments were deposited in an environment which was periodically exposed. The cryptalgal laminites (facies F1) are characteristic of regularly flooded muddy environments, such as the intertidal and supratidal zones of a tidal flat in which microbial mats are growing (Hamon, 2004; Matysik, 2016). The scarcity of bioclasts and coarse particles in facies F1 suggests limited storm-generated transport and a relatively long distance to the subtidal zone.

In the facies association F2 + F3 (Table 1), the abundance of the charophyte *Porochara douzensis* suggests brackish conditions (Tiss et al., 2019). The salinity of the palaeoenvironment of *P. douzensis* varies from oligo- to mesohaline (Tiss et al., 2019). Although *Darwinula* is typically a freshwater ostracod, this taxon can tolerate temporary increases of salinity and was reported in freshwater to mesohaline environments (Schudack, 2006). Ostracods from F2 frequently show an anatomical connection of their two valves (particularly visible in FS2), suggesting low hydrodynamic conditions and a short transport after the death, which is coherent with the deposition of the fine matrix particles (micrite and marls) under low energy conditions. The autochthony or para-autochthony of the taphocoenosis is also attested by the exquisite preservation of foliar remains (Fig. 8(C, D)). The root casts (F2) and cracks induced by pedogenetic activity (F3) suggest a shallow and subaerial environment. The abundance of terrestrial remains (e.g., conifer woods and cuticles), as well as the low share of marine organisms in the facies F2 and F3, suggest a paralic environment such as a protected and freshwater to brackish ponds which were most of the time disconnected from the sea.

In the facies F4, the marine organisms (e.g., corals, benthic foraminifera, echinoids) are strongly fragmented, rounded and quite micritised suggesting that they are allochthonous and were transported along a quite long distance from the place of life to the depositional environment. In the same facies, the abundance of diverse and well-preserved plant macro- and mesoremaines showing a conifer-dominated assemblage (e.g., large trunks of wood, leafy axes and cones) suggests a strong proximity of the depositional environment with littoral forests (well-marked in FS4). In the facies F4, by contrast with marine organisms, plant meso- and macroremaines are mainly autochthonous to para-autochthonous. This co-occurrence of marine and terrestrial plant fossils suggests a shallow and paralic environment such as a bay or a lagoon partially open to the sea. This is on the edge of this bay/lagoon that the sauropods from Castelbouc left their tracks. The presence of a callipurbeckiid or lepidotid ginglymodian fish is not a relevant indicator of salinity since these groups were reported from freshwater, brackish to marine environments (Cavin et al., 2020). However, the charophyte *P. douzensis* suggests brackish condition (Tiss et al., 2019). FS4 represents the only fossiliferous layer yielding palynomorphs. In total, 437 pollen grains and spores were counted. Ten taxa were identified (Table 4). After the Pinophyta (54% of the Cheirolepidiaceae *Classopollis classoides* and 1.1% of the Podocarpaceae *Podocarpidites verrucosus*), the Bryophyta, Monilophyta and Lycopodiophyta constitute the most abundant palynomorphs (16.7%,

16.7%, and 7.8%, respectively). Rare palynomorphs of Ginkgophyta were reported (0.2%). The fossiliferous layer FS4 shows a mixture of palynomorphs typically common in unconfined marine environments (e.g., *Classopollis classoides* that is the most abundant pollen; Srivastava, 1976) as well as palynomorphs characteristic of innermost environments (such as lowland, freshwater swamps and river banks; e.g., *Staplinisporites*; Gedl and Ziaja, 2012; Gary et al., 2009). The local and thin oolitic limestone lenses of the facies F4 show that this bay/lagoon was regularly affected by storms reworking material from the sea and transporting it into the paralic setting. In the facies association F5 + F6 (Table 1), the absence of terrestrial organisms, the abundance of fragmented and micritised marine organisms (bivalves, corals, bryozoans, benthic foraminifera, echinoids), as well as the presence of ooliths and intraclasts attest of relatively high hydrodynamic conditions (foreshore to shoreface).

## 5.2. Palaeobiocoenosis

The plant macro- and microremains (including wood trunks, cuticles and palynomorphs) in facies F2, F3 and F4 demonstrate that the local brackish ponds, bays and lagoons were bordered by conifer-dominated forests (or partially wooded areas) in which Cheirolepidiaceae were the main component.

Data obtained from the palynoflora and from Philippe et al. (1998) suggest that the Bathonian palaeophytocoenosis of the Causses area included diverse Bryophyta, Lycopodiophyta and Monilophyta. Several palaeobotanical studies also demonstrated the presence of bennettitaleans, cycads and horsetail remains in lignitic beds of the “Calcaires à stipites” Fm. (De Serres, 1845; Nicklès, 1907; Philippe et al., 1998). At Castelbouc, the very low proportion of *Ephedripites* (0.2%) and the absence of Ginkgoales macroremains could question the possible transport of these pollen grains by wind and water into the basin.

According to Garcia et al. (1998) and Philippe et al. (2010), the wood *Brachyoxylon traatii* was bound to littoral environments, where it might have been a mangrove-like tree (Barale et al., 1991). The good preservation of conifer leafy axes suggests that plant debris were not transported during a long time and under a long distance. As pointed by Philippe et al. (1998), *Brachyphyllum* and especially the species *B. crucis* represents 80% of leafy rests commonly reported in the lignitic clay of the “Calcaires à stipites” Fm. However, since plant remains are not strictly autochthonous, composition of the taphocoenosis needs to be carefully interpreted.

