
Increasing size and abundance of microbialites (oncooids) in connection with the K/T boundary in non-marine environments in the South Central Pyrenees

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* During the revision of this manuscript our dear friend and co-author Nieves López-Martínez passed away. Nieves was a wonderful colleague whose discoveries and stimulating conversations motivated our research. With her prolific work and the depth of her papers, she was a role model for all of us. We dedicate this paper to her memory.

| A B S T R A C T |

A layer rich in giant microbialites, developed within continental deposits of the Tremp Formation (South-Central Pyrenees) in the aftermath of the end-Cretaceous mass extinctions, is here reported for the first time. Its stratigraphic location just above the Latest Maastrichtian Reptile Sandstone unit, and a characteristic $\delta^{13}\text{C}$ anomaly, are clear proofs linking this so-called “z” layer to the K/T boundary. The great abundance of microbialites, their outsized dimensions (oncooids with coating thickness up to 1.2m; average >50mm), and the great lateral continuity of the “z” layer in the study zone, support the hypothesis that these giant microbialites may represent disaster forms linked to the latest Mesozoic crisis.

To our knowledge, this is the first time a record of this type is reported in continental realms. Other large continental oncooids and stromatolite constructions (*e.g.*, in the Late Palaeogene deposits of the Pyrenees, Ebro basin, and Mallorca island) differ from those of the “z” layer in occurring in carbonate rocks and in having less lateral continuity, but they could also have been favoured by palaeoenvironmental crises, such as the global Eocene hyperthermals, Early Eocene Climatic Optimum, Middle Eocene Climatic Optimum, and the climatic cooling of the Eocene-Oligocene transition. It is thus possible that some layers of microbialites may record biotic crises in continental series, as they do in the marine record.

KEYWORDS | K/T boundary. Oncooids. Non-marine environments. South Pyrenean basin.

INTRODUCTION

Numerous authors have made reference to a noteworthy increase in the abundance and extension of stromatolites and other microbialites in marine environments following periods of global biodiversity crises, such as the Late Ordovician (Sheehan and Harris, 2004), the Late Devonian (Whalen *et al.*, 2002), the Permo-Triassic (Schubert and Bottjer, 1992, 1995; Lehrmann, 1999; Baud *et al.*, 2005, 2007; Pruss *et al.*, 2006; Kershaw *et al.*, 2007; Mary and Woods, 2008), and other Phanerozoic crises (Kiessling, 2002). Proliferation of microbialites after great biotic crises, recorded by stromatolite beds of anomalous thickness and lateral continuity, has been related to a reduction of depredation and/or bioturbation on microbial communities following the decline of metazoan and other eukaryote organisms during such events. In response to biodiversity crises, ecosystems would return to early successional ecological conditions, in part comparable to those of the Precambrian or to particularly extreme environments, where microbialite-forming microorganisms proliferate (Schubert and Bottjer, 1992; Sheehan and Harris, 2004). The toxicity of cyanobacterial-forming microbialites, leading to metazoan mortality, has also been invoked as an additional factor related to mass-extinction events (Castle and Rodgers, 2009).

Stromatolites were first considered to be “disaster forms” by Schubert and Bottjer (1992) in relation to the Permo-Triassic mass extinction. The concept of disaster form (Fischer and Arthur, 1977) itself refers to opportunistic taxa whose populations, normally restricted to marginal, stressed environments, become widespread and very abundant during biotic crises.

However, studies describing significant microbial deposits at the K/T boundary are surprisingly few (*e.g.*, Pomonis-Papaioannou and Solakius, 1991, in central Greece; and Tewari *et al.*, 2007, in the Karst region of Italy and Slovenia). This apparent scarcity of microbialites related to this and other major crises, such as the end-Triassic one, casts some doubt on the “disaster form” model (Riding, 2005, 2006). Besides, all of the aforementioned papers refer to marine environments; reports concerning continental environments are lacking, although presumably similar phenomena may have occurred.

In this paper we report a particularly rich development of microbialites (oncoids, stromatolites) within a layer related to the K/T boundary (now, formally K/P boundary) that can be traced laterally for over 54km within mixed/siliciclastic continental deposits of the Tremp Formation in the South-Central Pyrenees. The possible relation of these deposits to the biotic crisis was suggested by Dr. D.H. Erwin (Erwin, 1997), but it has not yet been formally proposed. We herein

present evidence to show that these deposits can indeed be related to the environmental crisis of the Cretaceous-Tertiary boundary.

GEOLOGICAL SETTING

Microbialites have been recorded in the Pyrenean region in Upper Cretaceous to Lower Eocene transitional and continental deposits (Freeman *et al.*, 1982; Plaziat, 1984; López-Martínez *et al.*, 1998). The ones described herein, which crop out extensively and in excellent conditions, occur in the southern Pyrenees within the Tremp Formation (Fig. 1). This is a continental unit mostly made up of red lutites and sandstones, with minor conglomerates, limestones, and gypsum, intercalated and laterally interfingering with marine deposits of the Upper Campanian (Aren sandstone, Les Serres limestone), Paleocene and Lower Eocene (Ilerdian *Alveolina* limestone) (Figs. 2; 3).

The Tremp Formation was defined in a major allochthonous tectonic unit (the South-Pyrenean central unit, Fig. 1), but continental deposits correlatable to the Tremp Formation crop out throughout the Pyrenees (*e.g.*, “Vitolian”, “Garumnian”; Plaziat, 1984; Oms *et al.*, 2007). The palaeogeographic reconstruction indicates that these continental deposits formed a facies belt surrounding the Pyrenean marine proto gulf of Biscay, which occupied a central position and opened westwards to the North Atlantic (Baceta *et al.*, 2004; López-Martínez *et al.*, 2009).

Detailed studies carried out in the eastern, central and western part of the South-Pyrenean central unit (Oms *et al.*, 2007; Díaz Molina, 1987; Eichenseer, 1988; Krauss, 1990; Rossi, 1993; Álvarez-Sierra *et al.*, 1994; Robador, 2005) point to a transitional, coastal, or paralic origin for the Tremp Formation deposits. Dating of the continental sediments has been approached by bio-, chemo- and magnetostratigraphic data (Fig. 3; Galbrun *et al.*, 1993; López-Martínez *et al.*, 1998; Schmitz and Pujalte, 2003, 2007; Oms *et al.*, 2007; Pereda-Suberbiola *et al.*, 2009; Pujalte *et al.*, 2009) and by correlation with marine deposits (Ardèvol *et al.*, 2000; Vicens *et al.*, 1999, 2004).

The Tremp Formation reaches up to 1,000m in thickness in the Tremp syncline (its type area), becoming thinner to the south, in the Àger and Serres Marginals synclines (Fig. 1). It has been divided into four lithostratigraphic units (Figs. 2; 3), two light-coloured carbonate units (Units 1 and 3) overlain by two reddish terrigenous units (Units 2 and 4) (Galbrun *et al.*, 1993).

Unit 2, the most relevant of them for the purpose of this study, is up to 300m thick and is formed of ochre and reddish marls, lutites and hybrid sandstones, and minor lime-

stone and evaporite beds. Unit 2 corresponds to the Lower Red Unit of Oms *et al.* (2007) and Riera *et al.* (2009). Near its top, the main fine-grained calciclastic composition of the sandstones and siltstones changes to coarse-grained, siliciclastic hybrid arenites rich in feldspars, known as the Reptile Sandstone (Ullastre and Masrera, 1983) (Figs. 2; 3). This member is particularly continuous laterally and more than 15m thick in the Àger syncline, where it ends with conspicuous whitish arkosic sandstone beds, a lithological change recorded across the entire Pyrenean region (Oms *et al.*, 2007). The deposits of Unit 2 have been attributed to marginal lagoonal, floodplain, fluvial, and alluvial environments (Rosell *et al.*, 2001; Oms *et al.*, 2007). In the Àger syncline, these deposits show estuarine influences (bioclasts, sigmoidal structures; Álvarez-Sierra *et al.*, 1994), confirmed by geochemical data such as $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ (Fig. 3), and REE analyses (La/Yb versus La/Sm; Domingo *et al.*, 2007). A magnetostratigraphic study across Unit 2 carried out by Galbrun *et al.* (1993) in the Fontllonga section

identified magnetochrons C32 to C27, confirmed by additional magnetostratigraphic data of López-Martínez *et al.* (2006b) (Fig. 3).

The Cretaceous-Tertiary (K/T) boundary is located towards the upper part of unit 2, just above the Reptile Sandstone member, close to the C29n/C29r geomagnetic inversion. Fontllonga is the only section in the Àger syncline in which the upper boundary of chron C29r has been located. This 5m-thick upper part of the C29r interval is particularly interesting, as it successively contains: i) the last record of dinosaurs, ii) the first Palaeocene fossils and iii) a layer rich in oncoïds, marked by a rapid fall in $\delta^{13}\text{C}$, a geochemical anomaly correlated with the “z” event detected in the marine realm by Shackleton (Shackleton, 1986; López-Martínez *et al.*, 1998, 2006a, 2009; Domingo *et al.*, 2007; Fig. 3). Immediately below this layer “z”, the grey lutites have yielded numerous fossils of plants and freshwater organisms (“fish layer” at Fontllonga-3 and Figuerola-1 with

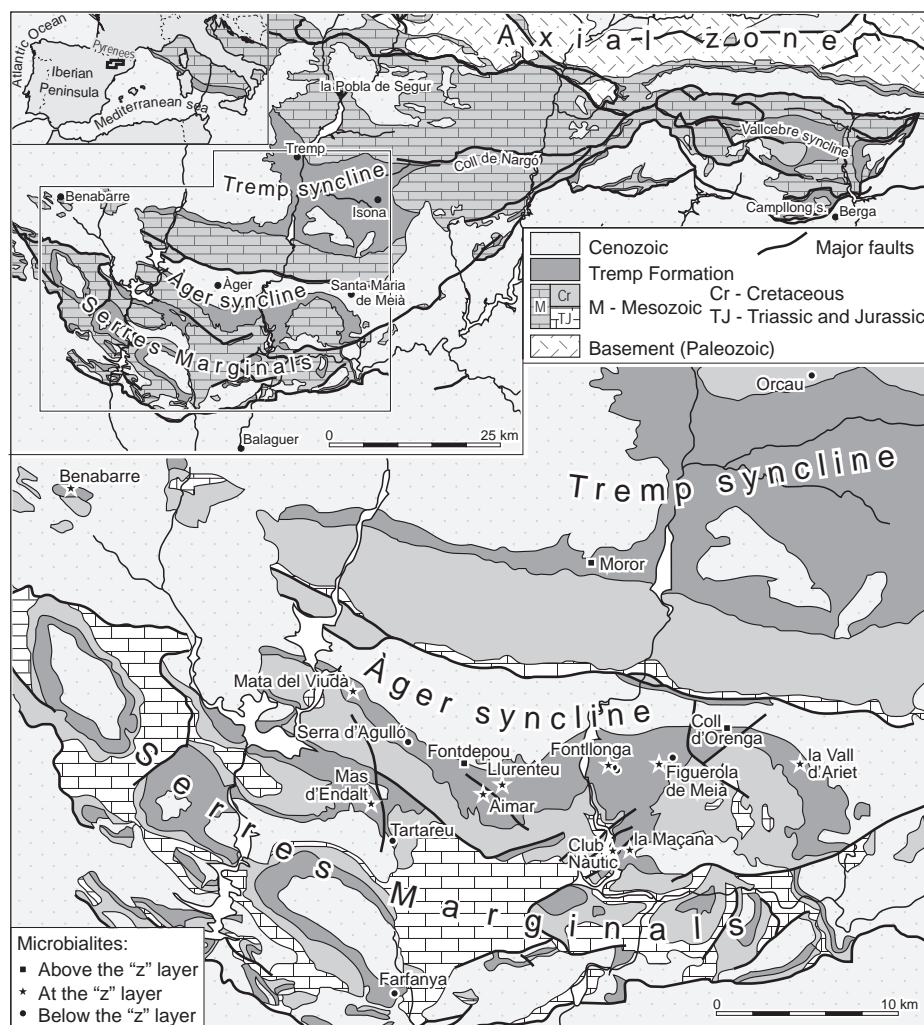


FIGURE 1 | Regional geological map of the study area.

fishes, ostracods, and charophytes) attributed to the Danian (López-Martínez *et al.*, 1999). The geochemical composition (Ba/Ca, $\delta^{13}\text{C}$, and $\delta^{18}\text{O}$ stable isotopes) of the skeletal micro-remains from the Fontllonga-3 site indicates high temperatures and a semiarid, seasonal climate (Domingo *et al.*, 2007). The dinosaur record in this sector ends abruptly at a 1–3-m-thick lutite interval below the “fish layer”; plants, in contrast, do not exhibit noteworthy changes in taxonomic composition across this interval (López-Martínez *et al.*, 1999; Mayr *et al.*, 1999; Fernández-Marrón *et al.*, 2004).

