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Chronostratigraphic synthesis of the latest Cretaceous dinosaur turnover in south-western Europe

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Abstract

In south-western Europe, the uppermost Cretaceous continental deposits in the different sedimentary basins of Iberia (Portugal and north and central Spain), the Pyrenees (Spain and France) as well as Languedoc and Provence (southern France) provide one of the few terrestrial records that allow a comprehensive study of the Campanian-Maastrichtian dinosaur assemblages. For the last years the southern Pyrenees has been the target of intense geological, palaeontological and geochronological research. Hundreds of fossil localities are now framed in high-resolution lithological sections.

The succession of these sites, most of them located in the Tremp Syncline, is based on the physical correlation of rock bodies, as permitted by the general outcropping conditions. Outside this syncline, correlation is supported by geochronologic and biostratigraphic data (mainly magnetostratigraphy and planktic foraminifera biostratigraphy). The integration of the entire dataset sheds new light on the Maastrichtian dinosaur turnover, characterized by a shift from a sauropod-dominated to a hadrosauroid-dominated faunal assemblage. This turnover was progressive and involved immigrants from North America, Eurasia and Gondwana, which probably reached the study area after a sea level drop. This faunal change was mainly triggered by the arrival of lambeosaurine hadrosauroids, a group that rapidly displaced the rest of the herbivorous clades of the region. Some of the extinction events suffered by the “pre-turnover” faunas during the Maastrichtian coincide with marine isotopic and sea-level drop events, suggesting that faunal competition was not the only cause of the observed changes in dinosaur composition. Despite this faunal replacement, the resulting ecosystem after the turnover shows no major loss of biodiversity before the Cretaceous-Paleogene extinction event.

Keywords: Pyrenees; dinosaur succession; Campanian and Maastrichtian stratigraphy; faunal changes

1. Introduction

One of the most important scientific controversies in the history of life concerns the mass extinction that took place at the end of the Cretaceous, approximately 66 million years ago (MacLeod et al., 1997; Brusatte et al., 2015). Since the early 1980s, researchers around the world have tried to decipher how and when this major extinction occurred (Archibald et al., 2010). The most widely accepted hypothesis is that the impact of an asteroid triggered a series of drastic environmental disturbances to ecosystems around the world (Alvarez et al., 1980; Schulte et al., 2010). The literature has also recognized massive volcanic eruptions (Duncan and Pyle, 1988), and changes in temperature and sea level (Miller et al., 2005) among other events that occurred at the end of the Maastrichtian which, isolated or combined (Richards et al., 2015), could have contributed to the extinction of thousands of species.

The most abundant and best-studied record of the terrestrial Cretaceous-Paleogene (K-Pg) boundary is in western North America, where for decades data have been collected and used to establish global hypotheses about the evolution of continental organisms before and after the extinction (Archibald, 2014; Fastovsky and Bercovici, 2016). Beyond this region, very little is known about how end-Cretaceous terrestrial communities were composed at the time when the disturbances occurred, either far away from the impact zone and/or in very different palaeogeographic settings.

Recently, however, the uppermost Cretaceous continental formations of present-day Romania, Spain and France have been systematically prospected, providing new data on their terrestrial vertebrates and ecosystems (Pereda-Suberbiola, 2009; Csiki-Sava et al., 2015). More importantly, new discoveries in the vertebrate-bearing successions of these regions are calibrated by an increasingly more precise and robust chronostratigraphy (e.g. Canudo et al., 2016; Csiki-Sava et al., 2016). This has made these regions, outside North America, among the best in the world to study the evolution of the Late Cretaceous vertebrates during the last ten million years prior to the extinction.

In terms of diversity, ecology and extinction patterns, the continental deposits of southwestern Europe provide one of the few terrestrial records that allow a comprehensive study of the Campanian-Maastrichtian dinosaur assemblages (López-Martínez, 2003;

Riera et al., 2009; Canudo et al., 2016; Vila et al., 2016). A very rich fossil record from hundreds of sites has been documented in the sedimentary basins of Iberia (Portugal as well as north and central Spain), the Pyrenees (Spain and France) as well as Languedoc and Provence (southern France; Fig. 1A). Towards the end of the Cretaceous, these basins, together with the surrounding exposed massifs, formed the Ibero-Armorican Island (Fig. 1B), the largest landmass (150,000-350,000 km²) of the western European archipelago (Philip et al., 2000). In this context, especially remarkable are the faunal changes observed here through the last 5-6 million years of the Cretaceous, and the potential migration events that seem to differentiate the Ibero-Armorican vertebrate assemblages from those of other European islands and from their continental contemporaries in Asia, North America or South America (Company et al., 2009; Pereda-Suberbiola, 2009; Csiki-Sava et al., 2015).

The first attempt to define such faunal changes in the study region within the Maastrichtian succession was carried out by Le Loeuff et al. (1994), who combined the dinosaur occurrences and chronostratigraphy. Since then, the analysis of the Maastrichtian faunal turnover has been successively improved by incorporating novel palaeontological, biostratigraphic and magnetostratigraphic data (e.g. Laurent et al., 2002; Pereda-Suberbiola et al., 2003; Vila et al., 2012, 2013). One of the key advances has been the improvement of the chronostratigraphy and dating of the non-marine formations of the main basins of north-eastern Iberia and southern France (Westphal and Durand, 1990; Galbrun et al., 1993; Ardèvol et al., 2000; López-Martínez et al., 1998, 2000; Garcia and Vianey-Liaud, 2001; Cojan and Moreau, 2006; Oms et al., 2007; Riera et al., 2009; Pereda-Suberbiola et al., 2009a; Vicente et al., 2015, 2016a, b; Corral et al., 2016; Fondevilla et al., 2016a, b; Puértolas-Pascual et al., 2018). The recent works carried out in the southern Pyrenees by Díez-Canseco et al. (2014) and Fondevilla et al. (2016a) have significantly improved the previous age constraints in the most famous basin, the Tremp Syncline, Catalonia (Fig. 1C). Such works provided accurate dating of tens of key fossil sites around the time interval in which the Maastrichtian faunal turnover took place. In light of these results, we review and update here the integrated stratigraphy (litho- and magnetostratigraphy) and the uppermost Cretaceous sedimentary successions of the southern Pyrenees, with special emphasis on those from the Tremp Syncline. We also gather all the newly available palaeontological and chronostratigraphical data from all the Ibero-Armorican localities to reappraise the

chronostratigraphic position of some of the most significant dinosaur localities and, therefore, to constrain the timing and duration of the Maastrichtian dinosaur turnover across the entire Ibero-Armorican region in the last 6 millions of years of the Cretaceous.

2. The chronostratigraphic framework of the Maastrichtian deposits in the southern Pyrenees

2.1. The transitional and continental units around the Cretaceous-Paleogene transition

The uppermost Cretaceous and lower Paleocene transitional and continental syntectonic deposits from the southern Pyrenees were first identified as ‘Garumnian’ following the work of Leymerie (1868) (see historical summary in Rosell et al., 2001). This informal nomenclature was later defined as Tremp Formation (Fm) by Mey et al. (1968) (Fig. 2). The unit was deposited atop the Campanian-Maastrichtian Arén Sandstone Formation (Mey et al., 1968) and its equivalents (e.g. the Les Serres Limestone Fm, Souquet, 1967).

Rosell et al. (2001) divided the former ‘Garumnian’ into four lithostratigraphic units (Fig. 2), which are from base to top: 1) the Grey Garumnian, a succession of grey marls and sandstones, limestones and coals with abundant invertebrate fauna. It has been interpreted as a transitional marine-to-continental setting that included swamp, lagoonal and tidal mudflat environments (Nagtegaal, 1972; Liebau, 1973; Díaz Molina, 1987; Cuevas, 1992; Rosell et al., 2001; Riera et al., 2009, 2010; Riera, 2010; Oms et al., 2016). The unit has been dated as early Maastrichtian following bio- and magnetostratigraphic studies (Rosell et al., 2001; Villalba-Breva et al., 2012; Oms et al., 2007), though it becomes younger towards the west due to facies migration during a regressive context (Liebau, 1973; Riera et al., 2009; Vila et al., 2013); 2) the “Lower Red Garumnian”, an alternation of brown, ochre and reddish marls with sandstones traditionally interpreted as fluvial deposits (Díaz-Molina, 1987; Cuevas, 1992; Rosell et al., 2001; Riera et al., 2009), but has also been considered as having formed in a perilagoonal environment (Eichenseer, 1988). More recently, the coastal origin of these deposits has been reinforced (Vila et al., 2013; Díez-Canseco et al., 2014; Blanco et al.,

2017). The unit has been dated as Maastrichtian on the basis of charophyte and planktic foraminifera biostratigraphy and magnetostratigraphy (Feist and Colombo, 1983; Galbrun et al., 1993; Rosell et al., 2001; Oms et al., 2007; Díez-Canseco et al., 2014), though the precise positions of these deposits within the Maastrichtian in the Tremp and the Àger synclines has been object of controversy (Fondevilla et al., 2016a; see below). It has been proposed that the K-Pg boundary occurs towards the top of the “Lower Red Garumnian” (Rosell et al., 2001), but other studies have proposed that the impact layer could be absent due to the presence of an important sedimentary hiatus around the K-Pg transition (at least for the Tremp Syncline; e.g. Baceta et al., 2004). In this respect, Díez-Canseco et al. (2014) have demonstrated that the first Paleocene deposits of the eastern Tremp Syncline belong to the upper Danian, implying a long hiatus around the K-Pg transition. The boundary has only been tentatively identified in the Àger Syncline (López-Martínez et al., 1998) using palynological and chemostratigraphic evidence, although no iridium anomaly has been identified so far; 3) the “Vallcebre Limestones and laterally equivalent strata”, represented by micritic limestones interpreted as coastal lake deposits (López-Martínez et al., 2006; Díez-Canseco et al., 2014). The unit can be highly diachronous throughout the different South-Pyrenean synclines. As mentioned above, it has been dated as late Danian in the Tremp Syncline (Díez-Canseco et al., 2014), but in the Vallcebre Syncline the unit is likely early Danian (Oms et al., 2007); 4) the “Upper Red Garumnian”, formed by red mudstones, sandstones and conglomerates interpreted as belonging to fluvial settings (Rosell et al., 2001). It has been dated as Selandian to Thanetian on the basis of its charophyte content and magnetostratigraphy (Galbrun et al., 1993; Vicente et al., 2016a). The Paleocene-Eocene Thermal Maximum has been identified towards the top of the unit in the Tremp Syncline (Schmitz and Pujalte, 2003; Domingo et al., 2009). The marine Eocene deposits of the Figols Group overlay the unit (Rosell et al., 2001). Gómez-Gras et al. (2016) characterized the palaeogeographic evolution of the uppermost Cretaceous formations of the study area, which accumulated in a single E-W oriented basin opened to the Atlantic during the early Maastrichtian. Due to its syntectonic evolution, this basin was progressively fragmented during the Maastrichtian into different sub-basins that correspond to the synclines currently recognized.

For the Tremp Syncline, Cuevas (1992) and Pujalte and Schmitz (2006) redefined the Tremp Fm as Tremp Group, and divided it into different formations that are more or

less equivalent to the informal “Garumnian” units of Rosell et al. (2001). Hence, the La Posa Fm represents the “Grey Garumnian”; the Conques and Talam formations are equivalent to the “Lower Red Garumnian”; the Suterranya and Sant Salvador de Toló Fm is equivalent to the “Vallcebre limestones”; and the Esplugafreda and Claret formations represent the “Upper Red Garumnian”. Colombo and Cuevas (1993) did the same for the Àger Syncline, replacing the Tremp Fm by the Fontllonga Group. In this case, the La Maçana Fm replaces the “Grey Garumnian”; the Figuerola Fm is equivalent to the “Lower Red Garumnian”; the Millà Fm is equivalent to the “Vallcebre limestones”; and the Perauba Complex can be related to the “Upper Red Garumnian”. These units and their equivalences are shown in Figure 2. Despite these formal lithostratigraphic divisions, the terms ‘Garumnian’, ‘Garumnian facies’ and Tremp Fm were widely used by researchers until recently (e.g., López-Martínez et al., 1998; Rosell et al., 2001; Oms et al., 2007; Gómez-Gras et al., 2016).

For an overview of the other Upper Cretaceous continental deposits of south-western Europe (rest of Iberia, southern France and Portugal) see the Supplementary Information text and Supplementary Figures 1-3.