The three large sauropod trackways reported by Moreau et al. (2019) in the Tunnel gallery demonstrated that these littoral palaeoecosystems were inhabited, at least periodically (e.g., seasonal foraging behaviour, migration), by titanosauriforms. The diverse and abundant flora was probably an attractive source of food for these mega-herbivorous dinosaurs. As proposed by Hummel et al. (2008) and Gee (2011), sauropods may preferentially have fed on conifers and the horsetail *Equisetum*. Although *Equisetum* was not reported in deposits from Castelbouc, this hygrophytic plant was locally observed in abundance in the “Calcaires à stipites” Fm., including locally as *in situ* rhizome wefts (Philippe et al., 1998). The genus *Equisetum* is known to tolerate low degrees of salinity (Husby et al., 2011) and was probably and locally abundant in freshwater to brackish ponds present along the coastline.

Besides ginglymodian fishes, vertebrate remains demonstrated the presence of atoposaurids, an extinct (Jurassic–Cretaceous) group of small-sized, terrestrial to semiaquatic crocodylomorphs (Buscalioni and Sanz, 1990; Karl et al., 2006). We may notice that Gand et al. (2018) reported crocodylomorph swimming tracks from “Le Capelan” tracksite (Lozère), 20 km south of the Castelbouc Cave N°4. Although sauropod body fossils remain unknown in the “Calcaires à stipites” Fm., few theropod teeth and a single tooth of ornithischian were reported by Kriwet et al. (1997) in the Gardies site (Table 3). Tracks of theropods and possible tracks of ornithopods were reported from several Bathonian tracksites of the Causses Basin (Sciau et al., 2006; Gand et al., 2007, 2018; Moreau et al., 2012; Moreau, 2017).

Additionally, in other palaeontological sites from the Causses Basin, the organic-rich layers from the “Calcaires à stipites” Fm. also yielded rare microremains of elasmobranchs and lissamphibians (Bleicher, 1872; Seiffert, 1969a, 1969b; Kriwet et al., 1997; Knoll et al., 2013, 2014; Knoll and López-Antoñanzas, 2014). Fragmentary pterosaur remains from Les Liquisses (Aveyron) were briefly mentioned by Saporta (1873: p. 249) but they were neither described nor figured.

### 5.3. Palaeoecophysiological implications

*Brachyphyllum* displays xerophytic features (e.g., fleshy shoots; short and small leaves pressed against the axis; thick cuticle; sunken stomata apparatuses with subsidiary cells forming a thick rim limiting the water-loss; and epidermal cells with papillae) which are typically those of floras from cyclically dry tropical climates with contrasted seasons (Thévenard et al., 2005; Moreau et al., 2021). This conifer leafy axis type was probably adapted to withstand intense sunlight and coastal environments exposed to desiccant conditions coupled with saline sea spray. As proposed by Philippe et al. (2017), the wood genus *Brachyoxylon* can probably be considered as indicative of warm subtropical climate. *Brachyoxylon* was also hypothesised as characteristic for tropophilous climate, with marked alternation between a wet and a dry season (Oh et al., 2011). Here, palynology also supports this hypothesis, with *Classopollis* being mainly reported from sediments deposited in a littoral context and under a warm tropophilous climate (Srivastava, 1976).

## 6. Conclusions

The track-bearing bed (Facies F4) of the Castelbouc cave yields a mixture of terrestrial and marine fossils, including amber drops, plant remains (charophyte gyrogonites, leafy axes and wood of conifers, pinnae of ferns, indeterminate seeds, diverse spores and pollen grains), crustaceans (chela of an indeterminate astacidean lobster and ostracod carapaces) and vertebrate remains (osteichthyan scales and reptile teeth). Analyses of microfacies and palaeontological content allowed to identify a relatively wide range of coastal palaeoenvironments along the Castelbouc stratigraphic section (showing freshwater, brackish to euhaline conditions). The track-bearing bed was deposited in a bay or a lagoon regularly affected by storms reworking material from the more open sea and transporting it into the paralic setting. The plant remains demonstrate that this area was bordered by a conifer-dominated forest that was probably an attractive source of food for mega-herbivorous dinosaurs. The palaeobotanical assemblage suggests a warm subtropical climate, probably tropophilous with marked alternation between wet and dry seasons.

## Declaration of competing interest

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

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### Table and Figure captions

**Table 1.** Microfacies of the Castelbouc Cave N°4 (Causses Basin, Southern France). Abbreviations: M, mudstone; P, packstone; W, wackestone.

**Table 2.** Mineralogical composition of bulk rock samples obtained by XRD and Rietveld calculation. Phyllosilicates identification reveals presence of illite (I), kaolinite (K) and vermiculite (V). Used fit criteria for Rietveld calculation: weighted residuals of the whole pattern (Rwp) and goodness of fit (GOF). <sup>a</sup>: Traces of chlorite or kaolinite were detected.

**Table 3.** Synthesis of the sites yielding vertebrate microremains from the “Calcaires à stipites” Formation (Bathonian), Causses Basin (Southern France).

**Table 4.** List and percentages of palynomorphs from the sample S-CAS +3A (layer FS4).

**Fig. 1. A.** Location of the palaeontological sites yielding vertebrate microremains from the “Calcaires à stipites” Formation (Bathonian) of the Causses Basin. **B.** Palaeogeographic map of Western Europe and location of the study area (modified after Brigaud et al., 2009).

**Fig. 2.** Topography of the Castelbouc Cave N°4 and location of the study area (entrance of the cave). **A.** Section. **B.** Map. Courtesy of Daniel André, Catherine Perret and Pierre Lemaitre for reproduction of the topography.

**Fig. 3.** Stratigraphy of the Castelbouc Cave N°4. **A.** Stratigraphic sections achieved inside the cave and details of deposits exposed in the study area (entrance of the cave) with location of the main fossiliferous beds (FS1 to FS4). **B.** Location of each stratigraphic section in the cave. Abbreviations: Fac., facies; Lith., lithology; Sa., location of samplings; Thi., thickness (m).