The $\delta^{13}\text{C}$ geochemical anomaly has also been detected in the Benabarre section (López-Martínez *et al.*, 1996, 1998; Fig. 1). In both cases, this geochemical anomaly coincides with the key “z” layer, typified by oncoids of great size (described below).

Above the $\delta^{13}\text{C}$ geochemical anomaly, the terrigenous deposits change abruptly and are substituted for red lutites, carbonates and evaporites, from the uppermost Unit 2 affected by edaphic processes up to its contact with the thick, extensive lacustrine limestones of Unit 3, which also show evidence of marine influence in this sector (Mayr *et al.*, 1999; López-Martínez *et al.*, 2006a).

Microbialites (oncolites and stromatolites) can also be found in units 1, 3 and 4 of the Tremp Formation but, as described below, their extension and development is never as extensive as in the “z” layer.

MATERIALS AND METHODS

Following Flügel (2004), we use “oncoïd” to designate individual grains, and “oncolite” to name a rock formed by a large number of oncoïds.

We have studied in detail several oncolite beds in the following sections of the Àger syncline: Fontllonga (FO), la Vall d’Ariet (LV), la Maçana (LM), and Coll d’Orenga (CO) (Figs. 1; 2). In each section, oncolite size, shape, surface, nucleus, lamination type, and microstructural, mineralogical, and petrological characteristics were studied. Additionally, microbialite (oncolite) layers have been sampled in the sections of Figuerola de Meià (FI) and Club Nàutic (Àger syncline), Farfanya, Fontdepou, and Tartareu (Serres Marginals), Orcau-E (Tremp syncline), and Campllong I and II and Coll de Pradell (eastern Pyrenees) (Figs. 1; 2). In these cases, our study was limited to ob-

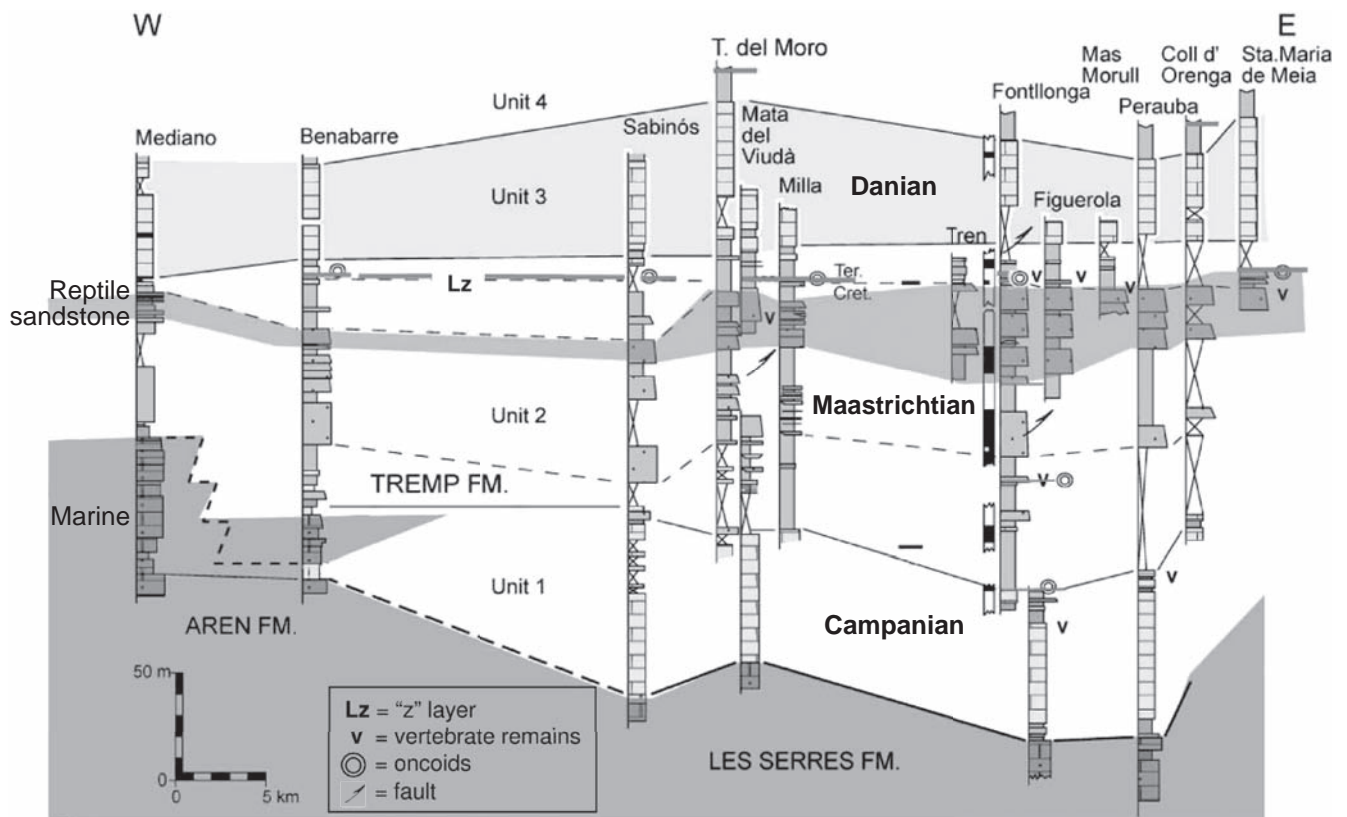


FIGURE 2 | Correlation panel of the lower–middle part of the Tremp Formation (Units 1 to 3) across the Àger syncline. (Modified from López-Martínez *et al.*, 1998, 2006).

servicing outcrop features and the external shape and size of the oncoïds.

We obtained 60 thin sections, 20 of which were stained with Alizarin Red S. Optical. Petrographic microscope observations were made with a binocular Leica MZ 16 microscope equipped with a DFC 320 digital camera, and with a Nikon Labophot T2-Pol petrographic microscope coupled to a Coolpix 4500 digital camera.

Several samples were analysed by X-ray diffraction (XRD) using a Philips PW-1710 diffractometer (University of the Basque Country) with Cu-ka radiation, automatic divergence slit, and a diffracted-beam graphite monochromator. Random powder samples were prepared for bulk mineralogical analysis.

To describe the oncoïds, we have followed the works of Nickel (1983), Leinfelder and Hartkoff-Fröder (1990), Zamarreño *et al.* (1997) and Arenas *et al.* (2007), among others. For oncoïd size, we use the classification of Arenas *et al.* (2007), somewhat modified: small oncoïds, <100mm; large, 100 to 400mm; and giant, >400mm. However, these authors refer to the maximum diameter of the oncoïds, whereas we apply these measurements to the minimum diameter. Besides, we add a new category, huge, for oncoïds over 800mm minimum diameter.

ONCOÏD-BEARING LAYERS

The noteworthy microbialite development in the Tremp Formation has principally been observed in the Àger syncline (Fig. 1). Distinct layers of oncoïds are found there in almost all units, and stromatolites have also been reported in Unit 4 (Llompart and Krauss, 1982; Rossi, 1993). One of the best-exposed sections described here is Fontllonga, across the road between Camarasa and Tremp (from 41°56'43.62"N-0°52'40.09"E to 41°59'37.26"N-0°50'48.37"E) (Figs. 2; 3; 4A; see fig. 7 in López-Martínez *et al.*, 2006a). Other sections are indicated in Figure 1.

The different microbialite-bearing layers are described here in chronological order, distinguishing three main groups: the aforementioned "z" layer, with small to huge oncoïds and stromatolites linked to the K-T boundary, and those situated below and above the "z" layer, bearing small oncoïds and stromatolites.

i) The microbialite beds below the "z" layer have only isolated oncoïds and no stromatolites. The oldest microbialite layer lies at the top of Unit 1 (Upper Campanian) and contains abundant small oncoïds. This first oncolite layer appears in the Fontllonga (FO1, Àger syncline), Orcau (Tremp syncline), and Tartareu sections (Serres Marginals)

(Figs. 1; 2; 3; 5; 6A-C). Palaeosols and dinosaur footprints can be observed in the Fontllonga section below the layer of the small oncoïds, indicating a continental origin.

The overlying marly and sandstone deposits of Unit 2 contain distinct oncoïd-bearing layers, with oncoïds increasing in size upsection. Most of these oncoïds formed around disarticulated shells of unionid bivalves (ear-shaped oncoïds) and gastropods. These layers appear in the following sections: Fontllonga (FO2 and FO3), Serra d'Agulló, Figuerola de Meià (Àger syncline), Tartareu, Farfanya (Serres Marginals), and Coll de Pradell with at least four oncoïd layers (Vallcebre syncline, eastern Pyrenees) (Figs. 1; 2; 3; 5; 6D-F). Magnetostratigraphic correlation at the Fontllonga and Vallcebre sections indicates that the FO2 and Coll de Pradell oncolite layers are Lower Maastrichtian (Galbrun *et al.*, 1993; Oms *et al.*, 2007).