2.2. Updated ages for the dinosaur-bearing sedimentary successions of the southern Pyrenees

In this section we integrate, discuss, and update all available chronostratigraphic data for the Maastrichtian South Pyrenean region and its different synclines in order to update the ages of the known dinosaur sites. We followed four main pieces of evidence for calibration and correlation purposes:

- Presence of non-reworked Maastrichtian planktic foraminifera in all the transitional successions of the Tremp (Díez-Canseco et al., 2014; Puértolas-Pascual et al., 2018) and Vallcebre synclines (Vicente et al., 2015). The identified Maastrichtian planktic foraminifera biozones are consistent with those of the western marine equivalents of Campo (Aragon; López-Martínez et al., 2001; Fondevilla et al., 2016a) and the distal marine deposits of Zumaia (Basque Country; Pérez-Rodríguez et al., 2012).
- Additionally, the Tremp Syncline lithostratigraphic units can be physically tracked towards the laterally equivalent marine units, which are also dated by

means of magneto- and biostratigraphic data (e.g. Ardèvol et al., 2000; López-Martínez et al., 2001 and Canudo et al., 2016; Fondevilla et al., 2016a).

- The available magnetostratigraphic studies carried out in the region provide reversal patterns that are consistent with planktic foraminifera biostratigraphy, allowing accurate correlations between lithostratigraphic units and the Global Polarity Time Scale (GPTS, Ogg and Hinnov, 2012; Oms et al., 2007; Fondevilla et al., 2016a, Canudo et al., 2016; Puértolas-Pascual et al., 2018).
- Additional age calibration support is provided by the occurrence of the *Hippurites radiosus*-bearing shelf (described in Vicens et al., 2004), a key horizon that appears just below the Maastrichtian successions of the study area. This conspicuous level, composed by an association of different rudist species, is identified throughout the different South Pyrenean synclines and has been dated as earliest Maastrichtian by means of strontium (Sr) stable isotopes, with an age between 72 and 71 Ma (Caus et al., 2016) in both Àger and Tremp synclines. In the Vallcebre Syncline, a robust magnetostratigraphic study also indicated a similar age for the rudist-bearing level (Oms et al., 2007). Hence, the *Hippurites radiosus*-bearing horizon has an earliest Maastrichtian age and represents an isochronous marker (as defended in Vicens et al., 2004, Caus et al., 2016 and Oms et al., 2016) or, at least, appears constrained within a very short temporal range between 72 and 71 Ma. The Fumanya Member (Mb), at the base of the La Posa and La Maçana Fm (Fig. 2) usually appears atop the mentioned rudist horizon. This member represents a tidal mudflat recognized over a distance of 40 km and is a reference level to study sauropod ichnology (e.g. Vila et al., 2005). Hence, some authors considered it as an isochronous stratigraphic unit (e.g. Oms et al., 2016).

In order to provide an easy-to-follow overview, the chronostratigraphic and palaeontological revision is arranged by synclines. Each syncline (Figs. 1, 3–5) has geological and palaeontological peculiarities that can be better explained in this way. We integrate 73 stratigraphic sections in different chronostratigraphic panels (Figs. 6–10) combined with the most up-to-date age calibrations. Section 1 is modified from Caus et al. (2016); sections 2, 4, 5, 9, 13, 16–18, 20–24, 26–31, 36, 38, 39 and 41–48 are modified from Riera et al. (2009); section 3 first appeared in Fuentes-Buxó (2012) and has been re-measured here; section 21 is modified from Prieto-Márquez et al.

(2019); sections 25, 32, 33 and 56 appear for the first time in this synthesis; section 6 was published in Fondevilla et al. (2016a) and Blanco et al. (2016), but its lower portion -section 37- was first published in Oms et al. (2014) together with section 35; sections 7, 8, 14, 19, 40 and 59 are modified from Vila et al. (2013); section 10 is modified from Dalla Vecchia et al. (2013); sections 11 and 12 are modified from Marmi et al. (2012); sections 15, 49 and 57 are modified from Riera (2010); section 34 is modified from López-Martínez et al. (2000); section 50 is modified from Blanco et al. (2016); sections 51 and 58 are modified from Gómez-Gras et al. (2016); section 52 is modified from Llompart (2006); section 53 is modified from Pons and Vicens (2006); sections 54 and 55 are modified from López-Martínez and Vicens (2012); sections 60, 62 and 64–73 are modified from Vila et al. (2011); and finally, sections 61 and 63 are modified from Oms et al. (2016).

2.2.1. *The eastern Tremp Syncline (Isona area)*

According to the chronostratigraphic framework of the Isona sector (eastern Tremp Syncline; Fig. 3), published in Riera et al. (2009) and Vila et al. (2012, 2013), the Maastrichtian stage was recorded without significant hiatuses in the eastern Tremp Syncline. However, this proposal was subsequently questioned and updated based on discoveries of Díez-Canseco et al. (2014) and Fondevilla et al. (2016a). Based upon these new data (Figs. 4, 6), the main features of the updated chronostratigraphic framework are:

- The recognition of the planktic foraminifera biozones of *Pseudoguembelina palpebra* and *Planoglobulina acervulinooides* in the northern sector of the Isona area (Díez-Canseco et al., 2014) indicates that most of the stratigraphic succession has an early Maastrichtian age. These biozones are correlated with the lower-middle and the end-part of chron C31r, respectively, in the marine deposits of Zumaia (see Pérez-Rodríguez et al., 2012 and Fig. 4). Hence, the reverse polarity zone identified in Fondevilla et al. (2016a) in the Orcau section (section 6 in Figs. 3 and 6) is calibrated with this chron (Figs. 4, 6). This implies that two-thirds of the transitional-continental sedimentary succession in this sector (the complete La Posa and Conques formations) belong to the early Maastrichtian, instead of the late Maastrichtian as considered by Vila et al.

(2012), Dalla Vecchia et al. (2014) and Sellés and Vila (2015). Most of the late Maastrichtian (chrons C31n to C30n) is not recorded in the sector (Figs. 4 and 6). The correlation levels represented by the rudists-bearing horizons with *Hippuritella castroi* and *Biradiolites chaperi* (Vicens et al., 2004) are thus calibrated with the lower and the mid-upper part of chron C31r (Fig. 6), respectively.

- The sedimentary succession of the central sector of the Isona area (around the villages of Figuerola d'Orcau and Conques, Fig. 3) can be directly correlated with the northern Orcau section following a laterally continuous sandstone unit placed at the base of the Talarn Fm (see it mapped in Fig. 3). The Sant Salvador de Toló and Suterranya Fm, placed at the top of the succession, presents some dating problems. The limestone levels that appear around the Suterranya village belong to the late Danian according to Díez-Canseco et al. (2014), but no accurate ages have been provided for the Sant Salvador de Toló limestone layers yet.
- The southern sector of the Isona area (located in the Noguera Pallaresa Valley at the foothills of the Montsec chain, Fig. 1C and 8) was originally considered late Campanian (Torices-Hernández, 2002). However, the top of the Arén Sandstone Fm and the base of the La Posa Fm cropping out there belong to the early Maastrichtian on the basis of Sr stable isotope geochemistry and the presence of the *Hippurites radiosus*-bearing horizon (Caus et al., 2016; Oms et al., 2016). In addition, the presence of the *Hippuritella castroi* and *Biradiolites chaperi* horizons at the top of the La Posa Fm allows us to consider this entire formation (and the lower part of the overlying Conques Fm) as early Maastrichtian (Fig. 8), likely within chron C31r.

These data imply that several dinosaur-bearing sites previously dated as late Maastrichtian (e.g. Sellés and Vila, 2015; Vila et al., 2016) now belong to the early Maastrichtian (lower and middle part of chron C31r). These include important fossil sites such as Els Nerets, Basturs Poble and Serrat del Rostiar-1 (Fig. 6). In addition, the Montrebei site can be dated as 'mid' early Maastrichtian (Fig. 8), younger than the age indicated in Torices et al. (2015), who considered the site as late Campanian-earliest Maastrichtian.

2.2.2. *The western Tremp Syncline*

This region (from E to W) is represented by the sections of Areny/Arén (Pereda-Suberbiola et al., 2009a), Iscles and Serraduy (Vila et al., 2012, 2013; Puértolas-Pascual et al., 2018) and Campo (Canudo et al., 2016). For these areas, clear magnetostratigraphic and biostratigraphic (planktic foraminifera) constraints and direct geological correlations are both available (Ardèvol et al., 2000; López-Martínez et al., 2001; Fondevilla et al., 2016a; Puértolas-Pascual et al., 2018). The continental record extends across chrons C30n and C29r, thus representing one of the most complete records of the late Maastrichtian in the southern Pyrenees. The most relevant sites are those of Blasi (Areny section), located in the upper part of chron C30n (see Canudo et al., 2016, fig. 2).

2.2.3. *The Coll de Nargó Syncline (Pinyes section)*

The Pinyes succession, located in the Coll de Nargó Syncline (Fig 4A), has yielded the richest dinosaur oological record from Europe. However, this 400 m-thick succession of red mudstones and sandstones has never been accurately dated. Magnetostratigraphic studies in this area have provided no reliable results. Marmi et al. (2016a) and Vicente et al. (2016b) placed the Pinyes succession in the mid-part of chron C31r based on the presence of the *Microchara punctata* charophyte biozone, considered by the authors as a non-basal Maastrichtian marker. This biozone is also found at the base of the La Posa Fm in the Tremp Syncline (Marmi et al., 2016a), which is dated as the earliest part of chron C31r according to Fondevilla et al. (2016a).

Riera (2010) and Riera et al. (2013) considered the Pinyes sedimentary succession as laterally equivalent to the Maastrichtian rocks of the Tremp Syncline, despite the fact that the Bóixols thrust separates these areas (Fig. 1C and 4). The fluvial red beds that characterize the Pinyes section resemble those of the easternmost Isona sector (the Coll de Faidella section, numbered as 56 in Figs. 1C and 6), suggesting an original lateral continuity between the Tremp and Coll de Nargó synclines (Fig. 4). This correlation is reinforced by the presence of the Fumanya Mb and the *Hippurites radiosus*-bearing horizon at the base of the Pinyes succession. Considering this last marker and the

charophyte content, the $\delta^{13}\text{C}$ isotope curve obtained from carbonate nodules from Pinyes (Riera et al., 2013) can be tentatively placed within chron C31r (see below).

2.2.4. The Àger Syncline (Fontllonga section)

The Fontllonga section of the Àger Syncline (Fig. 1C) was the first Maastrichtian succession dated by magnetostratigraphy in the southern Pyrenees. Galbrun et al. (1993) found a reversal pattern in the fluvial Figuerola Fm that was correlated with chrons C32n, C31r, C31n, C30r, C30n, C29r and C29n following the presence of Maastrichtian charophyte species in the local succession. Hence, these authors stated that all the late Maastrichtian chrons were represented in the Figuerola Fm and that it contained the K-Pg transition. The underlying lacustrine La Maçana Fm provided very limited magnetostratigraphic data, but was considered late Campanian in age. Villalba-Breva and Martín-Closas (2013) also dated the formation as late Campanian using charophytes. Nevertheless, its flora content, represented by the *Peckichara cancellata* biozone, is also compatible with an early Maastrichtian age (Villalba-Breva et al., 2012). The Maastrichtian age of the La Maçana Fm is confirmed by the presence of the *Hippurites radiosus*-bearing horizon, with an age between 72 and 71 Ma (Caus et al., 2016, see above) and the identification of the Fumanya Mb at the base of the formation (Oms et al., 2016). Hence, the La Maçana Fm is dated as early Maastrichtian instead of late Campanian. After this age recalibration, the magnetozones found in the Figuerola Fm by Galbrun et al. (1993) represent chrons C31n-C29n instead of chrons C32n-C29n interval. Hence, the latter formation only records the late Maastrichtian (Fig. 8).

The updated age of the Figuerola Fm implies that the Fontllonga-6 site no longer belongs to the base of chron C31r as proposed by Sellés and Vila (2015) as well as Torices et al. (2015). Instead, this site is allocated to chron C30r (late Maastrichtian). The Figuerola-2, -3 and Perauba-Figuerola sites remain in an undeterminate age around the mid-upper part of chron C31r, but are younger than the earliest Maastrichtian age previously proposed by Torices et al. (2015).

2.2.5. The Vallcebre Syncline

The Vallcebre Syncline (Fig. 5) contains the most continuous and well-dated record of the studied region. A well-defined magnetostratigraphy (Oms et al., 2007) between chrons C32n.1n and C29r is recorded here (Fig. 10), which is supported by planktic foraminifera (Vicente et al., 2015). No significant hiatus is detected in this syncline, in contrast to the Tremp Syncline. Despite the quality of the geological record and the diversity of the general palaeontological discoveries, no dinosaur fossils have been determined at the species level in the Vallcebre Syncline.