**Fig. 4.** Microfacies F1–F6, plane polarized light. **A.** Cryptalgal laminites (F1). **B.** Limestone with ostracods (F2). **C.** Marl with charophyte gyrogonites and ostracod carapaces (F3). **D.** Oolitic limestone (oosparite) lenses from the lignitic to oolitic marl (F4). **E.** Peloidic to bioclastic limestone (F5). **F.** Dolomite (F6). Scale bars: 1 mm.

**Fig. 5.** Crustacean microremains from the entrance of the Castelbouc Cave N°4, SEM pictures. **A.** *Darwinula* sp., inner view of a right valve, filled with sediment, UBGD.294177 (FS4). **B, C.** *Fabanella* cf. *bathonica*, outer view of a left valve (B), inner view of a compressed right valve, filled with sediment (C), UBGD.294178 and UBGD.294179 (FS4). **D, E.** Fragment of indetermined crustacean chela (probable astacidean lobster), outer and inner view of fixed finger, UBGD.294182 (FS1). Scale bars: 500 µm (A–C), 5 mm (D, E).

**Fig. 6.** Vertebrate microremains from the entrance of the Castelbouc Cave N°4 (FS4), SEM pictures. **A.** Fish scale, *Ginglymodi* indet., UBGD.294176. **B–G.** Crocodylomorph teeth, *Atoposauridae* indet.; each tooth in labial view, mesial or distal view and apical view, UBGD.294168 to UBGD.294173, respectively. **H.** Crocodylomorph osteoderm fragment, *Crocodylomorph* indet. UBGD.294174. Scale bars: 500 µm.

**Fig. 7.** Gyrogonites of charophytes, *Porochara douzensis* from the entrance of the Castelbouc Cave N°4 (FS1). SEM pictures in basal (A, C, E) and lateral (B, D, F) views. A–F: UBGD.294158 to UBGD.294163, respectively. Scale bars: 100 µm.

**Fig. 8.** Plant remains from the entrance of the Castelbouc Cave N°4, stereomicroscopic images and SEM pictures. **A, B.** Distal portion of a circinate pinna of fern, photograph (A) and interpretative sketch (B), UBGD.294157 (FS4). **C, D.** *Classostrobis* sp., ovoid cone

bearing helically arranged microsporophylls, photograph (C) and interpretative sketch (D), UBGD.294154 (FS4). **E, F.** *Brachyphyllum* sp., narrow shoots of showing persistent, helically arranged, highly appressed, imbricated and rhomboidal leaves, photograph (E) and interpretative sketch (F), UBGD.294151 (FS3). **G–J.** *Brachyphyllum* sp., isolated rhomboidal leaves, UBGD.294152 and UBGD.294153 (FS4). **K.** *Brachyphyllum* sp., SEM picture of abaxial surface of cuticle showing short papillae (FS4). **L.** Orange-brown, droplet-shaped grain of amber, UBGD.294150 (FS4). **M.** Coalified seed, UBGD.294156. Scale bars: 1 mm (A–J, L, M), 100  $\mu\text{m}$  (K).

**Fig. 9.** Palaeoenvironmental reconstruction of the littoral ecosystem from the Causses Basin during the Bathonian. Facies from the entrance of the Castelbouc Cave N°4 are located in their respective depositional environment. For each facies, proportions of organisms are reported (based on data from the entrance of the Castelbouc Cave N°4).

Table 1.

N°	Facies	Textures	Descriptions	Facies association	Depositional environments
F1	Cryptalgal laminites	M	Grey limestone locally showing thin laminites of microbial mats (alternation of micrite/microsparite). Microbial mats parallel to the bedding planes and wavy to planar. Rare ostracods and some foraminifera dispersed in the matrix. Abundant mud cracks sometimes filled by ooids.	F1	Intertidal to supratidal zone. Tidal flat. Periodic exposures and desiccation.
F2	Limestone with ostracods	M-W	Grey to yellow mudstone to micro-wackestone with ostracods. Locally tiny fragments of highly altered woods and abundant bioturbations (possible root casts). Charophyte gyrogonites and peloids. Rare foraminifera and brachiopods.	F2 + F3	Freshwater to brackish ponds rarely open to the sea. Periodic exposures for F3.
F3	Marl with plants and ostracods	W-P	Grey to green biomicrite with abundant ostracods, charophyte gyrogonites and plant remains (cuticles, wood). Abundant peloids. Some lithoclasts and gastropods. Rare thalli of charophytes. Rare vertebrate teeth, bivalves and foraminifera. Cracks induced by pedogenitic activity.		
F4	Lignitic to oolitic marl	M-W-(G)	Grey to black marls yielding abundant plant remains including wood (up to 30 cm wide compressed trunks), cuticles and rare tiny amber drops. Abundant ooliths/ooids. Some bivalves, gastropods, spines of echinoids, corals,	F4	Lagoon or enclosed bay. Occasionally affected by storms.

charophyte gyrogonites and vertebrate remains dispersed in the matrix. Rare crustacean remains. Locally abundant microquartz grains. Locally, lenses of oolitic limestone (oosparite) with intraclasts and rare micritised bioclasts (foraminifera, bivalves and gastropods).

F5	Peloidic to oobioclastic limestone	W-P	Grey to yellowish pelbiomicrite to oobiomicrite. Abundant fragments and micritised bioclasts including bivalves, brachiopods, corals, bryozoans, benthic foraminifera (miliolids), echinoderms (including some spines of echinoids). Some ooids and intraclasts.	F5 + F6	Shoreface to foreshore.
F6	Dolomite	W	Grey to yellowish dolomite bearing compacted and fully dolomitized ooids.		