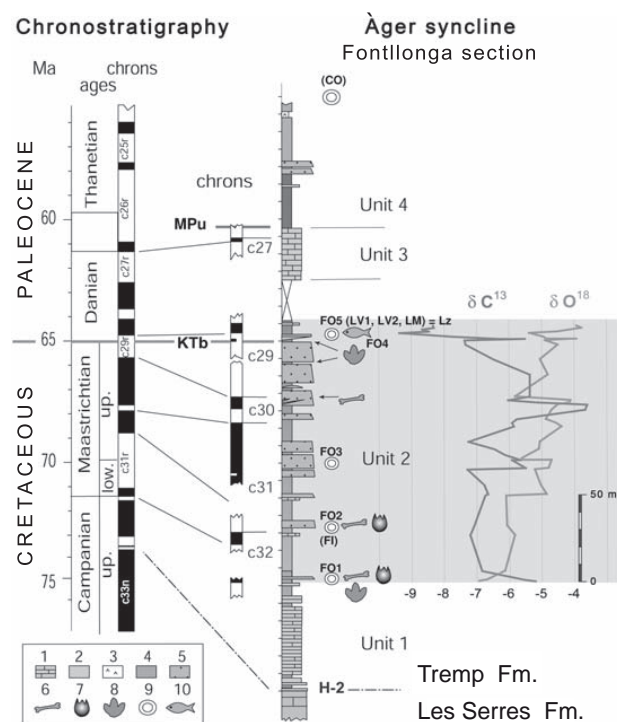


FIGURE 3 | Fontllonga partial stratigraphic log of the Tremp Formation, Àger syncline. 1: Peritidal limestones, 2: clay and mudstones, 3: gypsum, 4: grey marls, 5: reddish sandstones, 6: dinosaur bones, 7: dinosaur eggshells, 8: dinosaur footprints, 9: oncoïds, 10: fish remains. FO1-5: Fontllonga, Fl: Figuerola de Meià, LV1-2: la Vall d'Ariet, LM: la Maçana, CO: Coll d'Orenga. lz: "z" layer (FO5, LV1-2, LM), Ktb: Cretaceous-Tertiary boundary, MPu: Mid-Paleocene unconformity. (Modified from López-Martínez *et al.*, 1998, 2006a, b). The low isotopic values recorded throughout Unit 2 agree with the continental origin of waters, showing two transgressive episodes (sudden increase in $\delta^{13}\text{C}$ at chrons C31n and C30) and a general trend towards increasing marine influence (general increase in $\delta^{18}\text{O}$) interrupted by the $\delta^{13}\text{C}$ geochemical anomaly at the "z" layer. Palaeomagnetic data according to Galbrun *et al.* (1993).

ii) The extensive “z” layer can be followed along the Àger syncline over a distance of at least 54km from west to east, from the town of Benabarre (Huesca, Aragón) in the west to the limit of the South-Pyrenean central unit in the east (la Vall d’Ariet section), and stretches for at least 10km from north to south, from Mata del Viudà in the north to Mas d’Endalt in the south in the Serres Marginals sector (Fig. 1). The “z” layer has not been observed in the Tremp and eastern Pyrenees sectors, where evidence of the geochemical anomaly and the magnetochrons around the K/T boundary are also absent; this episode has either not been recorded in these sectors, or else removed by later erosion.

In the Fontllonga section, the “z” layer with large oncoïds (FO5, Figs. 3; 7C; 8A) lies on top of a lenticular sandstone body with grey marly lenses rich in fossil remains, separated from the underlying dinosaur-bearing Reptile Sandstone by 3m of red lutites. The base of the lenticular sandstone body contains an oncolite layer with intermediate-sized oncoïds (FO4, Figs. 3; 7A, B). FO4 is situated just below the first Palaeocene fossils (“fish level”) mentioned above, a few centimetres below the “z” layer with the large and giant oncoïds (López-Martínez *et al.*, 1998). The “z” layer at Fontllonga has been sampled at three different sites: FO5(1), FO5(2), and FO5(3) (Fig. 8A), which are separated by normal faults.

The “z” layer can be followed across various localities of the Àger syncline, being particularly well developed in the sections of Mas d’Endalt, Aïmar, la Vall d’Ariet (LV1), and la Vall d’Ariet West (LV2) near the town of Sta. Maria de Meià, as well as la Maçana and Club Nàutic (Figs. 3; 4B-C; 5; 7C-F; 8; 9). The largest oncoïds reach more than 1.5m minimum diameter, and specimens reaching 0.6m minimum diameter are relatively common. In contrast with large oncoïds described from other epochs, these have thick microbial coatings (*i.e.*, the size of the nucleus is negligible). Additionally, extensive stromatolitic crusts occur on top and around the uppermost oncoïds (observed at la Maçana, Aïmar and Mas d’Endalt sections, Figs. 4C; 8C; 9A). This layer can be more than 1.5m thick (Fig. 4), with the oncoïds embedded in siliciclastic-hybrid sandstones (FO, LM, LV1) or red clays (Aïmar).

The uppermost part of Unit 2 above the “z” layer, where carbonate and evaporite sedimentation dominates, does not show any other oncolite layers.

iii) The Upper Danian Unit 3 has a very scarce microbialite record despite being a carbonate-rich deposit from transitional environments, favourable for microbial development. Only the presence of microbial mudstones in the eastern sector of the Tremp syncline and packstones of oncoïds in the Coll de Nargó syncline have been recorded

(López-Martínez *et al.* 2006a, fig. 1). Upsection, the Upper Palaeocene Unit 4 has noteworthy amounts of microbialites in the Àger (Coll d’Orenga section, Figs. 5; 10), Tremp (Morror, see Soler-Gijón *et al.*, 2003), Serres Marginals (Fontdepou), and Vallcebre (Campllong I and II) sectors. In all these sectors, however, the oncoïds are sparse or grouped in marly or limestone oncolite and stromatolite lenses. According to Rossi (1993), Upper Palaeocene stromatolites and oncoïds in the Àger sector developed at the margins of mixed carbonate-evaporite coastal lakes.

Clearly, the extensive microbialite “z” layer of the Àger sector is unique because of its extensive lateral continuity, the giant and huge oncolite sizes, and due to its development within a terrigenous siliciclastic deposit.

DESCRIPTION OF ONCOIDS

Microbialites below the “z” layer

Fontllonga - FO1, FO2, FO3

The oncoïds pertaining to the lower layers (FO1, FO2, and FO3) are small (Figs. 5; 11; Table 1). Discoid and irregular ovoid shapes predominate in FO1 and FO2 oncoïds; subcylindrical-to-ovoid shapes are mainly common in FO3. Surfaces are smooth to slightly tubercular (Fig. 6A). In general, they develop on nuclei made up of bioclasts (charophyte, ostracod, and gastropod fragments) and micritic masses. Cortex spaces are filled with cement (spatic calcite) and terrigenous contribution is negligible (Fig. 6B, D, E). The nuclei of the FO3 oncoïds in many cases are gastropod shells and include a few scarce grains of detrital quartz and small lamellar twinning of authigenic gypsum. The FO3.2 sample is different in that it has a nucleus principally composed of terrigenous elements (quartz with wavy extinction, altered feldspars, chert, fragments of metamorphic rock, micas and tourmalines), in addition to pellets. The FO2.1 oncolite sample contains fragments of vertebrate eggshells.

Lamination in oncoïds is indicative of cyclical cyanobacterial growth, controlled by variations in different environmental factors such as detrital input, luminosity, salinity, and temperature. Light-coloured laminations are interpreted for this case as having formed during periods of more active cyanobacterial growth. Clear waters supersaturated in CaCO₃ and with high luminosity favoured the growth of vertical cyanobacterial filaments, forming microdomes. The dark laminations presumably represent unfavourable growth periods, with filaments mainly showing a horizontal pattern because of a decrease in luminosity and/or increasingly turbid conditions (Chafetz and Buczynski, 1992; Seong-Joo *et al.*, 2000).

In our case, the cortex is no more than 15mm thick. Microscopically, oncoids have zones of dense microfabric

and continuous calcitic lamination, made up of micrite with alternating light and dark bands as a result of fluctuating

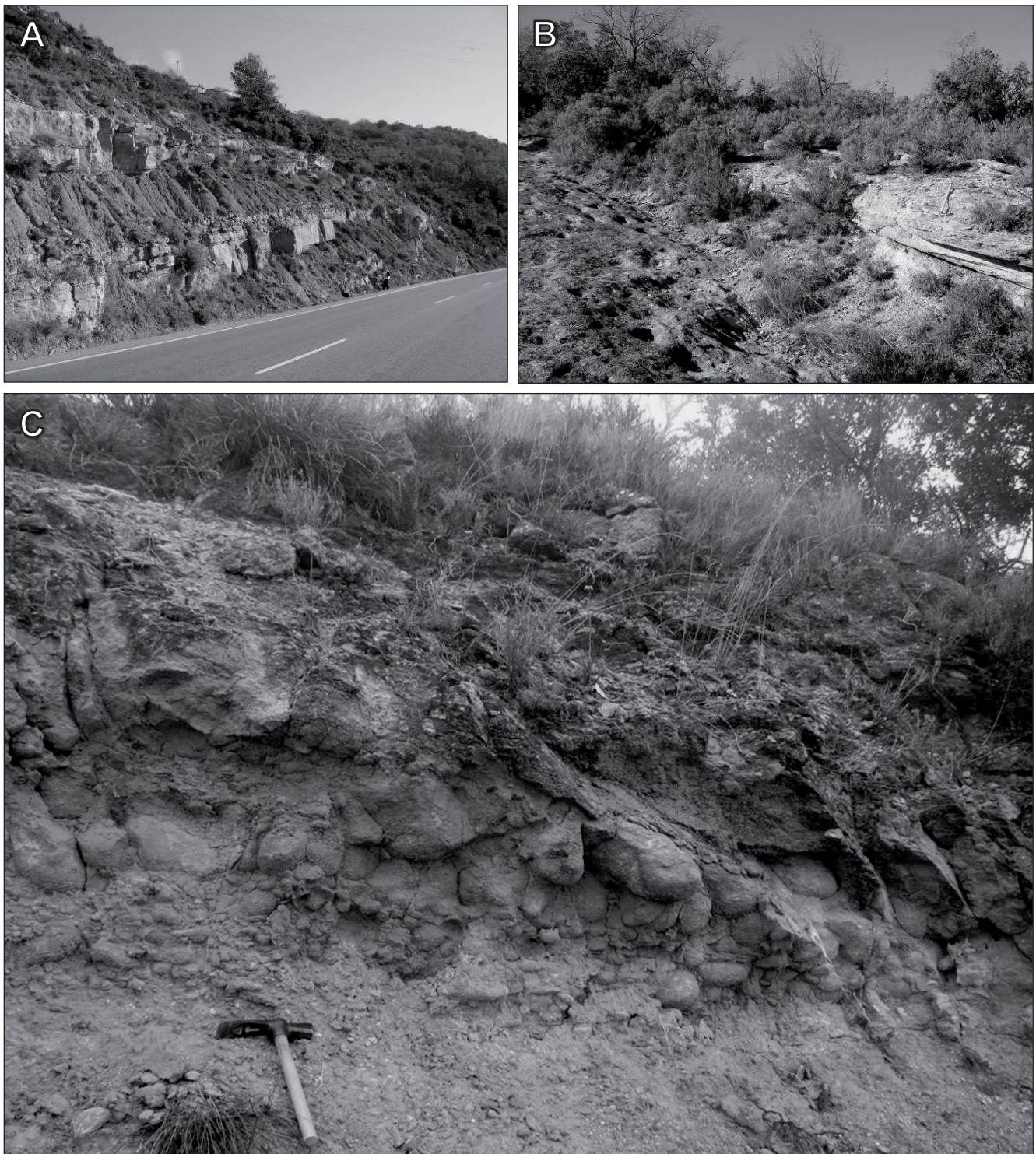


FIGURE 4 | Field view of oncooid layers, Àger syncline. A) Alternating reddish sandstones and mudstones containing FO2 layer, middle part of Unit 2 of the Tremp Formation, Fontllonga section. B) Intensely dinoturbated "Reptile Sandstone" (bottom left), marly interval at the K/T boundary, and oncooid "z" layer (LV1) at the top right stratum, upper part of Unit 2 in la Vall d'Ariet section (Sta. Maria de Meià). C) Oncooid "z" layer (LM), la Maçana section (hammer length= 30cm).