3. The Maastrichtian dinosaur turnover in south-western Europe

Le Loeuff et al. (1994) proposed that a major dinosaur faunal turnover took place between the early and the late Maastrichtian based on observations from the northern Pyrenees, France. These authors described the “lower” assemblages as those composed by titanosaurids alongside rhabdodontids and nodosaurids whereas the “upper” assemblages were dominated by hadrosauroids. The hypothesis was supported by many subsequent works from other Pyrenean areas (Buffetaut et al., 1997; Casanovas-Cladellas et al., 1995, Casanovas et al., 1999; Laurent et al., 2002; López-Martínez et al., 1999, 2001; Buffetaut, 2005; Vila et al., 2006). Recent studies have attempted to refine this succession on the basis of the original hypothesis and with the integration of updated chronostratigraphy and new occurrences available. Vila et al. (2016) postulated that an assemblage of titanosaurian sauropods, rhabdodontid ornithopods, nodosaurid ankylosaurians, abelisaurid and dromaeosaurid theropods dominated the late Campanian-early Maastrichtian landscapes until the early late Maastrichtian, (around the C31r-C31n reversal, ca. 69 Ma), when the appearance of a new assemblage in the Ibero-Armorican region composed by hadrosauroids and new titanosaurian taxa led to a very rapid faunal replacement.

Here, we re-evaluate the turnover by integrating the new stratigraphic data from the vertebrate localities of the southern Pyrenees combined with the contemporaneous records from other Iberian, as well as Languedoc and Provence areas. With the database of the most complete Campanian-Maastrichtian dinosaur succession of south-western Europe built so far (Fig. 11 and Supp. Table 1), we refine the chronostratigraphic occurrence of the dinosaur turnover. The new revision involves several clades of dinosaurs, whose chronostratigraphic ranges are established not only on the basis of

skeletal record but also on oological evidence. The “pre-turnover” communities are composed by a distinctive fauna of titanosaurs alongside rhabdodontid iguanodontians and nodosaurid ankylosaurians, which are no longer present in the fossil record after the turnover interval. By comparison, the “post-turnover” communities are composed by a distinctive and new fauna of titanosaurs alongside lambeosaurine hadrosaurids, which are absent in times preceeding the turnover. Finally, abelisauroid and maniraptoran theropods, and non-lambeosaurine hadrosaurs seem to occur in both the “pre-turnover” and “post-turnover” intervals. Below, the time ranges (including the lowest and highest stratigraphical occurrences) of each major dinosaur clades known in the region are reviewed and discussed, with special emphasis on the contribution of the Pyrenean record.

3.1. “Pre-turnover” communities

These include the communities that extend from the Campanian to the early late Maastrichtian (chron C30r).

3.1.1. *Nodosaurid ankylosaurians*

Nodosaurids are the ankylosaurians commonly known in several fossil sites from Campanian-Maastrichtian formations of south-western Europe (Csiki et al., 2015) (Fig. 11). Garcia and Pereda-Suberbiola (2003) defined the species *Struthiosaurus languedocensis* in the lower Campanian of the Villeveyrac-Meze Basin (Hérault, France). Nevertheless, due to the lack of diagnostic features most of the nodosaurid remains cannot be identified beyond higher taxonomic levels (Pereda-Suberbiola, 1992; Laurent et al., 2001; Laurent, 2003; Buffetaut, 2005). In Spain, only a single unnamed species, *Struthiosaurus* sp. (Pereda-Suberbiola, 1999a), has been described from the upper Campanian deposits of Laño. The controversial *Taveirosaurus costai* from the upper Campanian-Maastrichtian deposits of Taveiro, Portugal (Antunes and Sigogneau-Russell, 1991, 1996), was regarded by Pereda-Suberbiola (1999b) as *nomen dubium* due to the lack of diagnostic characters. In addition, Sellés and Galobart (2016) suggested that, on the basis of microstructural features and anatomical constrains, the endemic European egg-type *Cairanoolithus* could belong to European nodosaurid ankylosaurians.

The ankylosaurian record from southern Pyrenees is very scarce and fragmentary, being limited to a single humerus from the Suterranya-Mina de lignit locality (Martín-Jiménez et al., 2017), two armor plates from the Els Nerets site (Santafé et al., 1997), two isolated teeth from the Biscarri and Fontllonga-6 sites (López-Martínez et al., 1999, 2000), and some alleged partial eggs from the Coll de Nargó area (Sellés and Galobart, 2016). However, after the updating and calibration of the south-Pyrenean localities, the ankylosaurian chronostratigraphic framework becomes of pivotal importance. Thus, the chronostratigraphic position of the Fontllonga-6 locality (previously falling into the early Maastrichtian; López-Martínez et al., 1998) is significant as it is now considered the last appearance of the group in south-western Europe, in chron C30r (early late Maastrichtian). A similar age has been proposed for the ankylosaurian remains of Lestailats, in the Haute Garonne area of the northern Pyrenees (Laurent et al., 2002).

Lowest Occurrence: Villeveyrac, southern France (early Campanian, chron C33r); skeletal remains (bones).

Highest Occurrence: Fontllonga-6 and the Lestailats localities, southern Pyrenees, Spain, and southern France, respectively (early late Maastrichtian, chrons C31n to C30r); skeletal remains (a single tooth and bones, respectively).

3.1.2. *Rhabdodontid iguanodontians*

This category corresponds to four taxa of the Rhabdodontidae family known from the end-Cretaceous deposits of the Ibero-Armorican Island (we exclude for the analysis the isolated occurrence of rhabdodontids in the Early Cretaceous; Dieudonné et al., 2016). *Rhabdodon septimanicus* has only been found in the mid-Campanian of La Boucharde, (Provence; Chanthasit, 2010) and in the Campanian-Maastrichtian sites of Quarante and Montouliers (Lapparent, 1947; Chanthasit, 2010 and references therein). *Matheronodon provincialis* (Godefroit et al., 2017) has been identified from the upper Campanian beds of Velaux-La Bastide Neuve site, in Provence. *Rhabdodon priscus*, erected by Matheron (1869) on the basis of material from the lower Maastrichtian La Nerthe site (Pincemaille-Quillevere, 2002), has been identified in several French (Lapparent, 1947; de Broin et al., 1980; Buffetaut et al., 1996; Garcia et al., 1999; Pincemaille-Quillevere, 2002; Le Loeuff, 2005), and Iberian (Company et al., 2005; Pérez-García et al., 2016) localities. Finally, Parraga and Prieto-Márquez (in press) recently defined the species

Pareisactus evrostos in the lower Maastrichtian of Basturs Poble, in the southern Pyrenees.

The Figuerola-2 locality has yielded rhabdodontid remains, represented by a single unambiguous tooth (Llompart and Krauss, 1982). The site is placed around the early-late Maastrichtian boundary (ca. middle-upper part of chron C31r) of the Àger Syncline (Fig. 8). Despite of the fragmentary nature of the material, the Figuerola-2 tooth is highly significant as it represents the highest occurrence of the group in the entire Ibero-Armorican region together with the Basturs Poble remains.

Lowest Occurrence: Villeveyrac, southern France (early Campanian, chron C33r); skeletal remains (bones).

Highest Occurrence: Figuerola-2 locality, southern Pyrenees, Spain (early-?late Maastrichtian; ca. middle-upper part of chron C31r) and Basturs Poble, southern Pyrenees, Spain (early Maastrichtian, middle-upper part of chron C31r); skeletal remains (bones, single tooth).

3.1.3 “Pre-turnover” titanosaurians

This group is represented by the titanosaurians producers of the *Megaloolithus siruguei* and *M. aureliensis* eggs, whose temporal range expands from chron C33n (late Campanian) to chron C30r (early late Maastrichtian). The megaloolithid eggshells have been traditionally assigned to titanosaurian sauropods (Chiappe et al., 2001; Wilson et al., 2010; Grellet-Tinner et al., 2011). More particularly, *M. siruguei* and *M. aureliensis* most probably correspond to the titanosaurian taxa found in the middle-late Campanian and the earliest Maastrichtian localities of south-western Europe, including the taxa *Ampelosaurus atacis*, *Lirainosaurus astibiae*, *Atsinganosaurus velaucencis*, *Lohuecotitan pandafilandi*, and three new titanosaurian species pending definitive description (Knoll et al., 2013; Díez Díaz et al., 2015). Aside of *M. siruguei* and *M. aureliensis* these titanosaurian taxa could also have produced eggs referred to *Megaloolithus microtuberculata*.

In the southern Pyrenees, the skeletal record of the “pre-turnover” titanosaurians concentrates in chron C31r (early Maastrichtian) but is scarce and fragmentary and has been assigned to indeterminate titanosaurians. On the contrary, the egg record is profuse

with dozens of egg-levels containing *M. siruguei* and *M. aureliensis* (Vianey-Liaud and López-Martínez, 1997; Vila et al., 2011; Sellés et al., 2013; Sellés and Vila, 2015), the latter oospecies representing the highest occurrence (Fontllonga-6 locality, chron C30r) of the group in south-western Europe.

Lowest Occurrence: Chera locality, eastern Iberia, Spain (middle-late Campanian, chron C33n); skeletal remains (bones).

Highest Occurrence: Fontllonga-6 locality, southern Pyrenees, Spain (late Maastrichtian, chron C30r); eggshells.

3.2. “Post-turnover” communities

They include the dinosaur communities that extend from the early Maastrichtian (chron C31r) to the latest Maastrichtian (lower half of chron C29r).

3.2.1. *Lambeosaurine hadrosaurids*

Lambeosaurines are by far the most abundant and taxonomically diverse hadrosauroids in south-western Europe, being represented from the mid-part of chron C31r (early Maastrichtian) to the lower half of chron C29r (latest Maastrichtian) by five different species (*Pararhabdodon isonensis*; *Arenysaurus ardevoli*; *Blasisaurus canudo*; *Canardia garonnensis*, *Adynomosaurus arcanus*) as well as other material referred to indeterminate species. Prieto-Márquez et al. (2006) defined the species *Koutalisaurus kohlerorum*, but later Prieto-Márquez et al. (2013) regarded the specimen as an indeterminate lambeosaurine. Abundant track-bearing levels with the ichnogenus *Hadrosauropodus* (Riera, 2010; Vila et al., 2013) and some eggshell localities (with *Spheroolithus europaeus*; Sellés et al., 2014b) could be attributed to lambeosaurine hadrosaurids according to their stratigraphic positions, and because of the occurrence of indeterminate lambeosaurine embryos within spheroolithid eggs (Horner, 1999).

Fossils of lambeosaurine hadrosaurids are concentrated exclusively in the Pyrenees, and most abundantly in the southern basins. Aside the localities that yielded distinctive lambeosaurine species (Sant Romà d’Abella, Costa de les Solanes, Blasi, Tricouté 3 and Larcán; Prieto-Márquez et al., 2013; Prieto-Márquez et al., in press), dozens of sites from the Tremp Syncline, such as Els Nerets, Basturs Poble, Serrat del Corb, and Euroda Nord (Prieto-Márquez et al., 2013; Dalla Vecchia et al., 2014; Fondevilla et al.,

2018; Conti et al., 2018), produce abundant fossils. As the clade is uniquely represented in the Pyrenees, its lowest and highest occurrences in south-western Europe are exclusively set on this region.

Lowest Occurrence: Els Nerets, southern Pyrenees, Spain (early Maastrichtian, middle portion of chron C31r); skeletal remains (bones).

Highest Occurrence: Cingles del Boixader locality, southern Pyrenees, Spain (late Maastrichtian, lower half of chron C29r); footprints.

3.2.2. “Post-turnover” titanosaurs

This group includes titanosaurs producing the eggs *Megaloolithus mamillare* and *Fusioolithus baghensis*, found from the early to the late Maastrichtian (lower part of chron C31r to lower half of chron C29r). These titanosaurs probably correspond to indeterminate but distinctive taxa recovered from late Maastrichtian localities of the southern Pyrenees (Vila et al., 2012) such as Molí del Baró-2 and Serraduy in chrons C30n-C29r, an interval where the oospecies associated to the “pre-turnover” taxa are absent.

The southern Pyrenees are the region where most of the scarce record of such titanosaurs is found. It consists of usually fragmentary skeletal material (Presa de Tremp, Peguera-1, Molí del Baró-2, Serraduy localities), several egg sites (Basturs-1, -2, Suterranya-1, Barranc de la Boïga, Molí del Baró-1, Tossal de Sant Romà, Els Terrers; Sellés and Vila, 2015) and a few track sites (e.g. Serrat de Sanguín and Mirador de Vallcebre; Vila et al., 2013; Fondevilla et al., 2017a). Biostratigraphically, this region is significant in terms of its fossil record as it contains both the lowest and the highest occurrences of “post-turnover” titanosaurs. Outside of the Pyrenees, the fossil record of “post-turnover” titanosaurs corresponds uniquely to the occurrence of *Megaloolithus mamillare* and *Fusioolithus baghensis* in some localities of Iberia and Provence (Pol et al., 1992; Garcia and Vianey-Liaud, 2001).