**Table 2.**

Samples	Facies	Calcite	Dolomite	Quartz	Rutile	Phyllosilicates	Rwp	GOF	
S-CAS +8	F6	47 ± 1.6	53 ± 1.6				10.6 6	9.99	
S-CAS +7	F6	0.6 ± 0.7	96.8 ± 3.3			2.6 ± 3.3	12.2 1	10.9 8	
S-CAS +6	F2	100					7.49	6.1	
S-CAS +5	F4	35.8 ± 6.7		11.2 ± 2.2	1.1 ± 1.6	51.9 ± 6.7	I+ K	11.9 6	11.2

							+		
							V		
S-CAS +4	F5	97 ± 1.1	0.8 ± 0.6	1.3 ± 0.3		1 ± 1	7.57	6.29	
S-CAS +3B	F4	98.7 ± 0.7	0.7 ± 0.7	0.6 ± 0.2			7.87	6.52	
S-CAS +3A	F4	46.2 ± 5.9		4 ± 0.9	0.9 ± 1	48.9 ± 7.6	I <sup>a</sup>	9.37	8.4
S-CAS +2H	F2	96.8 ± 0.7	0.7 ± 0.4	0.9 ± 0.1		1.6 ± 0.6	6.02	4.97	
S-CAS +2B	F2	95 ± 1.1	0.9 ± 0.6	1.6 ± 0.2		2.5 ± 1	7.25	6.03	
S-CAS +1	F1	98.8 ± 0.5	0.7 ± 0.5	0.5 ± 0.2			7.17	5.92	
S-CAS -1	F1	96.3 ± 1.1		0.8 ± 0.2		3 ± 1.1	7.49	6.18	
S-CAS -2	F3	70.4 ± 5.4		2.2 ± 0.5		27.4 ± 5.4	I	9.06	7.78
S-CAS -3	F2	99.7 ± 0.2		0.3 ± 0.2			6.46	5.31	
S-CAS -4	F3	69 ± 4.6		2.7 ± 0.5		28.3 ± 4.6	I	8.88	7.61
S-CAS -5	F5	100					7.39	6.05	

Table 3.



			<b>Gardi</b>	<b>Les</b>	<b>Les</b>	<b>La</b>	<b>Cornh</b>	<b>Sai</b>	<b>Caste</b>	<b>Monp</b>	<b>Sourg</b>
			<b>es,</b>	<b>Liqu</b>	<b>Mouli</b>	<b>Baum</b>	<b>es,</b>	<b>nt-</b>	<b>lbouc</b>	<b>laisir,</b>	<b>uettes</b>
			<b>Nant,</b>	<b>isses,</b>	<b>nets,</b>	<b>e, La</b>	<b>Mostu</b>	<b>Ma</b>	<b>Cave</b>	<b>Le</b>	<b>cave,</b>
			<b>Aveyr</b>	<b>Nant</b>	<b>Nant,</b>	<b>Panou</b>	<b>éjouis,</b>	<b>rtin</b>	<b>N°4,</b>	<b>Rozie</b>	<b>Meyr</b>
			<b>on</b>	<b>,</b>	<b>Aveyr</b>	<b>se de</b>	<b>Aveyr</b>	<b>,</b>	<b>Saint</b>	<b>r,</b>	<b>ueis,</b>
				<b>Aveyr</b>	<b>on</b>	<b>Cerno</b>	<b>on</b>	<b>Rev</b>	<b>e-</b>	<b>Lozèr</b>	<b>Lozèr</b>
				<b>ron</b>		<b>n,</b>		<b>ens,</b>	<b>Enimi</b>	<b>e</b>	<b>e</b>
						<b>Aveyr</b>		<b>Gar</b>	<b>e,</b>		
						<b>on</b>		<b>d</b>	<b>Lozèr</b>		
									<b>e</b>		

**Crocodyl**  
**omorphs** Atoposau +  
ridae  
indet.

Crocodyl +  
omorpha  
indet.

**Pterosaur**  
**s** Pterosauri +  
a indet.

**Dinosaur**  
**s** Ornithisc +  
hia indet.

Theropod +  
a indet.