	Microbialites below the "z" layer (FO1, FO2, FI, FO3)	Microbialites at the "z" layer (FO4, FO5, LV1, LV2, LM)	Microbialites above the "z" layer (CO)	
Morphological criteria	Size (minimum diameter, cm)	small, 0.4 to 3.8	small, 0.5 to 7.4	
	Shape	discoidal and irregular ovoid (FO1, FO2), "ear-shaped" (FI), subcylindrical (FO3)	"ear-shaped", "swallow-nest", ovoid and sub-spherical	subcylindrical, ovoid
	Surface	smooth to slightly tubercular	rough surface or very wrinkled (pustular, rough warty) plastic deformation	smooth to slightly tubercular
	Nucleus	bioclasts and micritic masses (FO1), vertebrate eggshel fragments (FO2.1), isolated Unionidae valves (FI), gastropod shells, detrital quartz, authigenic gypsum (FO3), terrigenous (grainstone) (FO3.2)	isolated Unionidae valves (dissolved), occupied by prismatic sparite	wood remains, twigs
Cortex configuration and composition	Lamination type	wavy with alternating light and dark laminae, towards the periphery occasional "microdomes", fenestrae with quartz and <i>Microcodium</i>	wavy, domed and columnar, large elongated fenestrae with terrigenous (quartz, apatite, anhydrite)	wavy and domed
	Microfabric	micritic laminations, loosely clustered, bush-like and/or fan-shaped microbial structures, spherulites of iron (from framboidal pyrite), spaces cemented with spatic calcite or microsparite	micritic laminations, bush-like and/or fan-shaped microbial structures, spherulites of iron (from framboidal pyrite)	micritic laminations, microbial filamentous structures
	Microencrusters	no fauna associated	no fauna associated	no fauna associated
Surrounding sediment	Classification	mudstones and marls	sandstones	mudstones, limestones and evaporites
	Environment	continental, peritidal coastal lakes	estuarine environment, point bar-oxbow lake deposit	mixed carbonate-evaporite coastal lakes

FIGURE 5 | Classification of oncoids in the Tremp Formation (Åger syncline): Morphological criteria, cortex configuration and composition, surrounding sediment and depositional conditions are summarized.

organic contents (Fig. 6B). Wavy or irregular, crinkled dentate and micro-domal lamination (50–150µm thick) can be observed. Microdomes are more abundant towards the oncoid periphery, with elongate fenestrae developing between them, occupied by small detrital grains (quartz, micas, etc.) and bioclasts (*Microcodium* prisms). Loosely clustered and bush-like and/or fan-shaped fossil microbial filamentous structures are conserved (Fig. 6C-F). Stylolite development features and small spherulites of iron oxide are observed.

Other sections

In Orcau and Farfanya, the oncoids are also small, with subcylindrical, ovoid and discoid forms, as in FO1, FO2, and FO3. In Figuerola, Serra d'Agulló, and in one of the Coll de Pradell layers, the oncoid nuclei are unionid valves that have been dissolved by diagenesis; but the lamination is tighter and the thickness of the microbialite coating is modest (4–20mm).

Microbialites at the "z" layer

Fontllonga - FO4, FO5

These two oncoid layers correspond to the bottom and top sets of a mixed sandstone-marly unit showing lateral accretionary bodies with sigmoidal strata that pinch out laterally, interpreted as a point bar-oxbow lake deposit. The grey marly lens contains the Fontllonga-3 vertebrate

remains dated as earliest Danian (Domingo *et al.*, 2007; López-Martínez *et al.*, 2009).

Oncoids in this unit, particularly those from FO5 ("z" layer), are noticeably larger than those from the underlying layers, and some can reach large sizes (large oncoids, 100–400mm) (Figs. 5; 8A; 11; Table 1). Their surface is wrinkled (rough surface) or very wrinkled (knobby to tuberculate). Many are ear-shaped ("ear" oncoids, with a concave groove) due to the fact that isolated unionid shells served as the oncoid nuclei. These aragonite valves have disappeared by dissolution, and the space occupied by the shell can be partially or totally collapsed; in the former case, the space void is occupied by prismatic sparite (Fig. 7C, D). This type of nucleus is also common in some lower oncolite layers, such as Figuerola.

On some occasions, these oncoids acquire a form similar to the "swallow-nest" oncoids described by Leinfelder and Hartkoff-Fröder (1990). The Fontllonga oncoids are, however, somewhat more compressed and may exhibit either a concave-down or a concave-up orientation, as observed both in the field and in the laboratory, the cortex of the concave side being similar or thicker than the cortex of the convex side (Fig. 7A, C, D). In some cases, oncoids show plastic deformation.

Microstructurally, the FO4 and FO5 oncoids have predominantly domed and columnar lamination, with

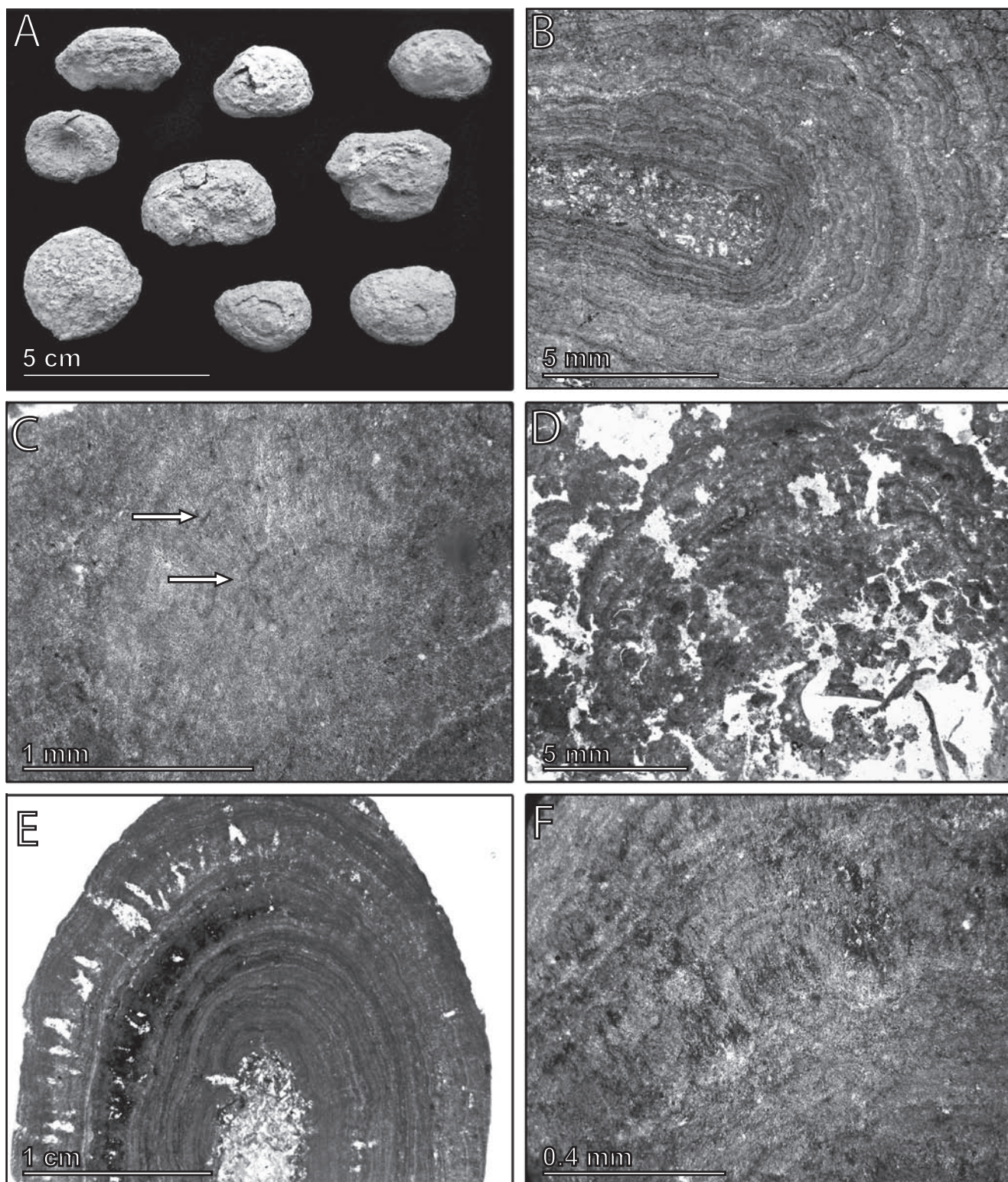


FIGURE 6 | Oncooids from the Fontllonga section (Tremp Formation, Àger syncline). A) F01 layer, top of Unit 1, external view. B, C) sectioned F01 oncoid: wavy or irregular thick lamination and associated microbial fossils (arrows). D) F02 layer, base of Unit 2, sectioned F02 oncoid: wavy and domed lamination. E) F03 layer, middle Unit 2, sectioned F03.1 oncoid showing micritic nucleus with authigenic gypsum, quartz and sparry calcite cement, wavy-crinkled dentate lamination in the internal part of the cortex and development of microcolumns and fenestrae towards the periphery. F) close-up view of microbial fossil filaments in F03.1.