Lowest Occurrence: Basturs-1, -2 localities, southern Pyrenees, Spain (early Maastrichtian, lower part of chron C31r); eggshells.

Highest Occurrence: El Portet locality, southern Pyrenees, Spain (late Maastrichtian, lower half of chron C29r); skeletal remains (bones).

3.3. Dinosaur taxa presumably not affected by the Maastrichtian turnover

3.3.1. *Abelisauroids*

The fossil record of large theropods in the Ibero-Armorican Island encompasses the late Campanian (upper part of chron C33n) to latest Maastrichtian (lower half of chron C29r) time interval, although it is still fragmentary and the specimens often have poor taxonomic resolution. For example, *Tarascosaurus salluvicus* from the lower Campanian of Provence (Le Loeuff and Buffetaut 1991; Tortosa et al., 2014) was first regarded as a ceratosaurian abelisaurid, but as a *nomen dubium* (Allain and Pereda-Suberbiola, 2003; Rauhut, 2003) and later referred to *Abelisauroidea incertae sedis* (Carrano and Sampson, 2008). More recently, Tortosa et al. (2014) placed the material in *Abelisauridae*. In addition, these authors identified a considerable diversity of abelisaurids in the Campanian-Maastrichtian of the Provence area, but they suggested that this variability could actually represent the same genus. Among these abelisaurids, *Arcovenator scotae* from the Pourrieres-Jas Neuf locality ranks as the most complete representative found so far in south-western Europe. Pérez-García et al. (2016) referred material previously classified as Theropoda indet. morphotypes 1 and 2 (Torices et al., 2015) from Armuña (late Campanian), Laño (late Campanian, chron C32n.2n), and Blasi (late Maastrichtian, chron C30n) to cf. *Arcovenator*. Similarly, two isolated large teeth reported at the sites 172-i/04e and Molí del Baró-1 (lower half of chron C29r) by Puértolas-Pascual et al. (2018) and Marmi et al. (2016b), respectively, were attributed to morphotype 1 of Torices et al. (2015), which in turn can be assigned to cf. *Arcovenator*. Thus, the temporal range of the abelisaurid material related to *Arcovenator* and cf. *Arcovenator* likely spans from the middle Campanian to the late Maastrichtian (Fig. 9).

The contribution of the southern Pyrenees to the large theropod record is remarkable as it preserves the only three localities with abelisauroid material from the upper Maastrichtian, in localities such as Blasi (chron C30n), Molí del Baró-1 or 172-i/04e (chron C29r). However, the fragmentary and usually disarticulated nature of most of the specimens (isolated shed teeth) in the region makes a more precise taxonomic resolution difficult, and the assumption that the abelisauroids were not involved in the Maastrichtian faunal changes of the region could be biased.

Lowest Occurrence: Le Beausset locality, southern France (early Campanian, upper part of chron C33r); skeletal remains (bones).

Highest Occurrence: Molí del Baró-1 locality, southern Pyrenees, Spain (late Maastrichtian, lower half of chron C29r); skeletal remains (single tooth).

3.3.2. *Maniraptorans*

The fossil record of maniraptoran theropods in the Ibero-Armorican region corresponds to small to medium size taxa that have been identified by means of fragmentary fossils and shed teeth. Apparently, as some of the identified taxa are present both in the upper Campanian-lower Maastrichtian and upper Maastrichtian assemblages and the fact that the current taxonomic resolution of the studied sample prevents to unambiguously differentiate them at species level, we can consider that they were most probably not affected by the faunal turnover.

In the upper Campanian-lower Maastrichtian assemblages, *Pyroraptor olympius* (Trets-La Boucharde, middle Campanian; Allain and Taquet, 2000) is the best represented taxon recovered to date. The Campanian-Maastrichtian *Variraptor mechinorum* (Le Loeuff and Buffetaut, 1998) from the French localities of Fox-Amphoux and Cruzy was considered a *nomen dubium* by Allain and Taquet (2000). Chanthasit and Buffetaut (2009) provisionally accepted the taxon, but commented that, as also possible in the case of other dinosaurs of the region, *P. olympius* and *V. mechinorum* could represent a single taxon due to the lack of diagnostic overlapping elements. Isolated teeth belonging to coelurosaurians (Coelurosauridae indet.), a distinct dromaeosaurid morphotype (Dromaeosauridae indet.), velociraptorines (Velociraptorinae indet.), the genus *Richardoestesia* and the troodontid *Paronychodon* have been reported in the late Campanian-early Maastrichtian localities of Laño, Lo Hueco, La Neuve, and Vitrolles-La Plaine (Supp. Table 1; Garcia et al., 2000; Valentin et al., 2012; Ortega et al., 2015; Torices et al., 2015). Antunes and Sigogneau-Russell (1991) defined the species *Euronychodon portucalensis*, now considered a synonym of *Paronychodon* (Rauhut, 2002), in the Campanian-Maastrichtian site of Taveiro. In addition, Antunes and Sigogneau-Russell (1992) identified seven different morphotypes of theropod teeth in Aveiro, Taveiro and Viso. The southern Pyrenees region yielded a poor record of maniraptorans in terms of skeletal remains but the isolated teeth of *Pyroraptor* in the lower Maastrichtian locality of Montrebei (middle C31r) expand the temporal range of

the genus into the Maastrichtian (Torices et al., 2015). Other isolated shed teeth of Coelurosauria indet. and cf. Dromaeosauridae indet. have been reported in Vicari-4 and Figuerola-2 (chron C31r) localities.

The skeletal fossil record of the late Maastrichtian maniraptorans in south-western Europe is scarce and is restricted exclusively to south-Pyrenean localities. The localities of Peguera-1 (around the boundary between chrons C31r-C30n), Blasi-2B (chron C30n) and Molí del Baró-1 (chron C29r) produced several shed teeth of maniraptorans attributed to indeterminate dromaeosaurids (including likely velociraptorines), indeterminate coelurosaurians and forms similar to *Richardoestesia* and *Paronychodon* (Baiano et al., 2014; Torices et al., 2015; Marmi et al., 2016b). These latter forms are also recognized in upper Campanian-lower Maastrichtian sites (Fig. 11).

Regarding the oological record, two distinct oossemblages from the “pre-” and “post-” turnover intervals can be differentiated (Sellés et al., 2014a). First, there are the maniraptorans producers of the oossemblage of *Prismatoolithus matellensis*, *P. tenuis* and *Ageroolithus fontllonguensis* (Vianey-Liaud and López-Martínez, 1997), which is temporally restricted to the interval extending from chron C33n (late Campanian) to chron C30r (early late Maastrichtian). These eggshells have been traditionally assigned to maniraptorans (López-Martínez and Vicens, 2012; Sellés et al., 2014a). Second, there are the maniraptorans producers of the *Prismatoolithus trempii* eggs, whose chronostratigraphic range encompasses the early Maastrichtian (lower part of chron C31r) up until the latest Maastrichtian (lower half of chron C29r). Prismatoolithid eggs are attributable to small to medium size maniraptorans, most probably to a variety of dromaeosaurids and related taxa (Norell et al., 1994; Varrichio et al., 2002; Araújo et al., 2013). Other ootaxa found in early-late Maastrichtian localities (*Sankofa pyrenaica*, *Montanoolithus labadousensis*; López-Martínez and Vicens, 2012; Vila et al., 2017) can be also attributed to maniraptorans, although because of their unique occurrence they cannot be unequivocally ascribed to either the “pre-” or the “post-turnover” assemblages.

Lowest Occurrence: Trets La Boucharde and other French localities (middle Campanian, chron C33n); skeletal remains (bones).

Highest Occurrence: Camí del Soldat locality, southern Pyrenees, Spain (late Maastrichtian, lower part of chron C29r); eggshells.

3.3.3. *Indeterminate hadrosaurids and non-hadrosaurid hadrosauroids*

The south-western European fossil record has yielded several hadrosauroid bones and teeth from localities in Iberia, the Pyrenees and Provence. This material, consisting of isolated cranial and postcranial elements assigned to indeterminate hadrosauroids and non-hadrosaurid hadrosauroids, is chronostratigraphically distributed from the late Campanian to the latest Maastrichtian. However, the scarcity of the fossils and the absence of continuous stratigraphic record throughout the Maastrichtian prevents any assessment of how the turnover affected these hadrosauroid taxa. Some of these taxa can be interpreted as hadrosauroids inhabiting Europe before the lambeosaurine arrival during the early Maastrichtian. The postcranial material from Vitrolles-La Plaine (Campanian-Maastrichtian) has been assigned to a non-euhadrosaurian hadrosaurid (Valentin et al., 2012) and a single tooth from Laño locality (late Campanian, chron C32n.2n) is referred to Hadrosauridae indet. (Pereda-Suberbiola et al., 2003, 2015). In the upper Maastrichtian, a dentary from the La Solana locality and the small-sized material of Serraduy del Pon/Beranuy (chron C29r) have been assigned to indeterminate hadrosaurids (Company et al., 1998, 2015; Pereda-Suberbiola et al., 2009b; Cruzado-Caballero et al., 2014), whereas the dentary from the Fontllonga-R locality (chron C29r) has been considered a possible non-hadrosaurid member of the Hadrosauroidea (Pereda-Suberbiola et al., 2009b). In a similar way, Blanco et al. (2015) considered that a morphotype of small dentaries found in the Basturs Poble site (chron C31r) could represent small hadrosauroid taxa that coexisted with larger lambeosaurines, but Fondevilla et al. (2018) claimed the material could belong to juvenile lambeosaurines.

4. Discussion

4.1. *Age, duration, and characteristics of the Maastrichtian dinosaur turnover in south-western Europe*

The combined chronological and geological data presented here refine the current scenario of the Campanian-Maastrichtian dinosaur succession in south-western Europe, and amend the timing and duration of the faunal turnover that took place here during the Maastrichtian. The time interval proposed for this replacement, or else the time of co-existence of both the “pre-” and “post-turnover” faunas, changed over time with each subsequent study. As such, the original proposal of Le Loeuff et al. (1994) did not

indicate the duration of the replacement. It is important to remark that these authors followed the GPTS of Haq et al. (1987), which placed the early-late Maastrichtian boundary around the C32n.1n-C31r reversal (the earliest Maastrichtian according to the GPTS of Ogg and Hinnov, 2012; Fig. 12). Vila et al. (2016) considered that the turnover was a short-term replacement that they set specifically around the C31r-C31n reversal. The present re-evaluation shows that, in fact, the turnover interval started earlier, in the early Maastrichtian, and ended in the early late Maastrichtian; thus, it took longer than previously recognized, and lasted about 2.5-2.8 millions of years (Fig. 12).

Le Loeuff et al. (1994) did not mention any replacement of titanosaurs between the early and the late Maastrichtian assemblages. The authors neither differentiated chronostratigraphic ranges for particular groups within hadrosauroids or theropods. According to Vila et al. (2016) and the newest evaluation, the titanosaurs experienced a clear replacement but no changes are observed for indeterminate hadrosaurids and non-hadrosaurid hadrosauroids, abelisauroids, and probably neither for small maniraptorans, at least based on the skeletal record. Moreover, in two of the analyzed groups the egg-type assemblages can be used as proxy for assessing faunal changes, as is common in the literature (Sellés et al., 2014a; Vila et al., 2016; Tanaka et al., 2016). Differences between the “pre-” and “post-turnover” egg assemblages, mainly those assigned to Megaloolithidae and Prismatoolithidae oofamilies, lead to speculate about plausible changes in the faunal composition of titanosaurs and small maniraptorans, respectively. Thus, the megaloolithid record can be used as proxy for assessing the replacement in titanosaurs. Given that the “pre-turnover” megaloolithid oospecies (*M. siruguei* and *M. aureliensis*) are endemic to Europe (Sellés et al., 2013) and those from the “post-turnover” (*M. mamillare* and *Fusioolithus baghensis*) have a global distribution (Vianey-Liaud et al., 2003; Fernández and Khosla, 2015), it seems likely that the appearance of the latter egg-producers were linked to some kind of migratory event. This hypothesis is supported by the fact that the post-turnover titanosaurian taxa show clear differences with those of pre-turnover times and some of them even show anatomical similarities with taxa from Asia (e.g. *Opisthocoelicaudia*, Vila et al., 2012). The “pre-turnover” assemblages would have been present on the region until the early late Maastrichtian (chron C30r), whereas the new “post-turnover” titanosaurs would have reached the island by the early Maastrichtian (basal part of chron C31r), with a time of coexistence with the former ones.