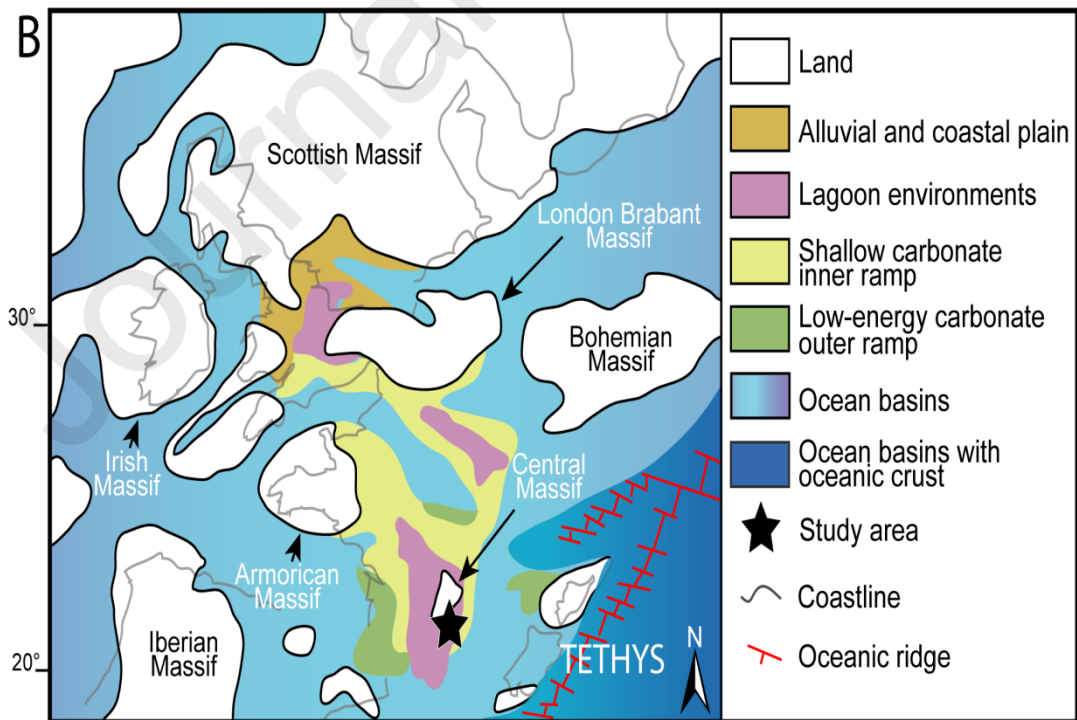
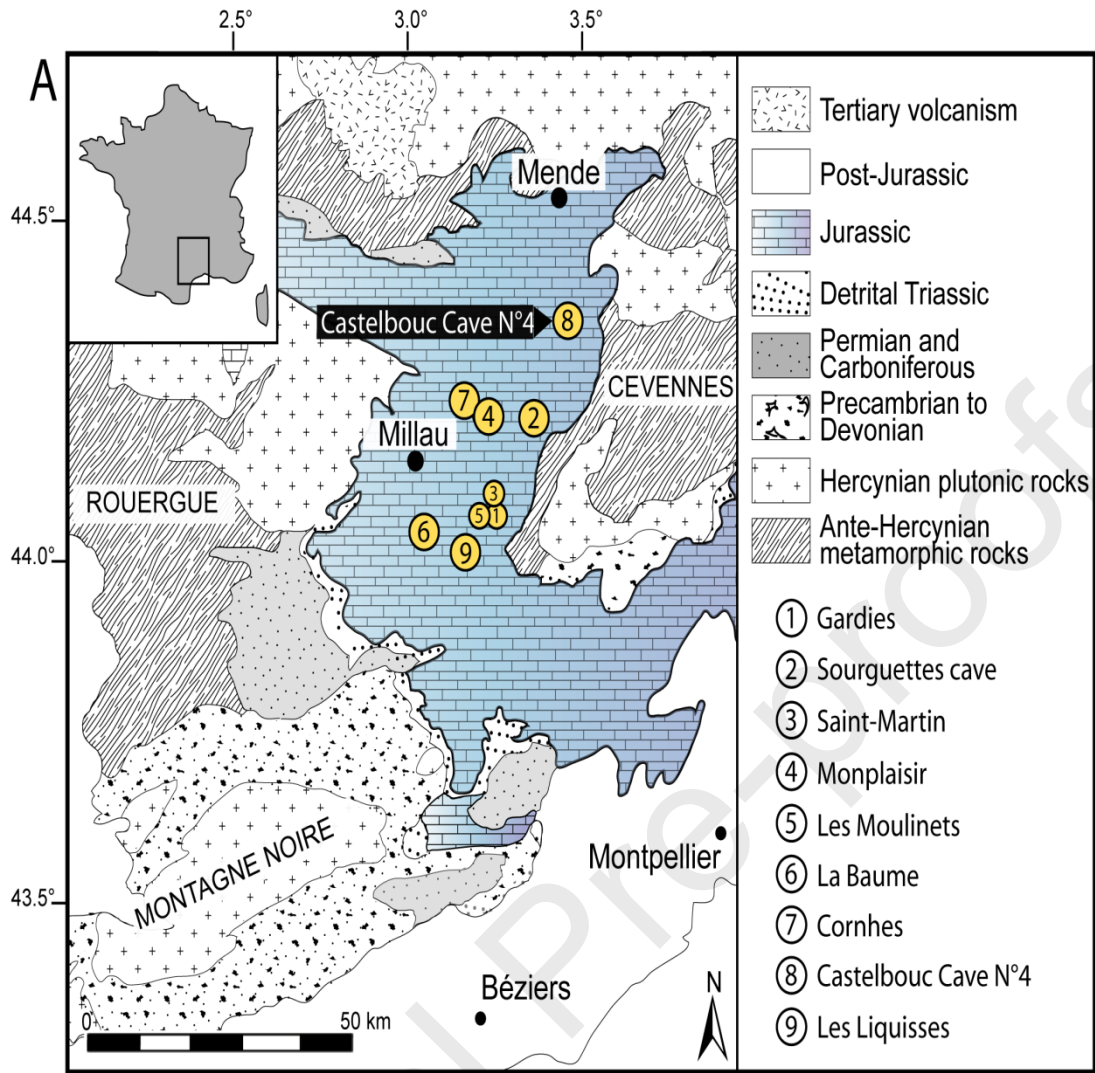
<b>Referenc</b> <b>es</b>	Seiffer t, 1969a, 1969b ; Kriwe t et al., 1997; Knoll and López - Antoñ anzas, 2014	Sapo rta, 1873	Knoll and López - Antoñ anzas, 2014	Knoll and López - Antoñ anzas, 2014	Knoll et al., 2014	Kno ll et al., 201 3	This study	Knoll and López - Antoñ anzas, 2014	Salvey re, 2007; Gand et al., 2018
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Table 4.