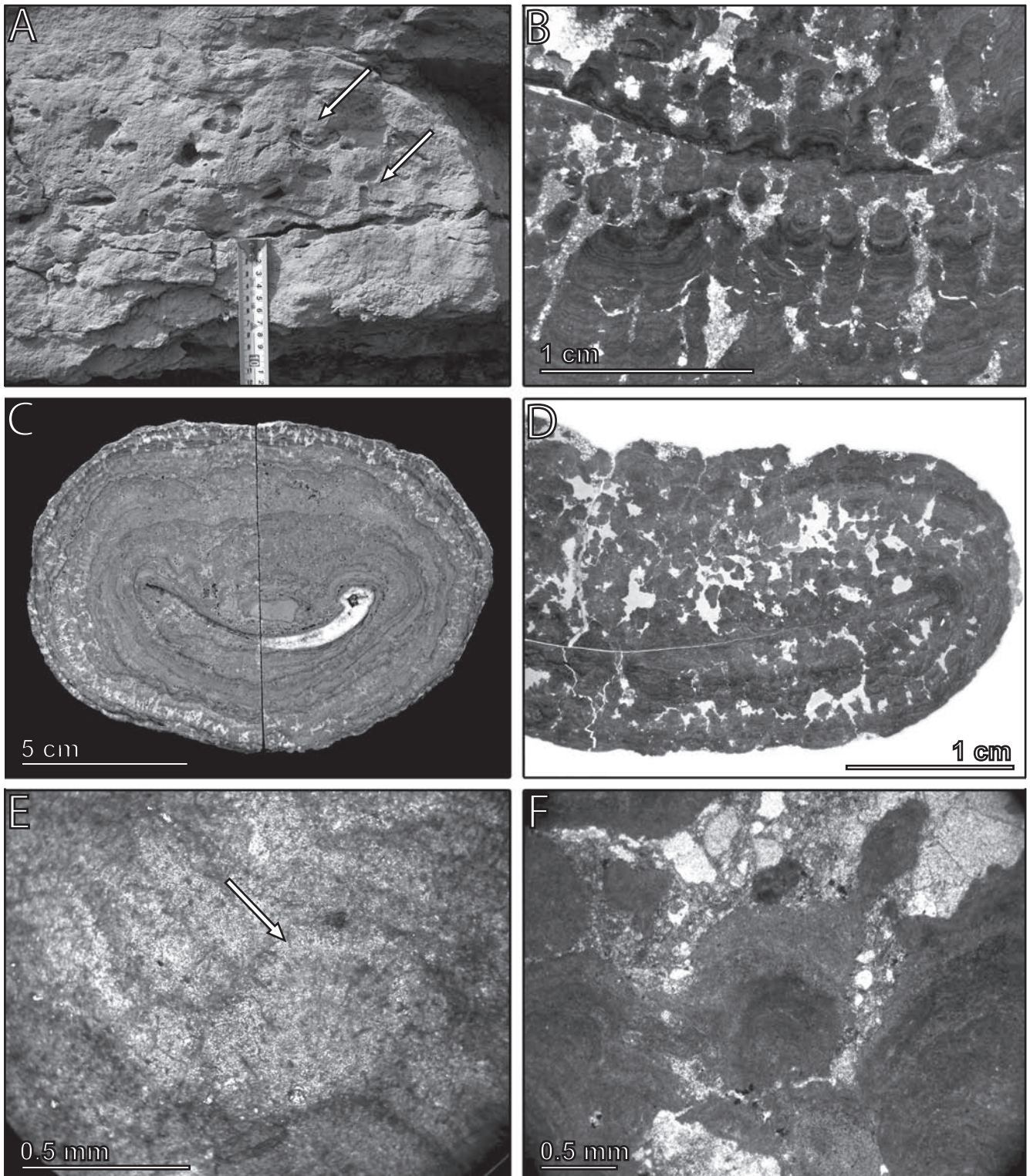


FIGURE 7 | Oncooids from the Fontllonga section, upper part of Unit 2 (Trep Formation, Ager syncline). A) Field view of F04 layer. Note the metastable position of oncooids, with the concavity orientated towards upsection (arrows). B) Thin-section of F04.2 oncooid showing the unionid shell cast, branching colloform growth of laminae, and detrital elements between microcolumns. C) Cross-sectioned F05 oncooid. The nucleus composed of a dissolved unionid valve is visible. D) Section of F05.2 oncooid showing wavy and columnar lamination around the nucleus, originally composed of a unionid valve. E) Close-up view of bush-like or fan-shaped fossil microbial filaments (arrow) in F05.1. F) Thin section showing the well-developed microcolumns limited by fenestrae filled with detrital quartz fragments and calcite cements.

large elongated fenestrae (Fig. 7B). In some zones, wavy lamination occurs, especially close to the nucleus. Spaces between domes are filled with terrigenous elements (quartz with signs of deformation; quartz with anhydrite and apatite inclusions, plagioclase feldspar, and bioclasts). Individual zircons and tourmalines have remained. They contain well-preserved associated bush-like or fan-shaped fossil microbial filamentous structures (*Phormidium*-like and *Schizothrix*-like, see Freydet and Verrecchia, 1998; Fig. 7E). FO4 and FO5 oncoids show no signs of bioerosion.

Radial fractures cemented with spatic calcite and small spherulites of dark ores (originally framboidal pyrite) have precipitated between layers during diagenesis.

Other sections

The characteristics of the oncoids from la Vall d'Ariet section are similar to those reported for FO4 and FO5. The mean oncoid size is notably larger than in FO1–FO3 (Figs. 5; 11; Table 1). Moreover, there are abundant extremely large samples, some showing plastic deformation. In LV1, there is a giant mass of oncoids 3m in diameter, with 1.5m minimum diameter almost exclusively composed of microbial crust (Fig. 8D).

The outcrop of la Maçana is clearly included in the “Reptile Sandstone,” and plainly shows the oncoid stacking pattern in this layer, reaching close to 1.6m in thickness. Large and giant oncoids are extremely abundant. The oncoids clearly increase in size upsection,

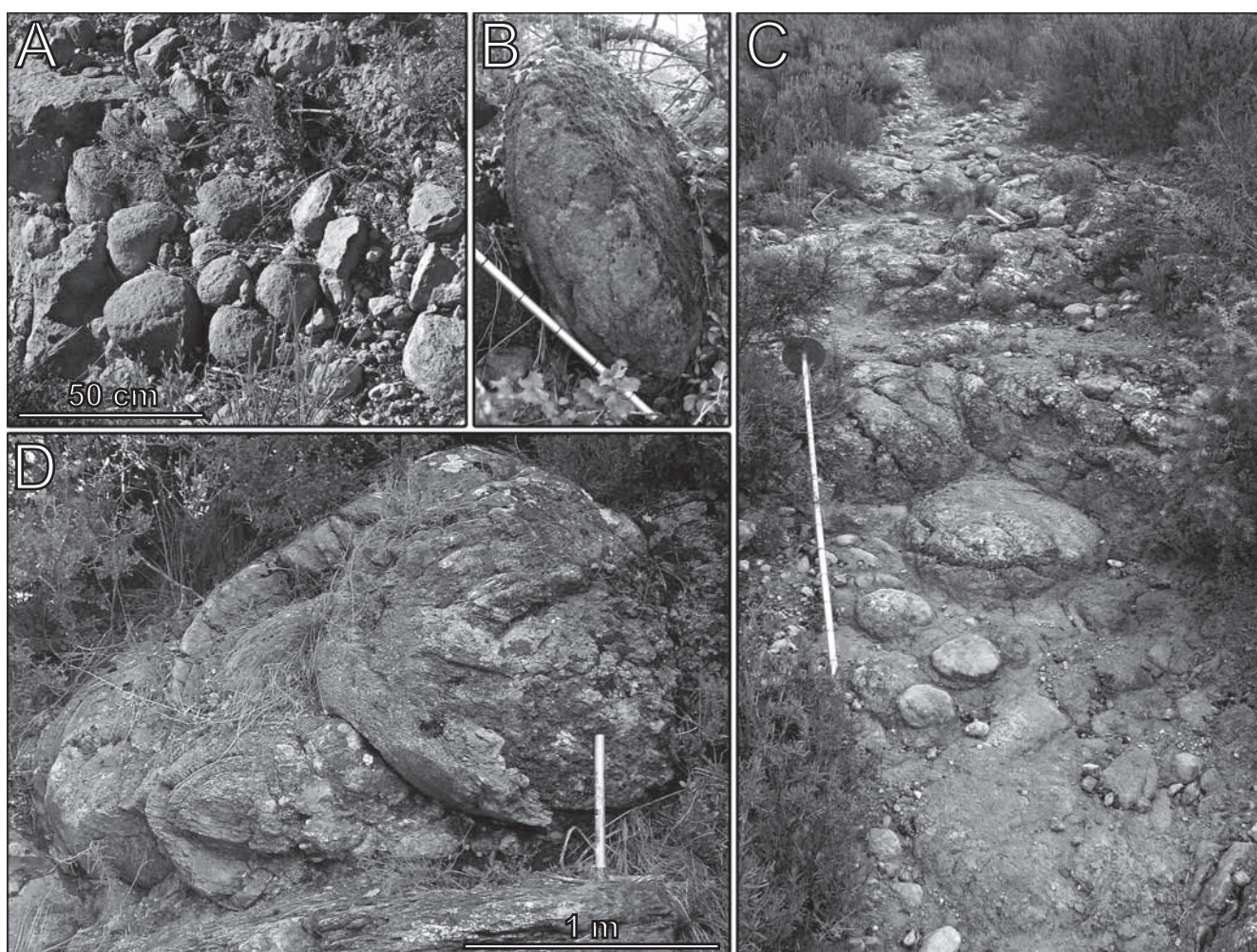


FIGURE 8 | Field views of “z” layer, upper part of Unit 2 (Tremp Formation, Ager syncline). A) Large oncoids, FO5, Fontlloga section. B) Huge oncoid, la Maçana section. Each division of the scale corresponds to 10cm. C) Top of the oncoid-stromatolite “z” layer, la Maçana section. (Scale length=150cm). D) Huge oncoid body, LV1: la Vall d'Ariet section.

with interspaces becoming more and more reduced until they form a continuous microbialite layer, fusing together large oncoids and continuous stromatolite crusts (Figs. 4C; 5; 8B, C; 11; Table 1).

Rather than constituting a laterally transported assemblage, this layer seems to be an in-situ microbial building since lithological heterogeneity is absent, oncoïd size increases from bottom to the top, and scars, fractures, or signs of wear/erosion are absent.

Recently discovered outcrops not yet studied in detail (Club Nàutic -located on the banks of the Camarasa

reservoir, approximately 1km northeast of la Maçana-Aimar in the Àger syncline, and Mas d'Endalt in the Serres Marginals) present a rich concentration of large to huge sub-rounded oncoids entirely made up of microbialite crust, some reaching more than 1m minimum diameter (Fig. 9).

Microbialites above the "z" layer

We have studied an Upper Palaeocene oncolite at Coll d'Orenga and observed additional lenses at Fondpou. Part of the oncolite from Coll d'Orenga is a lens of a continuous stromatolite mass; the other part presents abundant isolated

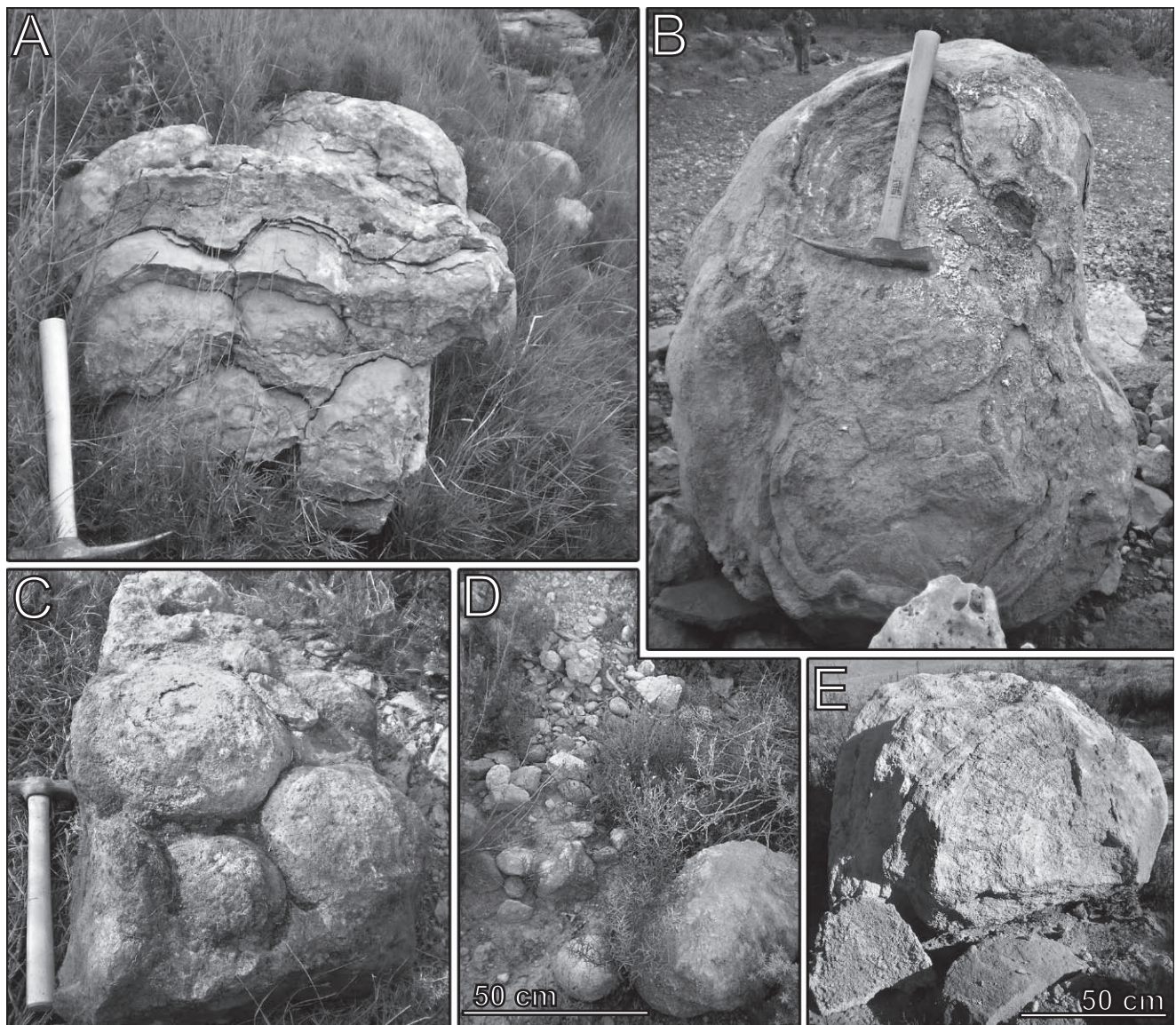


FIGURE 9 | Field views of "z" layer, upper part of Unit 2 (Tresp Formation., Àger syncline). A, B) Large, giant and huge oncoids, Mas d'Endalt section. C) Large oncoids, Aimar section. (Hammer length=30cm). D, E) Large, giant, and huge oncoids, Club Nàutic section.

oncoids that are small, mainly subcylindrical and ovoid in shape (Figs. 5; 10; 11; Table 1). The surface is smooth to slightly tuberculate (rough). The elongated oncoids probably grew around nuclei of little branches and twigs that are not preserved. In most cases, crust thickness does not exceed 5mm. Lamination is wavy and domed, and occasionally slightly wavy in some zones. Fossils of microbial microfilaments can be seen. In Fontdepou, small, subcylindrical oncoids predominate, as in Coll d'Orenga.