Regarding small theropods, the distinctive “pre-” and “post-turnover” oological associations may also suggest changes in the faunal composition of maniraptoran dinosaurs, as in the previous case. However, unlike titanosaurians, all primateolithid-eggs, either from “pre-” or “post-turnover” intervals, seem to be endemic to the region (Sellés et al., 2014a) and only the ootaxon *Montanolithus labadousensis* shows a North-American affinity (Vila et al., 2017). This fact prevents to link the replacement observed in oospecies assemblages with migratory events, as in the case of titanosaurians. In addition, the poor taxonomic resolution of most of the maniraptoran skeletal remains (rarely beyond the family level) and the long-time persistence of several groups in the Ibero-Armorican record hamper the establishment of a clear turnover pattern based on taxonomic species. It would be plausible that the different primateolithid associations of “endemic ootaxa” before and after the alleged turnover event could reflect changes in the communities of small theropods derived from a sympatric speciation. This evolutionary process is well established in Jurassic and Cretaceous theropod faunas of North America and Europe, and it is invoked when suggesting niche partitioning among theropod dinosaurs (Gerke and Wings, 2016; Hassler et al., 2018).

Considering the role of hadrosauroids, the original hypothesis of Le Loeuff et al. (1994) stated that the “hadrosaurs” were dominant and abundant in the “late Maastrichtian assemblages”, and Vila et al. (2016) indicated that the arrival of the hadrosauroids in the region occurred around the C31r-C31n interval, in the late Maastrichtian. The present work sets the first appearance of the lambeosaurine hadrosauroids earlier, in the early Maastrichtian (middle part of chron C31r) and does not rule out the possibility that a basal lineage of hadrosauroids was present in the region earlier in the late Campanian. The nodosaurid ankylosaurians and rhabdodontid iguanodontians were simply referred to taxa of the “early Maastrichtian assemblages” by Le Loeuff et al. (1994), whereas Vila et al. (2016) set the moment of their disappearance at around the C31r-C31n reversal. The present update most notably expands the chronostratigraphic range for the ankylosaurians up to the early late Maastrichtian (chron C30r), whereas the range of rhabdodontids remains unaffected.

The faunal changes that took place from the early to the late Maastrichtian involved a prolonged interval of coexistence between dinosaur groups instead of a rapid faunal replacement as previously stated. The episodes of extinction and new appearances (likely immigrant arrivals) took place diachronously for each main taxonomic group during the Maastrichtian. These changes or events can be summarized as follows (Figs. 13, 14):

- During Campanian and earliest Maastrichtian times (up to the beginning of chron C31r) the dinosaurian faunas of the Ibero-Armorican Island were dominated by several species of titanosaurian sauropods (the “pre-turnover titanosaurs”, including the likely producers of the oospecies *M. aureliensis* and *M. siruguei*), nodosaurid ankylosaurians, rhabdodontid iguanodontians and small- and medium-sized theropods. Hadrosauroids were extremely rare during this period and probably were represented by non-lambeosaurine taxa.
- During the early Maastrichtian (beginning of chron C31r), new titanosaurian sauropods (the “post-turnover” titanosaurs, including the likely producers of *M. mamillare* and *F. baghensis*) - arrived on the island. The “pre-” and “post-turnover” titanosaurian faunas cohabited the region until the end of the early late Maastrichtian (chron C30n, with the highest occurrence of *M. aureliensis*), when the “pre-turnover” taxa finally disappeared.
- Around 70 Ma (mid-part of chron C31r, still in the early Maastrichtian) lambeosaurine hadrosaurids first appeared in south-western Europe and rapidly became the most abundant herbivorous group (according to data from Vila et al., 2016).
- Ankylosaurians became extinct probably during chron C30r (ca. 68 Ma), coexisting with lambeosaurine hadrosaurids for about 2 Ma.
- Rhabdodontids became extinct before chron C31n (ca. 69 Ma), coexisting with “post-turnover” groups for about 1-2 Ma.
- The large theropod taxa (abelisauroids) and the small maniraptorans appear to be unaffected by any major change during this time interval as at least one of the Campanian forms was still present during the late Maastrichtian in the Ibero-Armorican Island. However, the poor taxonomic resolution of most of their fossil record and the distinct oospecies assemblages through the Maastrichtian imply that this statement should be considered with caution.

4.2. Palaeoenvironments and ecological competition during the turnover

The co-existence of “pre-“ and “post-turnover” faunas for more than 2 Ma entails the analysis of how dinosaurs might have been affected by ecological competition, or if, alternatively, they actually inhabited different palaeoenvironments and occupied distinct ecological niches. Vila et al. (2016) showed that lambeosaurines have the richest fossil record in the upper Maastrichtian of south-western Europe. Conversely, titanosaurian remains significantly reduce their abundance in that interval. After their arrival, lambeosaurines were present in all the available palaeoenvironments (cohabiting with the rest of the groups) of the Pyrenean area, but are mainly concentrated in tidal-influenced coastal and lagoonal settings (Laurent et al., 2002; Blain et al., 2010; Vila et al., 2013; Fondevilla et al., 2017b). The abundant lambeosaurine skeletal remains in these deposits coincide with the widespread presence of the track record linked to hadrosauroids (the *Hadrosauropodus* ichnogenus; Vila et al., 2013). However, it is important to remark that such observations are made exclusively in the Pyrenees, lambeosaurine remains being absent in other parts of Iberia and southern France. For instance, the Maastrichtian inland fluvial deposits of Provence (see Cojan, 1993) lack lambeosaurine remains, but contain several megaloolithid egg-bearing levels. Hence, making assumptions about a lambeosaurine dominance in the Ibero-Armorican Island based only in the Pyrenean record should be considered with caution, even more so when the group seems to show an apparent palaeoenvironmental preference for coastal settings in the region (concurring with the observation of Horner et al., 2004).

Regarding the hypothesis of competition between groups, some authors have raised the question of whether the lambeosaurine arrival was the triggering factor of the subsequent extinctions that took place at the end of the Maastrichtian faunal turnover. In this respect, Vila et al. (2016) considered that the demise of the nodosaurid ankylosaurians and the rhabdodontid iguanodontians could be the result of the more efficient hadrosauroid masticatory mechanism (Mallon and Anderson, 2013; but see Godefroit et al., 2017). Le Loeuff et al. (1994) explored the possibility of whether changes in the floral composition (from subtropical to temperate, following Ashraf and Erben, 1986) during the earliest Maastrichtian of the Ibero-Armorican Island were related to the observed changes in the dinosaur assemblages, possibly favouring

lambeosaurines over other herbivores. However, these floral changes have not been demonstrated (Marmi et al., 2016a).

Focusing on the turnover effect on the titanosaurs, Riera et al. (2009) and Riera (2010) proposed that the sauropod decline during the Maastrichtian was the consequence of a palaeoenvironmental bias. These studies considered that Ibero-Armorican titanosaurs preferred coastal environments (for instance, the Fumanya tidal flat; Vila et al., 2005; Marmi et al., 2014; Oms et al., 2016), so the apparent scarcity of such settings in the late Maastrichtian would explain the poor titanosaurian record after the turnover. However, a coastal habitat preference is not well supported for all titanosaurs in the region, because during the Campanian and the early Maastrichtian these sauropods were the dominant dinosaurs in fluvial deposits of Iberia and southern France (e.g. Le Loeuff et al., 1994; Garcia et al., 2010; Ortega et al., 2015). In addition, there is important evidence of sauropods living in inland and coastal settings (i.e. coastal plains, tidal-influenced fluvio-deltaic environments) in the Pyrenean area until the very end of the Cretaceous, just before the K-Pg extinction (Vila et al., 2013; Sellés et al., 2016; Fondevilla et al., 2017a). Thus, a palaeoenvironmental bias seems inconsistent to explain why sauropods reduced their presence, since both coastal and fluvial deposits were available during the entire Maastrichtian in the study area. Regarding the hypothesis of faunal interactions, Vila et al. (2016) suggested that the Maastrichtian sauropod decline could be the result of competition with hadrosauroids for space within the same palaeoenvironments, rather than for other resources (e.g. food) given the different body sizes, tooth morphology and masticatory mechanisms of the two groups. In this regard, the occurrence of pathologic sauropod eggs during the turnover could be a consequence of an increase in reproductive stress triggered by direct ecological competition between different dinosaur groups (Sellés et al., 2017).

4.3. Links with global events and palaeobiogeography

Regarding the causes and the palaeogeographical context of the turnover, Le Loeuff et al. (1994) proposed that the dinosaur turnover was related to environmental changes associated with a marine regression in the Ibero-Armorican Island. The Maastrichtian regression across the island is well documented (Bilotte et al., 1983; Ardèvol et al.,

2000; Laurent et al., 2001; Oms et al., 2007; Fondevilla et al., 2016a), and likely led to palaeogeographical changes in the landmasses that allowed the arrival of dinosaur immigrants (Le Loeuff et al., 1994; Prieto-Márquez et al., 2013; Vila et al., 2016). Here, the integration of the novel dinosaur chronostratigraphic ranges with the sea-level curve and the known marine isotopic events allows a better assessment of biogeographic events such as the dinosaur turnover (Fig. 13). In this regard, it is remarkable that the appearance of “post-turnover” forms coincide with marine isotopic events 4 and 5 of the Campanian-Maastrichtian Boundary Events (CMBE), recognized worldwide by $\delta^{13}\text{C}$ shifts in marine successions (Voigt et al., 2012) and caused by the combination of multiple factors (sea-floor spreading, opening of oceanic gateways, Campanian-Maastrichtian cooling, and changes in the global oceanic circulations; see Linnert et al., 2018). These global events in turn coincide with an important sea-level drop (up to 25 m) recorded in the early Maastrichtian (Miller et al., 2005), which could have favored the arrival of the new faunas (mainly lambeosaurine hadrosauroids but also new titanosaurs) to south-western Europe by opening passages between landmasses.

It has been hypothesized that the appearance of lambeosaurine hadrosaurids in the Pyrenean area (and also in the entire Ibero-Armorican Island) corresponds to at least two dispersal events (Csiki-Sava et al., 2015). In this regard, Asian representatives such as tsintaosaurin and aralosaurin lambeosaurines (*P. isonensis* and *C. garonnensis*, respectively; Prieto-Márquez et al., 2013) and other Asian or North American-related forms (like *A. ardevoli* and *B. canudoii*; Prieto-Márquez et al., 2013; Cruzado-Caballero et al., 2013) arrived the westernmost island of the European archipelago at different times during the Maastrichtian. The non-lambeosaurine taxa found in the Pyrenees, Iberian and Provence areas, just as further basal hadrosauroid taxa found in other Campanian-Maastrichtian landmasses of the archipelago (e.g., *Tethyshadros insularis*, from the Adriatic-Dinaric Island, Italy; Dalla Vecchia, 2009), could represent relict forms that inhabited Europe during the Late Cretaceous prior to the arrival of the lambeosaurines (Pereda-Suberbiola, 1999b) in the early Maastrichtian; they likely evolved separately in each island of the archipelago through vicariance rather than dispersal.

Apparently, the titanosaurian producers of *M. mamillare* and *F. baghensis* appeared in the early Maastrichtian of south-western Europe prior to the arrival of the

lambeosaurine hadrosaurids (Fig. 13). In the Isona sector, this difference is represented by at least 140 meters of stratigraphic succession between the lowest occurrence of *M. mamillare* and that of the lambeosaurine remains (Fig. 5; that is, about 0.8 Ma earlier based on the sedimentation rates calculated in Fondevilla et al., 2016a). Therefore, the different dispersal events (e.g. the arrival of new titanosaurians, and lambeosaurine hadrosaurids) that triggered the faunal turnover were not time-coincident between the different dinosaur groups. Palaeobiogeographically, the presence of *F. baghensis* in south-western Europe evidences a direct Gondwanan titanosaurian connection during the Maastrichtian since this oospecies is also found in the Upper Cretaceous of India and Argentina (Khosla and Sahni, 1995; Vianey-Liaud et al., 2003; Sellés et al., 2013; Fernández and Khosla, 2015; Dhiman et al., 2018).