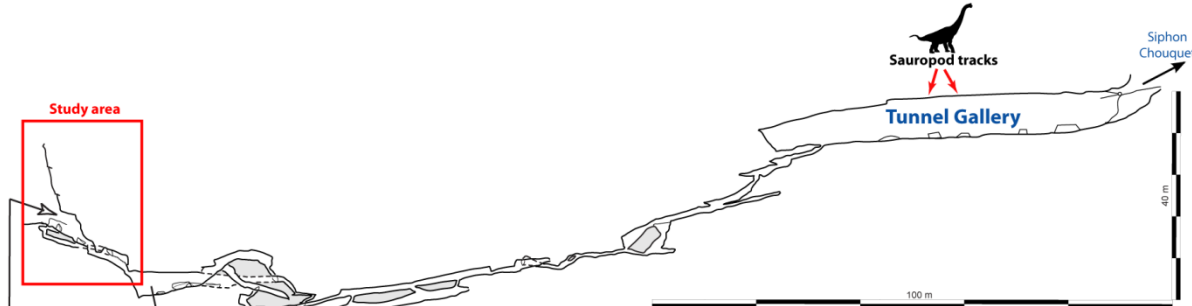
Phylum	Taxon	Environment	N	%
Bryophyta	<i>Staplinisporites caminus</i>	River bank, freshwater swamps	73	16.7
Monilophyta	<i>Cyathidites minor</i>	Lowland	34	7.8
Monilophyta	<i>Ischyosporites variegatus</i>	Lowland	28	6.4
Monilophyta	<i>Osmundacidites tuberculatus</i>	Lowland	8	1.8
Monilophyta	<i>Osmundacidites wellmanii</i>	Lowland	3	0.7
Ginkgophyta	<i>Ephedripites</i> sp.	Arid to semi-arid coastline	1	0.2
Lycopodiophyta	<i>Densoisporites velatus</i>	Coastal with tidal influence (halophytic area)	34	7.8
Marchantiophyta or Lycopodiophyta	<i>Neoraistrickia truncata</i>	River bank	8	1.8
Pinophyta	<i>Classopollis classoides</i>	Arid to semi-arid coastline	23	54.0
Pinophyta	<i>Podocarpidites</i> sp.	Upland	5	1.1