DISCUSSION

Oncolite and stromatolite layers occur in upper Cretaceous and early Paleogene coastal and inland deposits of the Tremp Formation, a time span of nearly 17 million years. These oncoids are generally small and occur in marly and limestone deposits. In contrast, the oncoids of the “z” layer occur in terrigenous deposits, mixed siliciclastic-bioclastic sandstones and clays, and are larger on average, with huge maximum sizes (Figs. 5; 11; Table 1). Besides, the “z” layer oncoids tend to encapsulate more terrigenous elements and to have -perhaps as a consequence- a more domed and columnar lamination and a rougher external surface than younger and older oncoids.

The “z” layer oncoids are most highly developed in the la Maçana, Aimar, and Mas d'Endalt sections (Figs. 4C; 8; 9), where they are enclosed in continuous stromatolite layers linking together huge individual oncoids and oncolite masses. The structure of this building is similar to the oncolite “pavement” described by Masari (1983) in the “Ammonitico Rosso” marine sequences (Middle–Upper Jurassic) of the Venetian Alps in Italy. Sometimes, these microbialites were also associated with thin shells or bivalve fragments. However, the microbialite “z” layer developed in non-marine environments and can be even thicker than the above-mentioned Jurassic marine microbial layer.

We therefore postulate that the exceptional microbialite development observed in the “z” layer could be directly related, in terms of cause and effect, to the environmental crisis of the K/T boundary. The following evidence supports this hypothesis:

i) In the Fontllonga and Benabarre sections, the “z” layer coincides with a rapid fall in the $\delta^{13}\text{C}$ carbonate values (López-Martínez *et al.*, 1996, 1998; Fig. 3). In the marine environment, this decrease in $\delta^{13}\text{C}$ values is usually interpreted to represent a fall in organic productivity. In the Fontllonga section, this geochemical anomaly can be closely correlated to the magnetic inversion between chrons C29r and C29n (López-Martínez *et al.*, 1998). Therefore,

this geochemical anomaly coincides with that recorded in other marine and continental sections all around the globe at or immediately after the K/T boundary, which has been interpreted as a sign of an abrupt environmental change in the ecosystems linked to the biotic crisis.

ii) The “z” layer has extensive lateral continuity along the Àger syncline, extending as a guide layer over a distance of at least 54km from the Benabarre to the la Vall d'Ariet outcrops (Figs. 1; 2).

iii) The average size of “z” layer oncoids is much larger than in other layers of the same geological formation. Maximum sampled sizes are much bigger here than in other layers (Fig. 11; Table 1). Moreover, huge individual oncoids and oncolite masses, exclusively made up of pure microbial crust, reach the largest sizes ever reported for such structures. The huge oncolite size here is not determined by the dimensions of the nucleus on which microbial growth is produced. Instead of developing on large nuclei (*e.g.*, big tree trunks; Arenas *et al.*, 2007), the oncoids of the Tremp Formation frequently grew around small bioclasts and micritic masses or on thin unionid valves. The observed size increase seems to be a real trend since: the mean thickness of “z”-layer oncoids -perpendicular to their maximal length, therefore not linked to the unionid size- is greater than that found in other layers (Fig. 11; Table 1); giant and huge oncoids and oncolite masses reaching up to 3m in diameter made up of pure microbial crust can be seen only in the “z” layer (Figs. 4C; 8; 9). The microbialite construction of the “z” layer is similar in structure to those described in marine environments, but larger in size, which is exceptional for non-marine environments.

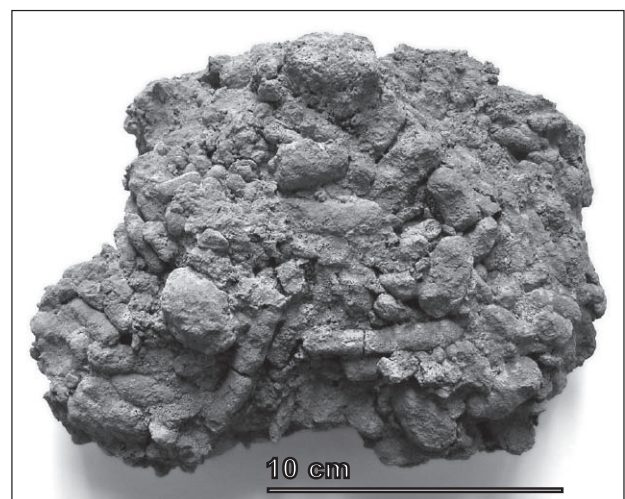


FIGURE 10 | Coll d'Orenga section, oncolite layer, Unit 4 (Upper Palaeocene, Tremp Formation, Àger syncline). External view of CO.2 sample, rudstone of oncoids.

iv) Notably, this impressive assemblage of microbialites occurs within and on top of a siliciclastic deposit (the Reptile Sandstone, in the upper part of Unit 2 of the Tremp Formation) (Figs. 2; 3; 4) instead of in the common carbonate facies favourable for the development of these bio-sedimentary structures.

Therefore, the huge development, widespread extension, and unusual siliciclastic environment of the microbialites in the “z” layer at the Ager syncline, and their coincidence with the geochemical anomaly of the Cretaceous-Tertiary boundary within geomagnetic chron 29r, connect these geobiomarkers as “disaster forms” with this major palaeoenvironmental crisis.

An important question could be raised in relation to this hypothesis: Could a particular depositional environment

favour the formation and accumulation of microbialites instead of being involved in a post-mass extinction scenario as “disaster forms”? Concerning this question, large microbialite structures can be found in diverse circumstances and might not necessarily be witness to a post-mass extinction scenario. For instance, stromatolite-oncolite buildings with oncoids that developed on unionid valves, similar to those in the “z” layer, have been reported by Plaziat (1984) in Lower Eocene continental deposits in the northern Pyrenean-Provençal region (Cuisian-Lutecian of Aude and Hérault). According to this author, large oncoids formed on quiet banks and on top of abandoned fluvial channels. Other cases of oncolites have been studied by Nickel (1983) from the Middle Eocene Guarga formation (Tremp-Graus basin, southern Pyrenees) and by Zamarreño *et al.* (1997) of stromatolites in Upper Palaeocene and Eocene fluvial deposits of the eastern Ebro basin. Their abundance and variety of occurrence (oncoids, domes, laminated crusts, and locally irregular bioherms) were interpreted in hydrodynamic, sedimentological, and palaeoenvironmental terms. Similarly, Arenas *et al.* (2003, 2007) described oncoids in non-marine carbonate deposits that are occasionally gigantic in size (because of their growth around large tree trunks) and stromatolites in Middle Eocene and Oligocene littoral-lacustrine and fluvio-lacustrine deposits from Mallorca island.

However, there are important differences between our “z”-layer microbialites and other Cenozoic continental microbialites, three of which are particularly relevant: the highly continuous “z” layer, in contrast with the generally local and much less extensive microbialite layers in the other cases; the size of the microbial crust, being much larger in the “z” layer than in the largest ones from other cases (see Zamarreño *et al.*, 1997; or Arenas *et al.*, 2007); and the lack of bioerosion signs in the studied samples of “z” layer oncoids, whereas they are present as tubes, pores, and cavities filled with sparite, bored by small organisms in many other cases, such as those reported by Arenas *et al.* (2003, 2007) as flat-convex microspar and spar calcite bodies attributed to insect tubes similar to chironomid larval tubes. The absence of bioturbation features in our “z” layer, together with the abundance of disarticulated unionid valves and the scarcity of other fossils (either trace fossils or body fossils) could indicate a much more stressed environment, compatible with the biotic crisis of the K/T boundary, than the other Cenozoic cases. It is interesting to point out that, in modern freshwater microbialite occurrences, summarized by Gischler *et al.* (2008, table 3), grazer gastropods are always present, in contrast to our microbialites in the “z” layer.

Moreover, as already mentioned, another important difference corroborates our hypothesis that the “z” layer records a major event compared to local Cenozoic micro-

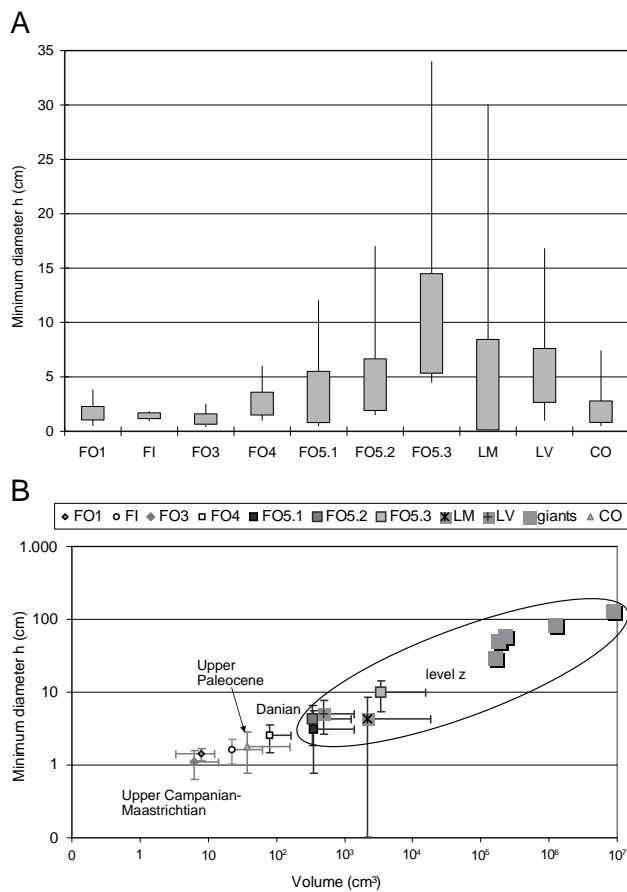


FIGURE 11 | Graphs showing the size distribution of oncoids throughout the Tremp Formation (Ager Syncline, Lleida). A) Minimum diameter (height h, cm); bars represent max, min and mean ± standard deviation. B) Volume (length * width * height, cm³) related to height (h); note the logarithmic scale for volume; negative values of mean-st. dev. are not shown. Values of giant oncoids from the “z” layer (FO5 = LV1 = LM) are not included in A to avoid image distortion. (FO: Fontllonga, FI: Figuerola de Meià, LM: la Maçana, LV: la Vall d’Ariet, CO: Coll d’Orenga). See Table 1.