Regarding the extinction of the “pre-turnover” dinosaur forms, we note that their disappearance took place shortly after the Mid-Maastrichtian isotopic events (MME; see Voigt et al., 2012). Some titanosaurians (the producers of *M. siruguei*) and the rhabdodontids disappeared at the beginning of the MME, so these events could have acted as a *coup de grâce* for these dinosaurs. Other titanosaurians (producers of *M. aureliensis*) and the nodosaurid ankylosaurians survived the event but became extinct shortly after. The direct effects of the MME in the Ibero-Armorican ecosystems could be potentially identified in the $\delta^{13}\text{C}$ isotopic curve by Riera et al. (2013, here recalibrated in Fig. 13), where a negative shift is suggested at the beginning of chron C31n. A climate shift has also been found for this time interval in the western distal marine depositional equivalents at Zumaia (Dinarès-Turell et al., 2013).

Finally, Vila et al. (2016) explored the possibility of whether the short-term ecological changes that occurred in the herbivorous dinosaur communities, which took place during the latest Cretaceous in south-western Europe and in North America, could have made them vulnerable to a global environmental/biotic crisis such as the K-Pg event. The progressive nature of this turnover, as documented in south-western Europe, can be a key point to understand ecosystem dynamics previous to the final extinction of the dinosaurs.

5. Conclusions

A relatively high-resolution time framework for the Late Cretaceous dinosaur successions is obtained from the Pyrenean area. This permits to constrain several uncertainties of other complementary successions such as those from the rest of Iberia or Provence. The review of the uppermost Cretaceous sedimentary successions, datings and fossil occurrences from the Ibero-Armorican Island (south-western Europe) provides an improved record of the last 10 million years of dinosaur evolution before the K-Pg extinction event. Based on this updated overview, the end-Cretaceous dinosaur succession is thus characterized by:

- 1) A faunal turnover occurred during the Maastrichtian, which was the result of a prolonged interval of coexistence between several groups of herbivorous dinosaurs (titanosaurian sauropods, rhabdodontid iguanodontians, nodosaurid ankylosaurians and hadrosauroids).
- 2) The appearance of lambeosaurine hadrosauroids was followed by a dramatic decrease in abundance (Vila et al., 2016) of their ecologic equivalents (rhabdodontid iguanodontians and nodosaurid ankylosaurians, and probably titanosaurian sauropods) during and after the turnover event.
- 3) There was a loss of diversity at higher-level clades of herbivores after the turnover due to the disappearance of ankylosaurians and rhabdodontids.
- 4) The time-comparison between climatic changes and the gradual pattern of the dinosaur turnover indicates a partial correlation of faunal changes with global isotopic events (CMBE and MME) and sea-level drops.
- 5) The dinosaur faunal turnover documented here is a first milestone to integrate the European dinosaur succession at a global scale for the end-Cretaceous.

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FIGURE CAPTIONS

Figure 1. Geographical and geological context of the latest Cretaceous fossiliferous areas from south-western Europe. **A**, present day geography of France, Portugal and Spain, with location of the main fossiliferous areas considered here. 1, Tresp, Àger and Coll de Nargó synclines; 2, Vallcebre Syncline; 3, Aude and Corbières; 4, Haute Garonne; 5, Hérault-Languedoc; 6, Arc Syncline-Provence; 7, La Solana-València; 8, Chera-València; 9, Lo Hueco-Cuenca; 10, Laño-Treviño; 11, Armuña-Segovia; 12, Burgos area; 13, Viso, Aveiro and Taveiro. **B**, palaeogeography of the Ibero-Armorican Island of south-western Europe during the latest Cretaceous. **C**, schematic geological map of the southern Pyrenees, showing the Tresp, Àger, Coll de Nargó and Vallcebre synclines and the location of the stratigraphic sections with Maastrichtian vertebrate sites. A and B are modified from Philip et al. (2000) and Vila et al. (2016); C is

modified from López-Martínez and Vicens (2012).

Figure 2. Stratigraphic scheme of the end-Cretaceous and Paleocene formations from the southern Pyrenees according to different authors. Modified from Riera (2010).

Figure 3. Detailed geological map of the Isona sector (eastern Tremp Syncline), with location of the studied sections. Modified from Berástegui and Losantos (2001, 2004) and Riera et al. (2009). *Hc* correlation level refers to the *Hippuritella castroi* horizon.

Figure 4. Geological setting of the Coll de Nargó Syncline. A, detailed geological map of the uppermost Cretaceous units of Coll de Nargó. Modified from Riera et al. (2013). B, correlation scheme of the Tremp and Coll de Nargó synclines. The Tremp Syncline data is modified from Fondevilla et al. (2016a). Correlation modified from Riera et al. (2013).

Figure 5. Detailed geological map of the Vallcebre Syncline, with location of the studied sections. Modified from Oms et al. (2004, 2007).

Figure 6. W-E correlation panel of the northern sector of the Isona area (Tremp Syncline), with indication of the fossil sites (plants, bones, tracks and egg remains). The identified oospecies are also indicated. Sections 32, 33 and 36 are projected in the panel. Correlation modified from Riera et al. (2009), Riera (2010) and Vila et al. (2013). Palaeomagnetism after Fondevilla et al. (2016a). Sites: a, Les Serretes; b, Camí de les Planes, Serrat de Santó; c, Compuertas, Sant Bartomeu, Presa de Sant Antoni; ç, Vicari-4; d, Els Nerets; e, Suterranya-Mina de lignit, Suterranya-Camí de Montesquiú; f, La Llabusta; g, Suterranya-1 ('Abeller ; h, Orcau-1; i, Costa Roia; j, Serrat de Sanguín; k, Serrat de Sanguín-1, -2; l, Els Esfons; m, Torrent de Carant; n, Casa Fabà; o, Orcau-3; p, Orcau-2; q, Barranc de Torrebilles-2; r, Barranc de Torrebilles-5; s, Serrat del Rostiar-1, -3; t, Costa de la Coma; u, Serrat del Rostiar-2; v, Magret; w, Basturs Poble, Basturs Est; x, Les Feixes; y, Costa de les Solanes; z, La Llau de la Costa; aa, Els Pous; ab, Les Torres, Les Torres-2; ac, Mare de éu de l'Àrrec; aç, Barranc de la Costa Gran; ad, Barranc de la Boïga; ae, Basturs-1, -2; af, Lo Bas-1, -2; ag, Euroda Nord; ah, Tossal de Sant Romà; ai, Molí del Baró-1; aj, Molí del Baró-2; ak, Les Llaus; al, Serrat del Corb; am, Planta del Mestre; an, Tossal del Gass ; ao, Sant Romà d'Abella; ap, Costa de Santa lúcia; aq; Barranc de la Fonguera-1, -2; ar, Isona Sud; as, Julí; at, Coll de Faidella.

Figure 7. N-S correlation panel of the central sector of the Isona area (Tremp Syncline), with indication of the fossil sites (bones, tracks and egg remains). The identified oospecies are also indicated. This sector is correlated with section 6 from the northern sector (Fig. 6). Correlation modified from Riera et al. (2009), Riera (2010), Vila et al. (2013) and Blanco et al. (2016). Palaeomagnetism after Fondevilla et al. (2016a). Sites: au, Camí del Soldat; av, Barranc de Guixers-2; aw, Barranc de Guixers-1; ax, Barranc de Guixers-3; ay, Masia de Ramon; az, Masia de Ramon petjades; ba, Cabana de Gori-2; bb, Cabana de Gori-1; bc, Costa de Castelltallat; bç, Costa de la Serra-2; bd, Costa de la Serra-1; be, Serrat del Pelleu.

Figure 8. W-E-NE correlation panel of the southern margin of the Tremp Syncline, with indication of the fossil sites (bones, tracks and egg remains). The identified oospecies are also indicated. This sector is correlated with section 36 from Figure 6. Correlation modified from Riera et al. (2009), Riera (2010), López-Martínez and Vicens (2012) and Vila et al. (2013). Sites: bf, Montrebei-1 (Montr-1); bg, Montrebei, Montrebei-2 (Montr-2); bh, 'Estany; bi, Moror A; bj, Moror B; bk, Moror; bl, Moror-1; bm, Serrat Pedregós; bn, Urbanització Montsec; bo, Biscarri.

Figure 9. Updated chronostratigraphic framework of the latest Cretaceous of the Àger Syncline, with indication of the palaeontological sites (bones, tracks and eggshell remains). The identified oospecies are also indicated. Palaeomagnetic data from Galbrun et al. (1993) have been reinterpreted. GPTS after Ogg and Hinnov (2012). Sites: bp, La Mata del Viudà; bq, Fontllonga-3; br, Fontllonga-R; bs, Fontllonga-6; bt, Fontllonga-L; bu, La Maçana; bv, Blancafort; bw, Figuerola-2; bx; Figuerola-3; by, Perauba-Figuerola; bz, Figuerola-4.

Figure 10. Correlation panel of the continental exposures of the Vallcebre Syncline, with indication of the palaeontological sites (plants, bones, tracks and eggshell remains). The identified oospecies are also indicated. Correlation modified from Vila et al. (2011). Palaeomagnetism after Oms et al. (2007). Sites: ca, Cingles del Boixader, Reptile sandstone, El Portet; cb, Mirador de Vallcebre; cc, La Pleta nord, La Pleta resclosa; cd, La Nou-1; ce, Torrent de l'Esdavella (E-MUN06); cf, Peguera (P2-COL01); cg, Peguera-1; ch, Coll de Jou L-ESP10; ci, Mina Esquirol; cj, Font del Bullidor (A-FIG05); ck, Fumanya Sud (B-FUM10); cl, Fumanya Sud (tracks); cm, Fumanya Nord (E-MUN05); cn, Lower Tumí (E-MUN-02); co, Lower Tumí (E-MUN-01); cp, Lower Tumí (E-MUN-03); cq, Les Quijoles (I-COM04); cr, Les Quijoles (I-COM09); cs, Els Terrers (J-BAR01); ct, Els Terrers (J-BAR03); cu, Els Terrers (N-MAÇ03); cv, Els Terrers (N-MAÇ17, N-MAÇ18, N-MAÇ16, N-MAÇ15, N-MAÇ14, N-MAÇ13, N-MAÇ02, N-MAÇ12, N-MAÇ07, N-MAÇ08, N-MAÇ11, N-MAÇ10, N-MAÇ06, N-MAÇ09, N-MAÇ04).

Figure 11. Dinosaur succession of the Campanian-Maastrichtian from the Ibero-Armorican Island (south-western Europe), with indication of the temporal occurrence of the main fossil sites. See Supp. Table 1 for taxonomic and chronostratigraphic references. First and last occurrences of indeterminate remains are not included. Ranges are approximate. GPTS after Ogg and Hinnov (2012). Those sites from the Tremp Syncline include also the codes (letters) used in Figures 6-10. Sites: 1, Serraduy del Pon/Beranuy; 2 ai, Molí del Baró-1, -2; 3, Fontllonga-R; ao, Sant Romà d'Abella; arcan; 6, Tricouté 3; 7, Serraduy; 8, Blasi 3.4; 9, Blasi-1,-2,-3; 10 bs, Fontllonga-6; 11 cf, Peguera-1; 12 c, Presa de Sant Antoni; 13 bw, Figuerola-2; 14 bg, Montrebei; 15 ç, Vicari-4; 16 w, Basturs Poble; 16 y, Costa de les Solanes; 17, Gourg de l'Encantado; 18, Bellevue; 19, Lo Hueco; 20, Laño; 21, Jas Neuf; 22, Fox Amphoux; 23, Trets-La Boucharde; 24, Velaux-La Bastide Neuve; 25, Le Beausset; 26 g, Suterranya-1 ('Abeller; 27, Vitrolles-La Plaine; 28, Albières; 29, Vitrolles-Couperigne; 30, Chera; 31, Cruzy; 32, Porcieux; 33, La Neuve; 34, Armuña; 35, Sacedón; 36, Villeveyrac-Meze. GPTS after Ogg and Hinnov (2012). The dinosaur fossil

record from Portugal has not been included due to the poorly known age calibration of the Viso, Aveiro and Taveiro sites, although their palaeontological content is included in the main text.

Figure 12. Comparison of different proposals (A, B and C) regarding the timing and duration of the dinosaur turnover in south-western Europe.

Figure 13. Biostratigraphic ranges of the main dinosaur groups from south-western Europe during the late Campanian and the Maastrichtian. Ranges in orange represent the new dinosaur groups that arrived to the island during the late Campanian and the early Maastrichtian. Ranges include all available data (skeletal remains, eggshells and footprints). The marine $\delta^{13}\text{C}$ record from Gubbio, Italy (after Voigt et al., 2012) is depicted and compared to the south Pyrenean $\delta^{13}\text{C}$ record of Coll de Nargó (spanning tentatively chron C31r, see text) and Vallcebre (spanning chrons C31n-C29r). $\delta^{13}\text{C}$ values from the southern Pyrenees are taken from Riera et al. (2013). The isotopic events known as Late Campanian Event (LCE), Campanian-Maastrichtian Boundary Events (CMBE) and mid-Maastrichtian Events (MME) are also shown, including their different episodes marked with numbers (see Voigt et al., 2012). Sea-level curve is taken from Miller et al. (2005). GPTS after Ogg and Hinnov (2012).