undetermined	damaged spores	-	7	1.6
			<b>43</b>	<b>100</b>
			7	

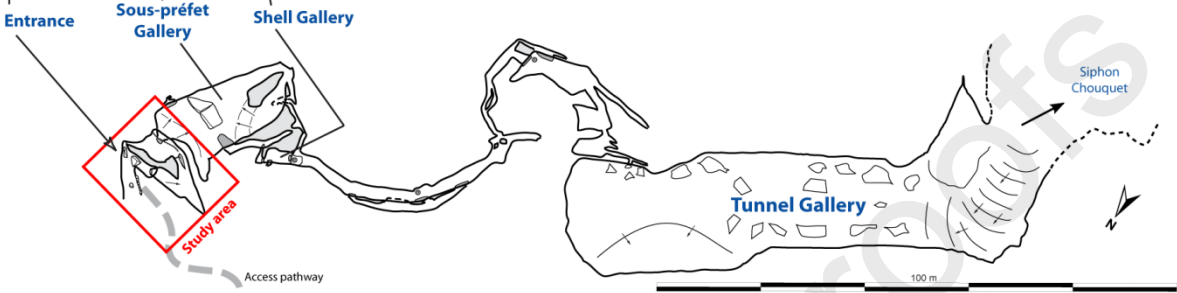
Journal Pre-proofs



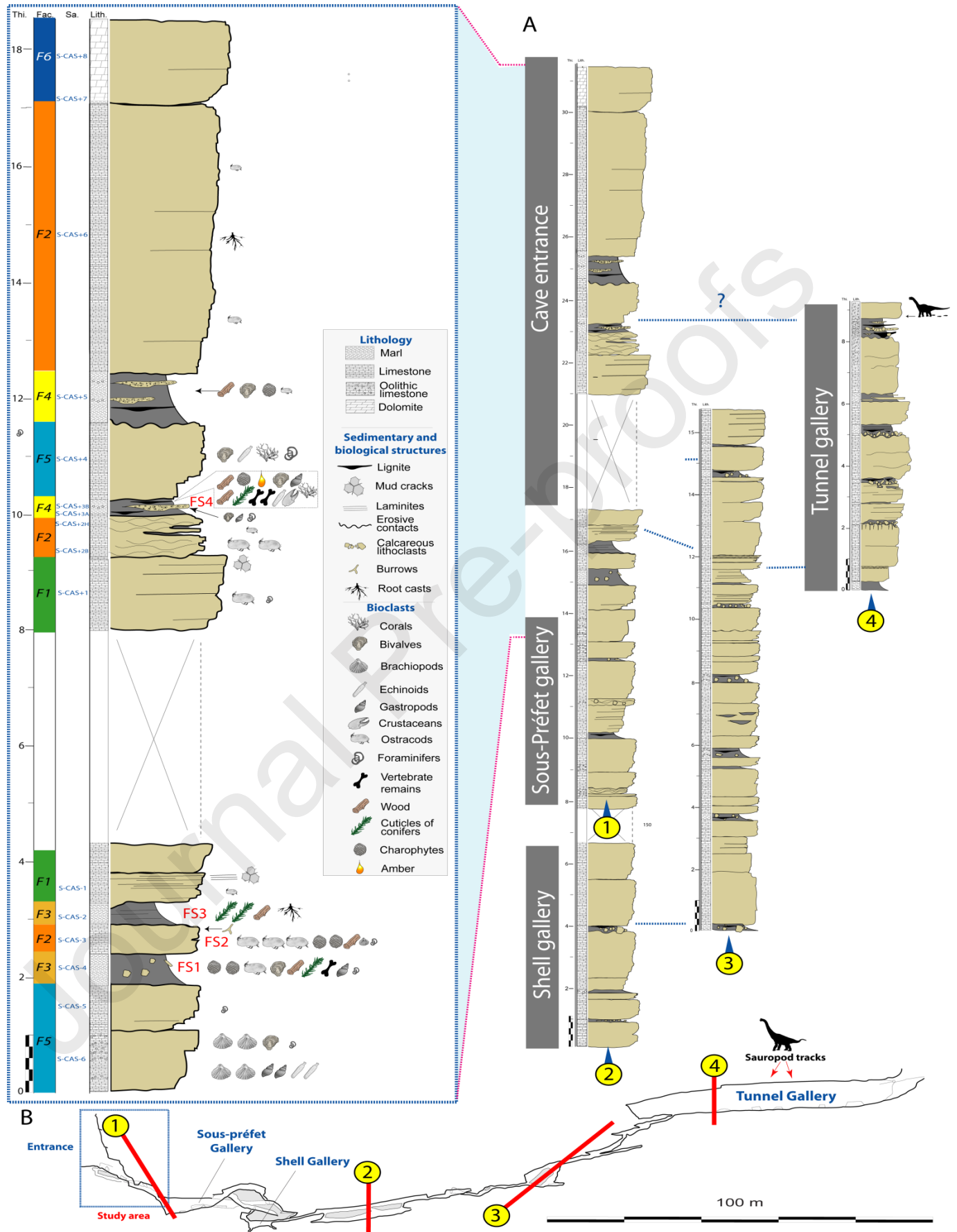
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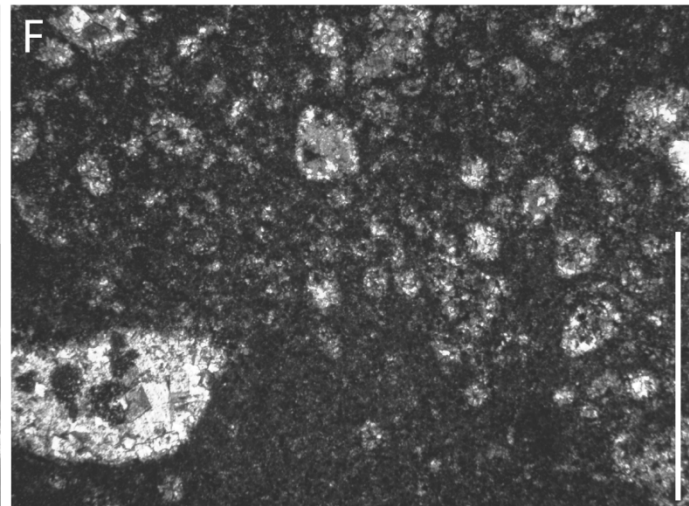
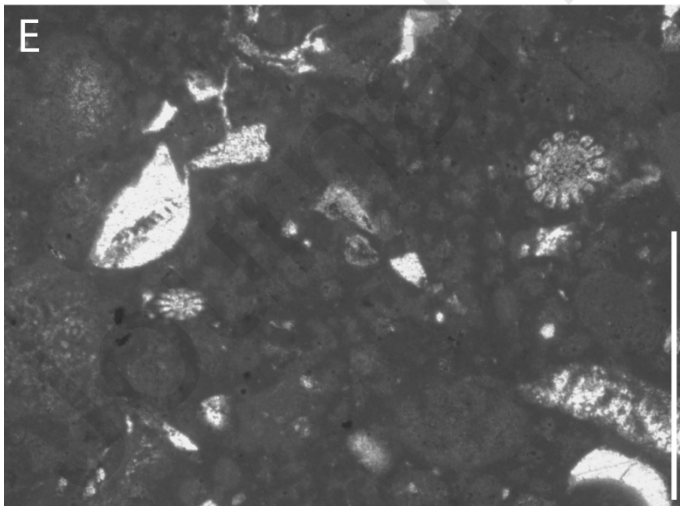
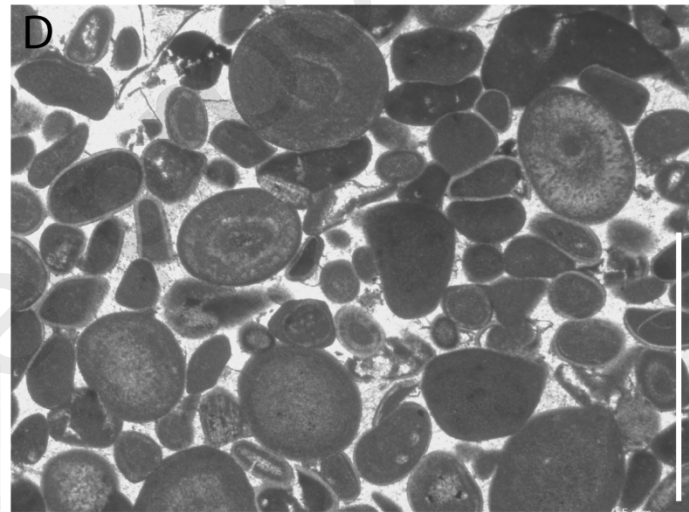
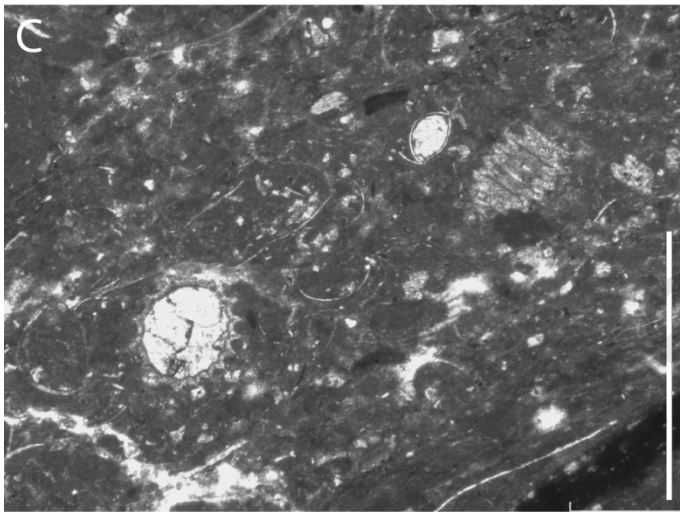
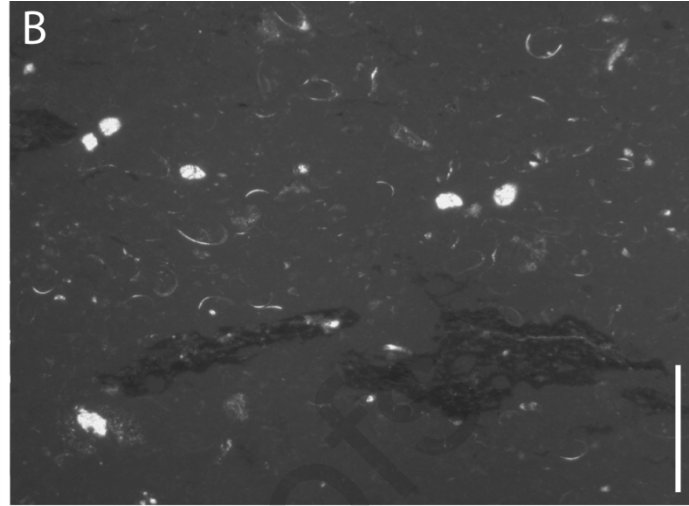
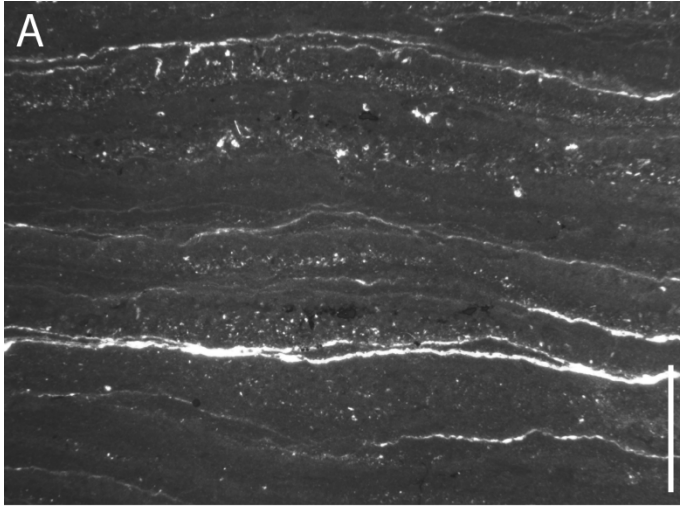