TABLE 1 | Minimum diameter of oncoids (height, cm) and volume (length*width*height, cm³) from successive layers of the Tremp Formation in the Àger syncline, sections of Fontllonga (FO1, FO3, FO4, FO5), Figuerola (FI), la Maçana (LM), la Vall d'Ariet (LV), and Coll d'Orenga (CO). The “z” layer of López-Martínez *et al.* (1998) corresponds to FO5, LV (LV1, LV2), and LM. In this table giant and huge oncoid dimensions of the “z” layer have not been included

minimum diameter	Up. Camp.		Maast.		lowermost Danian					Up. Pal.
	FO1	FI	FO3	FO4	FO5.1	FO5.2	FO5.3	LM	LV	CO
N	11	100	100	99	51	100	62	101	104	102
Maximum	1.85	3.80	2.50	6.00	12.00	17.00	34.00	30.00	16.80	7.40
Minimum	0.95	0.50	0.40	1.00	0.50	1.50	4.50	0.80	1.00	0.50
Mean	1.41	1.65	1.12	2.72	3.14	4.27	9.90	4.28	5.12	1.78
Standard error	0.08	0.06	0.05	0.21	0.33	0.24	0.58	0.42	0.24	0.10
Standard deviation	0.28	0.63	0.47	2.13	2.37	2.39	4.58	4.18	2.49	1.00
volume	level z									
Maximum	14.67	351.12	43.75	486.00	7,128.00	8,406.50	93,500.00	159,870.00	8,235.36	1,141.30
Minimum	1.86	0.39	0.20	4.50	8.75	7.20	216.00	2.40	2.16	1.15
Mean	7.79	22.37	6.22	267.11	353.77	339.87	3,409.68	2,159.91	485.68	37.86
Standard error	0.08	0.25	0.05	11.81	9.27	5.68	94.15	99.33	5.51	0.76
Standard deviation	4.44	39.35	7.79	1,883.99	1,056.01	906.29	11,822.47	15,919.64	896.49	121.76

Up. Camp: Upper Campanian; Maast: Maastrichtian; Up. Pal: Upper Paleocene

bialite layers described in previous works. This difference derives from the fact that the “z”-layer microbialites are found within a mostly siliciclastic unit. In contrast, all other continental microbialites (Palaeogene of Mallorca, Pyrenean, and eastern Ebro basin) have been found in carbonate rocks.

Consequently, we propose that the “z”-layer microbialites of the Tremp Formation are “disaster forms” after a major palaeoenvironmental crisis linked to the $\delta^{13}\text{C}$ anomaly after the K/T boundary mass-extinction event (Erwin, 1997, “a Precambrian scenario”).

Moreover, the important local microbialite records reported by previous authors in continental Palaeogene deposits could also be related to environmental crises in addition to being linked to specific environmental and sedimentological contexts. They might be associated with climatic and biotic changes around the Palaeocene/Eocene boundary (the highest global temperatures of the entire Cenozoic), Eocene hyperthermals, and the Eocene-Oligocene transition (cooling and climatic continentalization) (Miller *et al.*, 1987; Hooker *et al.*, 2004; Zanzazi *et al.*, 2006; Zachos, *et al.*, 2008), and they could also be indicators of a stressed environment following critical episodes of mass deaths. However, the $\delta^{13}\text{C}$ values of the Palaeogene continental microbialites reported in other areas do not represent any anomalies within the sedimentary context in which they occur (Zamarreño *et al.*, 1997; Arenas *et al.*, 2007).

The absence of extensive microbialite deposits linked to the K/T boundary in other parts of the world has been noted by authors when testing the significance of these geobiomarkers as “disaster forms” (Riding, 2005, 2006).

An explanation for this generalized absence is proposed. On the one hand, the abundance of carbonate-shelled organisms in Cretaceous seas has been invoked as a factor of Ca^{+2} depletion that hampered marine microbial calcification (Arp *et al.*, 2001). Coastal and inland environments (richer in Ca^{+2}) could therefore have been an alternative for calcimicrobial development, which would explain its development in the non-marine Tremp Formation. On the other hand, the metazoan mass extinction after the Cretaceous-Tertiary crisis would favour the release of Ca^{+2} and microbialite development. However, microbial calcification could have been impeded by the acidic marine waters linked to the “z” event (volcanism, winter impact, etc., Pope *et al.*, 1998) in the post-impact scenario.

CONCLUSIONS

The extensive “z”-layer microbialites in the continental Tremp Formation (huge oncoids and stromatolites made up of thick microbial crusts), which occur in relation to the K/T boundary recorded by magneto- and chemostratigraphy in the Àger syncline and Benabarre (south-central Pyrenees), are here attributed to the biotic crisis that occurred during this critical episode of Earth’s history. Other interpretations, such as a relationship between oncoid size and nucleus size, or a connection with local, particularly extreme conditions, or elevated concentrations of carbonate in surrounding waters, can be discarded. These microbialites therefore represent “disaster forms,” witnessing an interval depleted of eukaryotic life during the recovery of devastated ecosystems.

Our report would consequently be the first to document extensive microbialite formations in relation to the biodi-

versity crisis of the K/T boundary. Up to now, all studies describing the proliferation of microbialites after a global biodiversity crisis have been carried out on marine environments. This paper thus represents the first case in which the record of a similar process is reported for continental environments. The K/T boundary crisis would thus be indicated by microbialite proliferation on land rather than in the sea, probably hampered by the acidic environment in the post-impact scenario as well as the significant siliciclastic inputs that dominated the latest Cretaceous platform demises in many regions.

It is usually more difficult to detect past ecological crises in continental deposits than in marine ones due to more gaps and lack of palaeontological and geochemical signals in the continental record than in the marine one. In this regard, we propose that specific, important layers of microbialites (“disaster forms”) may constitute a record of such events and could help to detect biotic crises in continental series. More detailed research will provide more solid proof of this and related hypotheses aiming to reveal the multiple connections within geobiological processes.

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REFERENCES

- Álvarez-Sierra, M.A., Arribas M.E., Ardèvol, L., Civis, J., Daams, R., Krauss, S., López-Martínez, N., De La Peña, A., Soler, R., Vianey-Liaud, M., Lacasa, A., Marandat, B., Peláez-Campomanes, P., Sevilla, P., Sigé, B., 1994. El límite Cretácico-Terciario en la sección de Fontllonga (cuenca de Àger, provincia de Lérida). *Jaca (Spain)*, II Congreso del Grupo Español del Terciario, Comunicaciones, 23-26.
- Ardèvol, L., Klimowitz, J., Malagón, J., Nagtegaal, P.J.C., 2000. Depositional sequence response to foreland deformation in the Upper Cretaceous of the Southern Pyrenees, Spain. *American Association of Petroleum Geologists Bulletin*, 84(4), 566-587.
- Arenas, C., Cabrera, L., Ramos, E., 2003. Fluvial-lacustrine microbialites from the Cala Blanca Formation (Oligocene, Mallorca, Western Mediterranean). In: Valero-Garcés, B.L. (ed.). *Limnogeology in Spain: A tribute to Kerry R. Kelts*. Madrid (Spain), Consejo Superior de Investigaciones Científicas (CSIC), Colección Biblioteca de Ciencias, 119-150.
- Arenas, C., Cabrera, L., Ramos, E., 2007. Sedimentology of tufa facies and continental microbialites from the Paleogene of Mallorca Island (Spain). *Sedimentary Geology*, 197, 1-27.
- Arp, G., Reimer, A., Reitner, J., 2001. Photosynthesis-Induced Biofilm Calcification and Calcium Concentrations in Phanerozoic Oceans. *Science*, 292, 1701-1704.
- Baceta, J.I., Pujalte, V., Serra-Kiel, J., Robador, A., Orue-Etxebarria, X., 2004. El Maastrichtiense final, Paleoceno e Ilerdiense inferior de la Cordillera Pirenaica. In: Vera, J.A. (ed.). *Geología de España*. Madrid (Spain), Sociedad Geológica de España-Instituto Geológico y Minero de España, 308-313.
- Baud, A., Richoz, S., Marcoux, J., 2005. Calcimicrobial cap rocks from the basal Triassic units: western Taurus occurrences (SW Turkey). *Comptes Rendus Palevol*, 4, 569-582.
- Baud, A., Richoz, S., Pruss, S., 2007. The Lower Triassic anachronistic carbonate facies in space and time. *Global and Planetary Change*, 55, 81-89.
- Castle, J.W., Rodgers, J.H., 2009. Hypothesis for the role of toxin-producing algae in Phanerozoic mass extinctions based on evidence from the geologic record and modern environments. *Environmental Geosciences*, 16(1), 1-23.
- Chafetz, H.S., Buczynski, C., 1992. Bacterially induced lithification of microbial mats. *Palaios*, 7, 277-293.
- Díaz Molina, M., 1987. Sedimentación sintectónica asociada a una subida relativa del nivel del mar durante el Cretácico superior. In: Sanz, J.L. (ed.). *Geología y Paleontología (Arcosaurus) de los yacimientos cretácicos de Galve (Teruel) y Tremp (Lérida)*. Estudios Geológicos, Special Volume, 69-93.
- Domingo, L., López-Martínez, N., Soler-Gijón, R., Grimes, S.T., 2007. A multi-proxy geochemical investigation of the early Paleocene (Danian) continental palaeoclimate at the Fontllonga-3 site (South Central Pyrenees, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 256, 71-85.
- Eichenseer, H., 1988. Facies geology of Late Maastrichtian to Early Eocene coastal to shallow-marine sediments, Tremp-Graus basin, Northeastern Spain. Doctoral Thesis. Tübingen, University of Tübingen, unpublished, 237pp.
- Fernández-Marrón, M.T., López-Martínez, N., Fonollá-Ocete, J.F., Valle-Hernández, M.F., 2004. The palynological record across the Cretaceous-Tertiary boundary in differing palaeogeographical settings from the southern Pyrenees, Spain. In: Beaudoin, A.B., Head, M.J. (eds.). *The Palynology and Micropaleontology of Boundaries*. London, Geological Society, 230 (Special Publications), 243-255.
- Fischer, A.G., Arthur, M.A., 1977. Secular variation in the pelagic realm. In: Cook, H.E., Enos, P. (eds.). *Deep-water carbonate environments*. Society of Economic Paleontologists and Mineralogists, 25 (Special Publications), 19-51.
- Flügel, E., 2004. *Microfacies of Carbonate Rocks. Analysis, Interpretation and Application*. Berlin, Springer-Verlag, 976pp.
- Freeman, T., Rosell, J., Obrador, A., 1982. Oncolites from lacustrine sediments in the Cretaceous of north-eastern Spain. *Sedimentology*, 29, 433-436.