- The ages of south-Pyrenean Late Cretaceous Maastrichtian successions are reviewed.
- The dinosaur occurrences of south-western Europe are integrated in a new chronostratigraphy.
- The timing of the Maastrichtian dinosaur faunal turnover is reviewed and updated.
- A possible link between global events and faunal changes is proposed.

ACCEPTED MANUSCRIPT

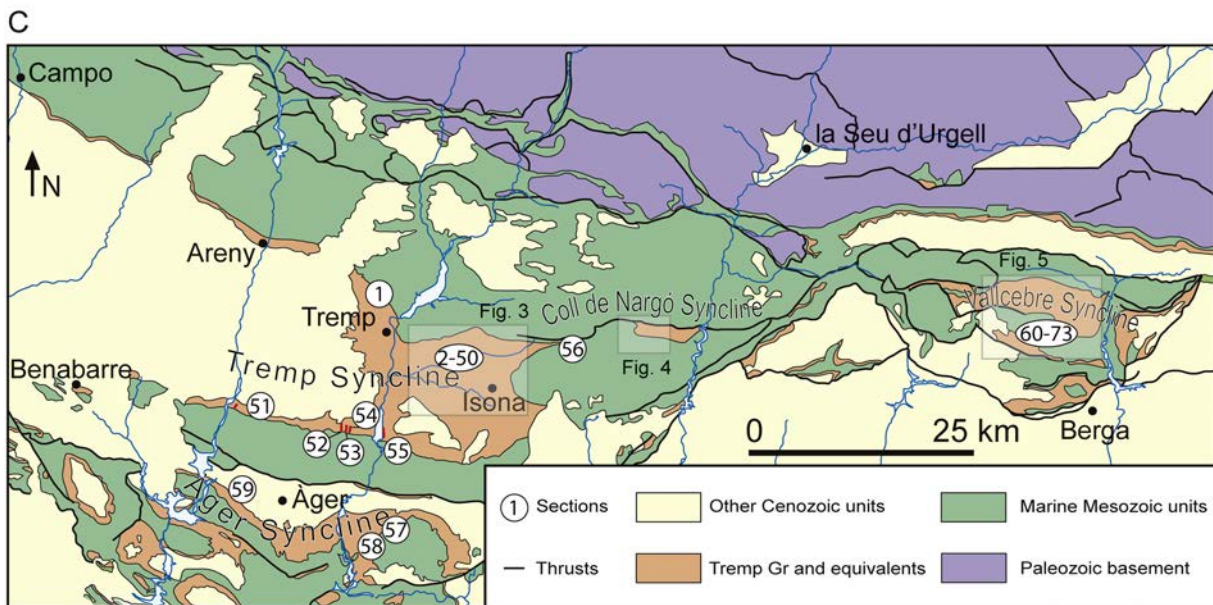
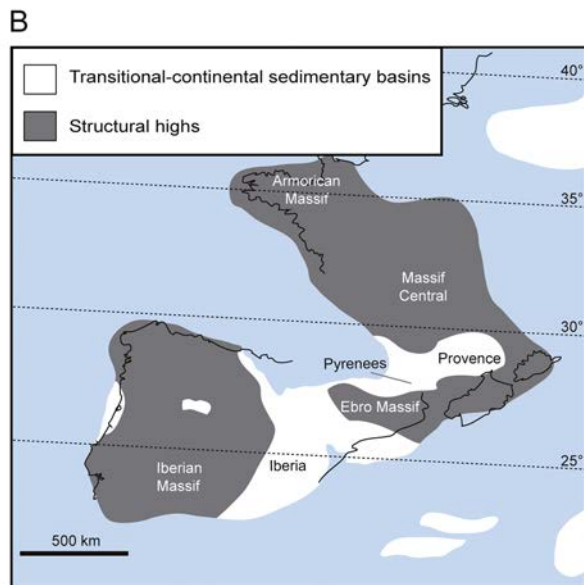
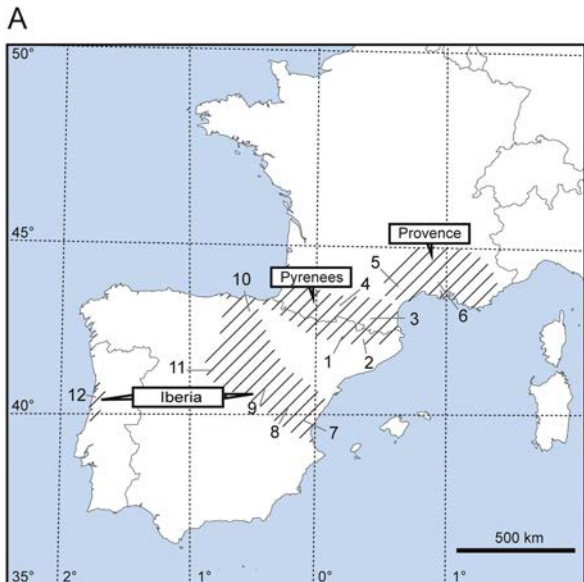


Figure 1

All synclines		Tresp Syncline		Àger Syncline
Mey et al. (1968)	Rosell et al. (2001)	Cuevas (1992)	Pujalte & Schmitz (2005)	Colombo & Cuevas (1993)
Tresp Fm	"Upper Red Garumnian"	La Guixera Mb	La Guixera Mb	Perauba Complex
		Claret Fm	Claret Fm Clg. Claret Mb	
	Esplugafreda Fm	Esplugafreda Fm	Calcàries Millà Fm.	
	"Vallcebre limestone & equivalents"	St. Salv. de Toló Fm ?		
"Lower Red Garumnian"	Talarn Fm.	Talarn Fm.	Figuerola Fm	
	Tossal Doba Mb	Tossal Doba Mb		
"Grey Garumnian"	Conques Fm	Conques Fm	La Maçana Fm	
	Basturs Mb	Basturs Mb		
Arén Fm & others	Arén Fm & others	Arén Fm	Arén Fm	Bona/Calc. Serres Fms

Figure 2

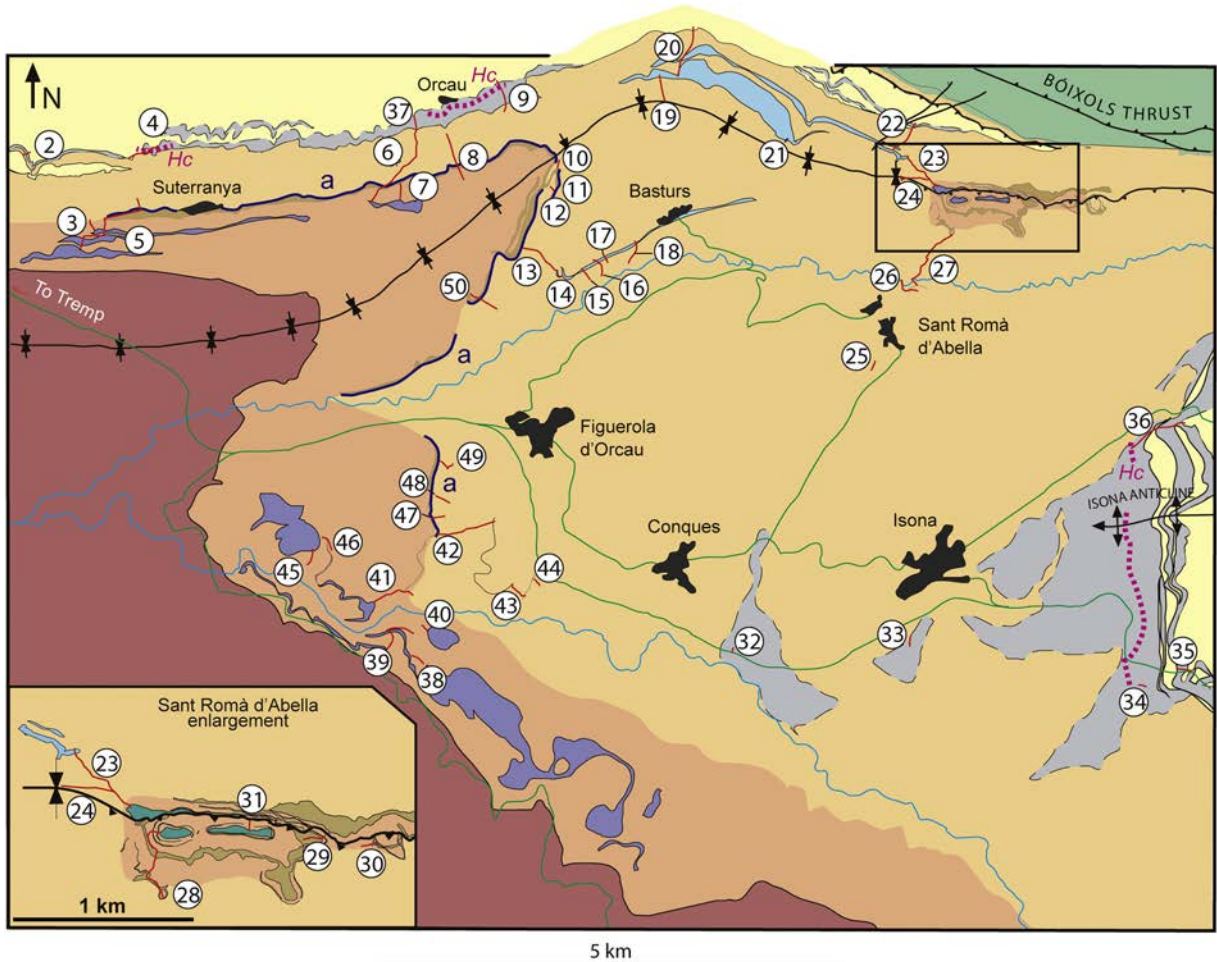
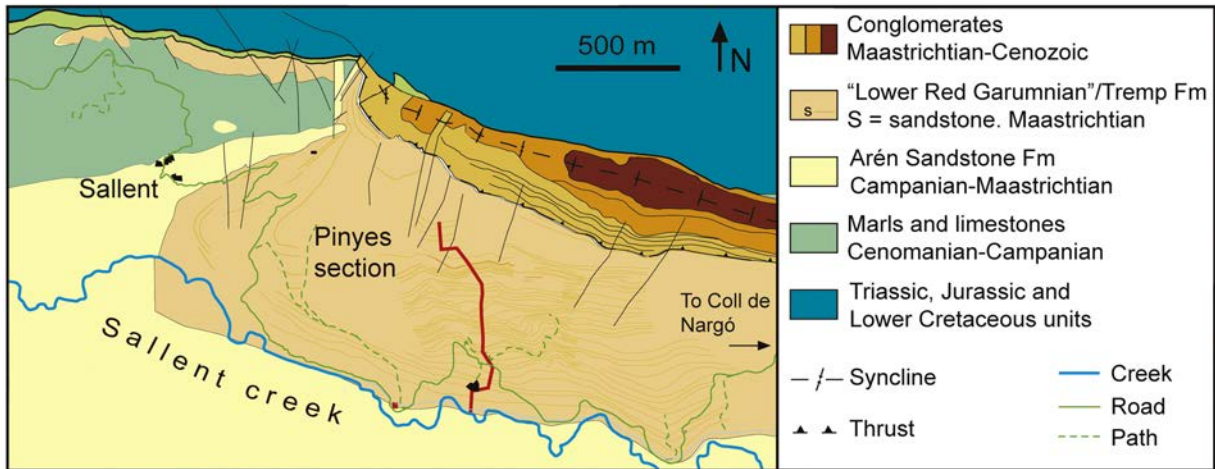