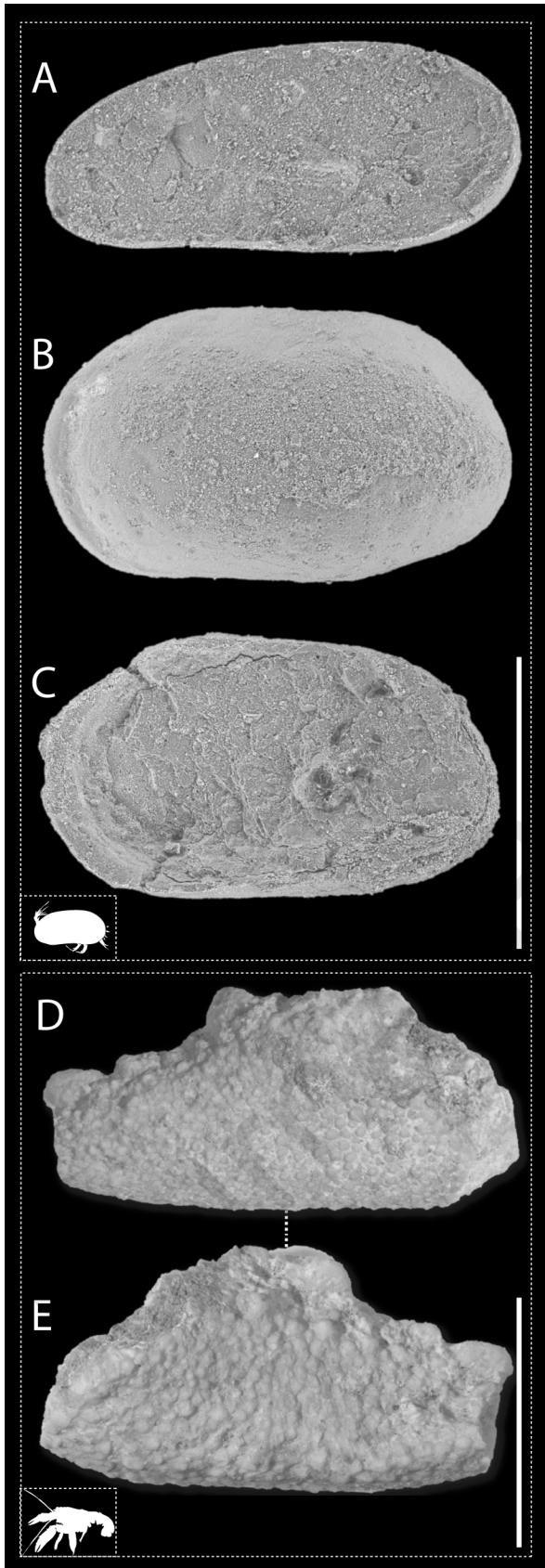
B



Journal Pre-proofs







re-proofs