- Freytet, P., Verrecchia, E.P., 1998. Freshwater organisms that build stromatolites: a synopsis of biocrystallization by prokaryotic and eukaryotic algae. *Sedimentology*, 45, 535-563.
- Galbrun, B., Feist, M., Colombo, F., Rocchia, R., Tambareau, Y., 1993. Magnetostratigraphy and biostratigraphy of Cretaceous-Tertiary continental deposits, Àger basin, province of Lerida, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 102, 41-52.
- Gischler, E., Gibson, M.A., Oschmann, W., 2008. Giant Holocene Freshwater Microbialites, Laguna Bacalar, Quintana Roo, Mexico. *Sedimentology*, 55, 1293-1309.
- Hooker, J.J., Collinson, M.E., Sille, N.P., 2004. Eocene-Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. London, *Journal of the Geological Society*, 161, 161-172.
- Kershaw, S., Li, Y., Crasquin-Soleau, S., Feng, Q., Mu, X., Collin, P.-Y., Reynolds, A., Guo, L., 2007. Earliest Triassic microbialites in the South China block and other areas: controls on their growth and distribution. *Facies*, 53, 409-425.
- Kiessling, W., 2002. Secular variations in the Phanerozoic reef ecosystem. In: Kiessling, W., Flügel, E., Golonka, J. (eds.). *Phanerozoic Reef Patterns*. Society of Economic Paleontologists and Mineralogists, 72 (Special Publications), 625-690.
- Krauss, S., 1990. Stratigraphy and facies of the "Garumnian" - Late Cretaceous to Early Paleogene - in the Tremp region, Central Southern Pyrenees. *Tübingen Geowissenschaft Arbeiten*, 11, 1-152.
- Leinfelder, R.R., Hartkoff-Fröder, Ch., 1990. In situ accretion mechanism of concavo-convex lacustrine oncoids ("swallow nests") from the Oligocene of the Mainz Basin, Rhineland, FRG). *Sedimentology*, 37, 287-301.
- Lehrmann, D.J., 1999. Early Triassic calcimicrobialmounds and biostromes of the Nanpanjiang basin, south China. *Geology*, 27, 359-362.
- Llompert, C., Krauss, S., 1982. Restos de moluscos y dinosaurios en formaciones estromatolíticas garumnienses al S. del Montsec (Prov. de Lérida). *Boletín Geológico y Minero*, 93, 371-378.
- López-Martínez, N., Ardèvol, L., Arribas-Mocoroa, M.E., Civis, J., González-Delgado, J.A., 1996. Transición Cretácico-Terciario en depósitos continentales de la cuenca de Tremp-Graus: datos preliminares de isótopos estables de C y O. *Geogaceta*, 20(1), 62-65.
- López-Martínez, N., Ardèvol, L., Arribas, M.E., Civis, J., González-Delgado, A., 1998. The geological record in non-marine environments around the K/T boundary (Tremp Formation, Spain). *Bulletin de la Société Géologique de France*, 169(1), 11-20.
- López-Martínez, N., Arribas, M.E., Robador, A., Vicens, E., Ardèvol, L., 2006a. Los carbonatos danienses (Unidad 3) de la formación Tremp (Pirineos sur-centrales): paleogeografía y relación con el límite Cretácico-Terciario. *Revista de la Sociedad Geológica de España*, 19(3-4), 213-255.
- López-Martínez, N., Dinarès-Turell, J., Elez, J., 2006b. Chronostratigraphy of the continental Paleocene series from the South Central Pyrenees (Spain): new magnetostratigraphic constraints. In: Caballero, F., Apellaniz, E., Baceta, J.I., Bernaola, G., Orue-Etxebarria, X., Payros, A., Pujalte, V. (eds.). *Climate and Biota of the Early Paleogene*. Bilbao, University of the Basque Country, Volume of Abstracts, 83.
- López-Martínez, N., Fernández-Marrón, M.T., Valle, M.F., 1999. The succession of vertebrates and plants across the Cretaceous-Tertiary boundary in the Tremp Formation, Àger valley (South-central Pyrenees, Spain). *Geobios*, 32(4), 617-627.
- López-Martínez, N., Galobart, À., Vicens, E., 2009. Upper Cretaceous continental deposits of South-eastern and South-central Pyrenees. In: Alcalá, L., Royo-Torres, R. (eds.). *Mesozoic Terrestrial Ecosystems in Spain*. *Fundamental Teruel*, 14, 1-91.
- Mary, M., Woods, A.D., 2008. Stromatolites of the Lower Triassic Wash Formation, CA: Evidence for Continued Post-Extinction Environmental Stress in Western North America through the Spathian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 261, 78-86.
- Massari, F., 1983. Oncoids and Stromatolites in the Rosso Ammonitico Sequences (Middle-Upper Jurassic) of the Venetian Alps, Italy. In: Peryt, T.M. (ed.). *Coated Grains*. Berlin, Springer-Verlag, 358-366.
- Mayr, C., Thümmel, B., Windmaier, G., Altenbach, A.V., Köhler, H., Tiedemann, R., 1999. New data about the Maastrichtian/Danian transition in the Southern Pyrenees (Àger Basin, Catalonia, Spain). *Revista Española de Micropaleontología*, 31(3), 357-368.
- Miller, K.G., Fairbanks, R.G., Mountain, G.S., 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. *Paleoceanography*, 2, 1-19.
- Nickel, E., 1983. Environmental Significance of Freshwater Oncoids, Eocene Guarga Formation, Southern Pyrenees, Spain. In: Peryt, T.M. (ed.). *Coated Grains*. Berlin, Springer-Verlag, 308-329.
- Oms, O., Dinarès-Turell, J., Vicens, E., Estrada, R., Vila, B., Galobart, A., Bravo, A.M., 2007. Integrated stratigraphy from the Vallcebre Basin (southeastern Pyrenees, Spain): New insights on the continental Cretaceous-Tertiary transition in southwest Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 35-47.
- Pereda-Suberbiola, X., Canudo, J.I., Cruzado-Caballero, P., Barco, J.L., López-Martínez, N., Oms, O., Ruiz-Omeñaca, J.I., 2009. The last hadrosaurid dinosaurs of Europe: A new lambeosaurine from the Uppermost Cretaceous of Aren (Huesca, Spain). *Comptes Rendus Palevol*, 8, 559-572.
- Plaziat, J.C., 1984. Le domaine Pyrénéen de la fin du Crétacé à la fin de l'Éocène. *Stratigraphie, paléoenvironnements et évolution paléogéographique*. Doctoral Thesis. Orsay, Université Paris-Sud, 2885, unpublished, 1362pp.
- Pomoni-Papaioannou, F., Solakius, N., 1991. Phosphatic hardgrounds and stromatolites from the limestone/shale boundary section at Prossilion (Maastrichtian-Paleocene) in the Parnassus-Ghiona Zone, Central Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 86, 243-254.

- Pope, K.O., D'Hondt, S.L., Marshall, C.R., 1998. Meteorite impact and the mass extinction of species at the Cretaceous/Tertiary boundary. *Proceedings National Academy Sciences USA*, 95, 11028-11029.
- Pruss, S.B., Bottjer, D.J., Corsetti, F.A., Baud, A., 2006. A global marine sedimentary response to the end-Permian mass extinction: Examples from southern Turkey and the western United States. *Earth-Science Reviews*, 78(3-4), 193-206.
- Pujalte, V., Schmitz, B., Baceta, J.I., Orue-Etxebarria, X., Bernaola, G., Dinarès-Turell, J., Payros, A., Apellaniz, E., Caballero, F., 2009. Redefinition of the Ilerdian Stage (Early Eocene). *Geologica Acta*, 7(1-2), 177-194.
- Riding, R., 2005. Phanerozoic reefal microbial carbonate abundance: comparisons with metazoan diversity, mass extinction events, and seawater saturation state. *Revista Española de Micropaleontología*, 37(1), 23-39.
- Riding, R., 2006. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sedimentary Geology*, 185, 229-238.
- Riera, V., Oms, O., Gaete, R., Galobart, À., 2009. The end-Cretaceous dinosaur succession in Europe: The Tremp Basin record (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 283, 160-171.
- Robador, A., 2005. El Paleoceno e Ilerdiense inferior del Pirineo Occidental: Estratigrafía y Sedimentología. Doctoral Thesis. Leioa-Bilbao, Universidad del País Vasco, unpublished, 456pp.
- Rosell, J., Linares, J., Llopart, C., 2001. El 'Garumniense' preprienaico. *Revista de la Sociedad Geológica de España*, 14, 47-56.
- Rossi, C., 1993. Sedimentología y diagénesis del Paleoceno superior-Eoceno inferior en la Cuenca de Àger (Sierras Marginales, Prepirineo de Lérida). Doctoral Thesis. Madrid, Universidad Complutense, unpublished, 324pp.
- Schmitz, B., Pujalte, V., 2003. Sea-level, humidity, and land-erosion records across the initial Eocene thermal maximum from a continental-marine transect in northern Spain. *Geology*, 31, 689-692.
- Schmitz, B., Pujalte, V., 2007. Abrupt increase in seasonal extreme precipitation at the Paleocene-Eocene boundary. *Geology*, 35, 215-218.
- Schubert, J.K., Bottjer, D.J., 1992. Early Triassic stromatolites as post-mass extinction disaster forms. *Geology*, 20, 883-886.
- Schubert, J.K., Bottjer, D.J., 1995. Aftermath of the Permian-Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 116, 1-39.
- Seong-Joo, L., Browne, K.L., Golubic, S., 2000. On stromatolite lamination. In: Riding, R.E., Awramik, S.M. (eds.). *Microbial Sediments*. Berlin, Springer, 16-24.
- Shackleton, N.J., 1986. Paleogene stable isotope events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 57, 91-102.
- Sheehan, P.M., Harris, M.T., 2004. Microbialite resurgence after the late Ordovician extinction. *Nature*, 430, 75-78.
- Soler-Gijón, R., Recio, C., López-Martínez, N., Arribas, M.E., Cuezva, S., 2003. Registro isotópico de oncolitos continentales del tránsito Cretácico-Terciario (Formación Tremp, Pirineos sur-centrales): Inferencias paleoambientales y paleoclimáticas. Morella, XIX Jornadas de la Sociedad Española Paleontología, Abstracts Book, 161-162.
- Tewari, V.C., Stenni, B., Pugliese, N., Drobne, K., Riccamboni, R., Dolenc, T., 2007. Peritidal sedimentary depositional facies and carbon isotope variation across K/T boundary carbonates from NW Adriatic platform. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 77-86.
- Ullastre, J., Masriera, A., 1983. Le passage Crétacé-Tertiaire dans les régions sud-pyrénéennes de la Catalogne: données nouvelles. *Géologie Méditerranéenne*, 10, 277-281.
- Vicens, E., Ardèvol, L., López-Martínez, N., Arribas, M.A., 2004. Rudist biostratigraphy in the Upper Cretaceous of the Southern Pyrenees, Spain. *Courier Seckenberg*, 247, 113-127.
- Vicens, E., Ardèvol, L., López-Martínez, N., 1999. The Rudists as biostratigraphic markers: an example from the Late Cretaceous of the Southern Pyrenees, Spain. *Erlanger geologische Abhandlungen*, 3, 74-75.
- Whalen, T.W., Day, J., Eberli, G.P., Homewood, P.W., 2002. Microbial carbonates as indicators of environmental change and biotic crises in carbonate systems: examples from the Late Devonian, Alberta basin, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 181, 127-151.
- Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451, 279-283.
- Zamarreño, I., Anadón, P., Utrilla, R., 1997. Sedimentology and isotopic composition of Upper Palaeocene to Eocene non-marine stromatolites, eastern Ebro Basin, NE Spain. *Sedimentology*, 44, 159-176.
- Zanazzi, A., Matthew, J., Kohn, M.J., Macfadden, B., Terry, D.O., 2006. Large temperature drop across the Eocene-Oligocene transition in central North America. *Nature*, 445, 639-642.

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