Figure 3

A



B

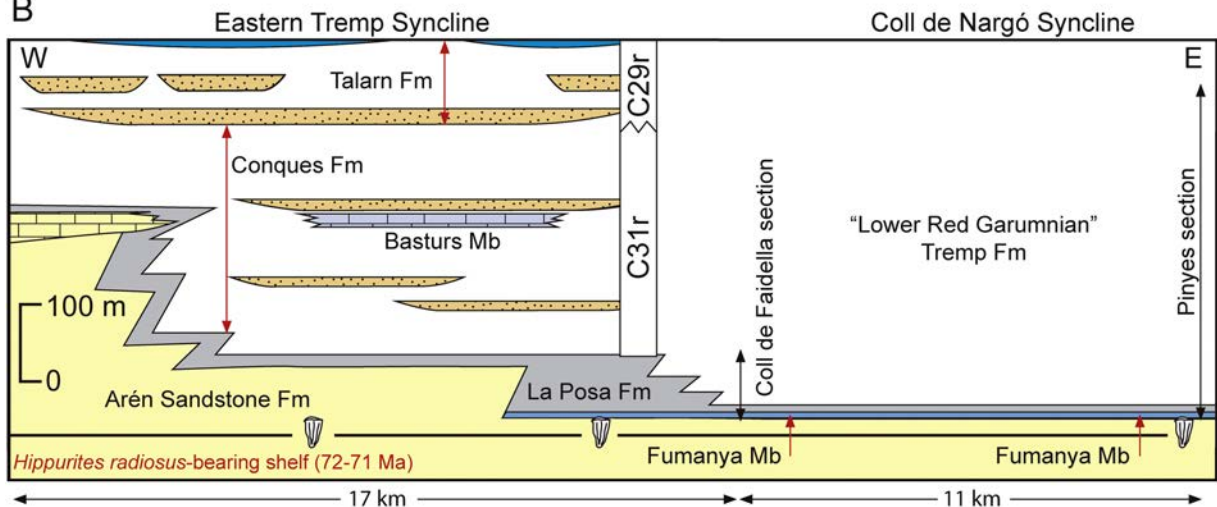


Figure 4

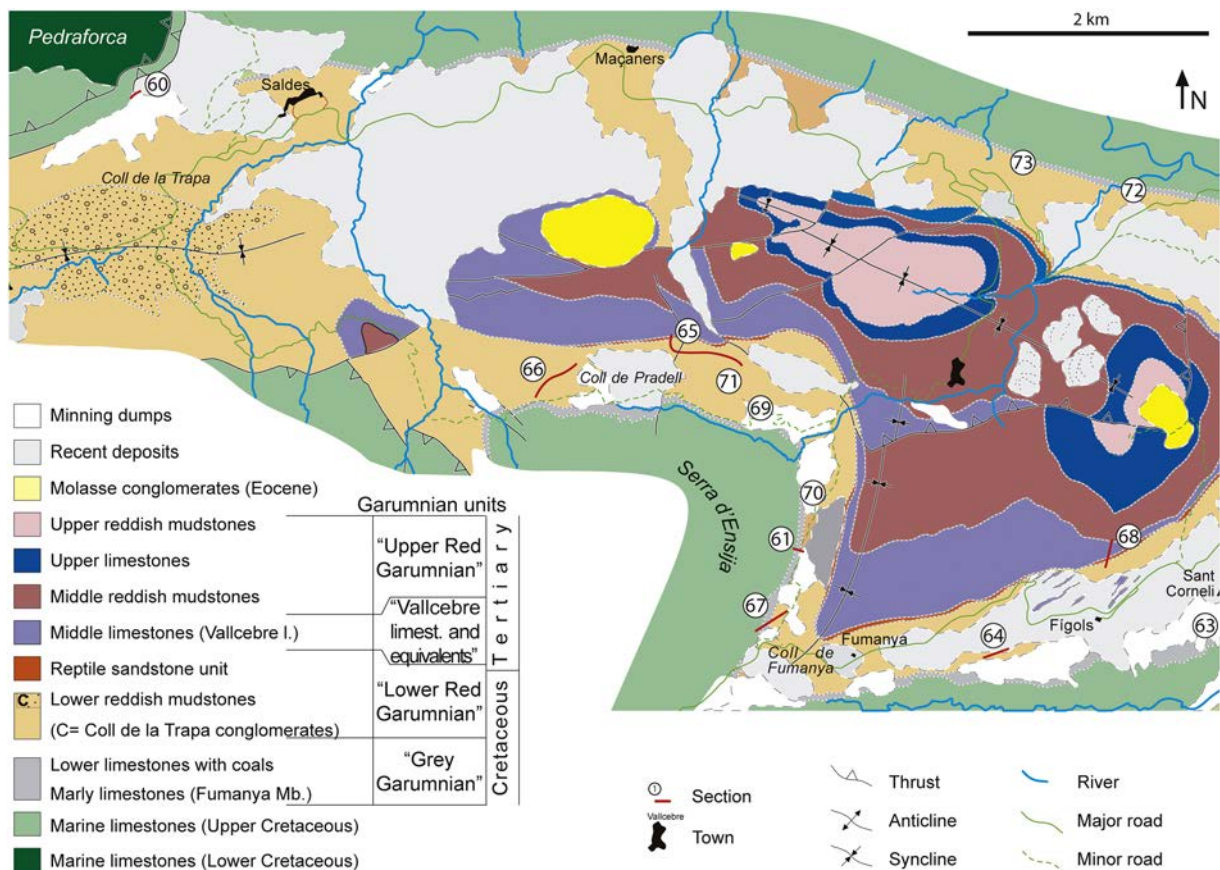


Figure 5

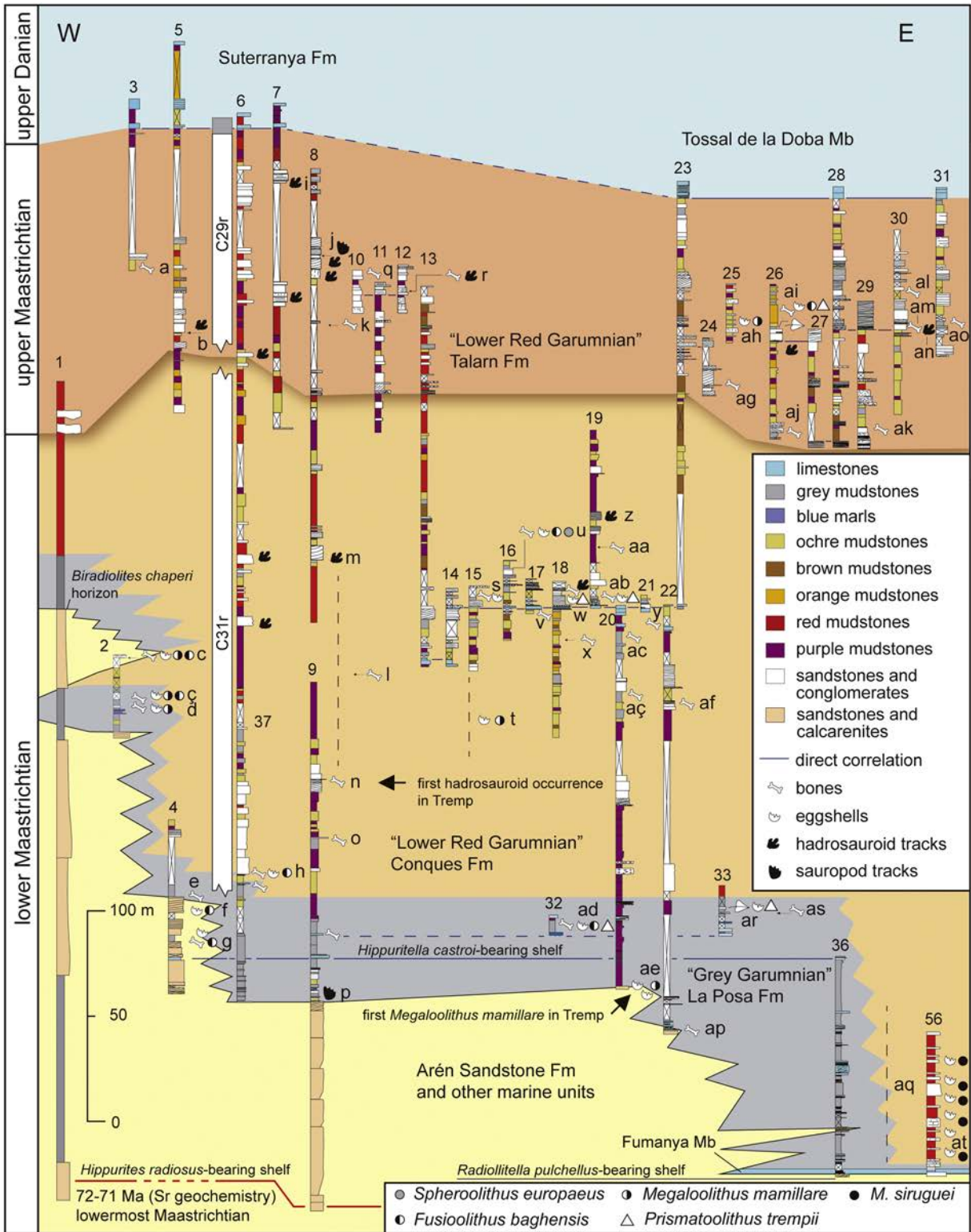


Figure 6

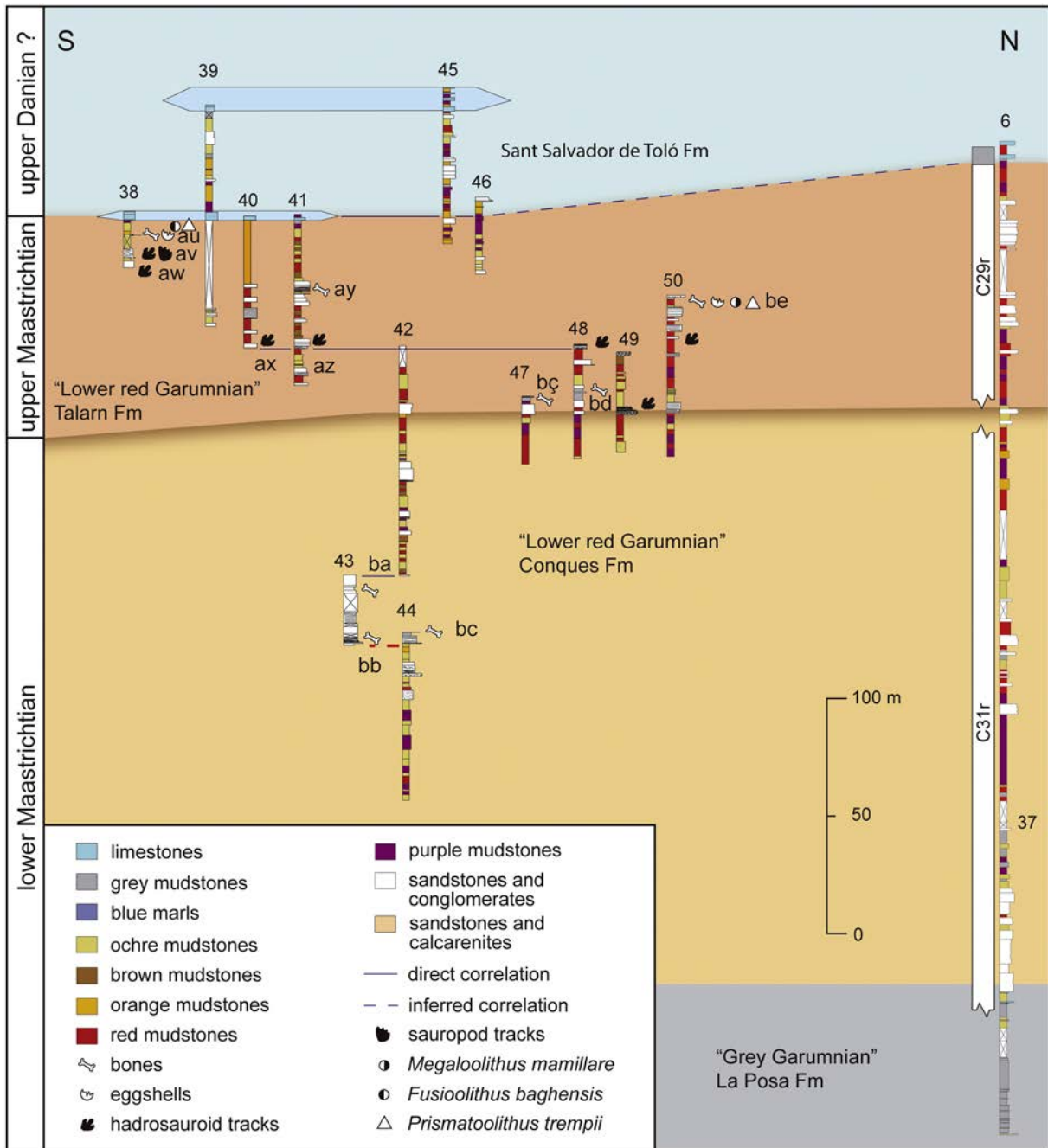


Figure 7

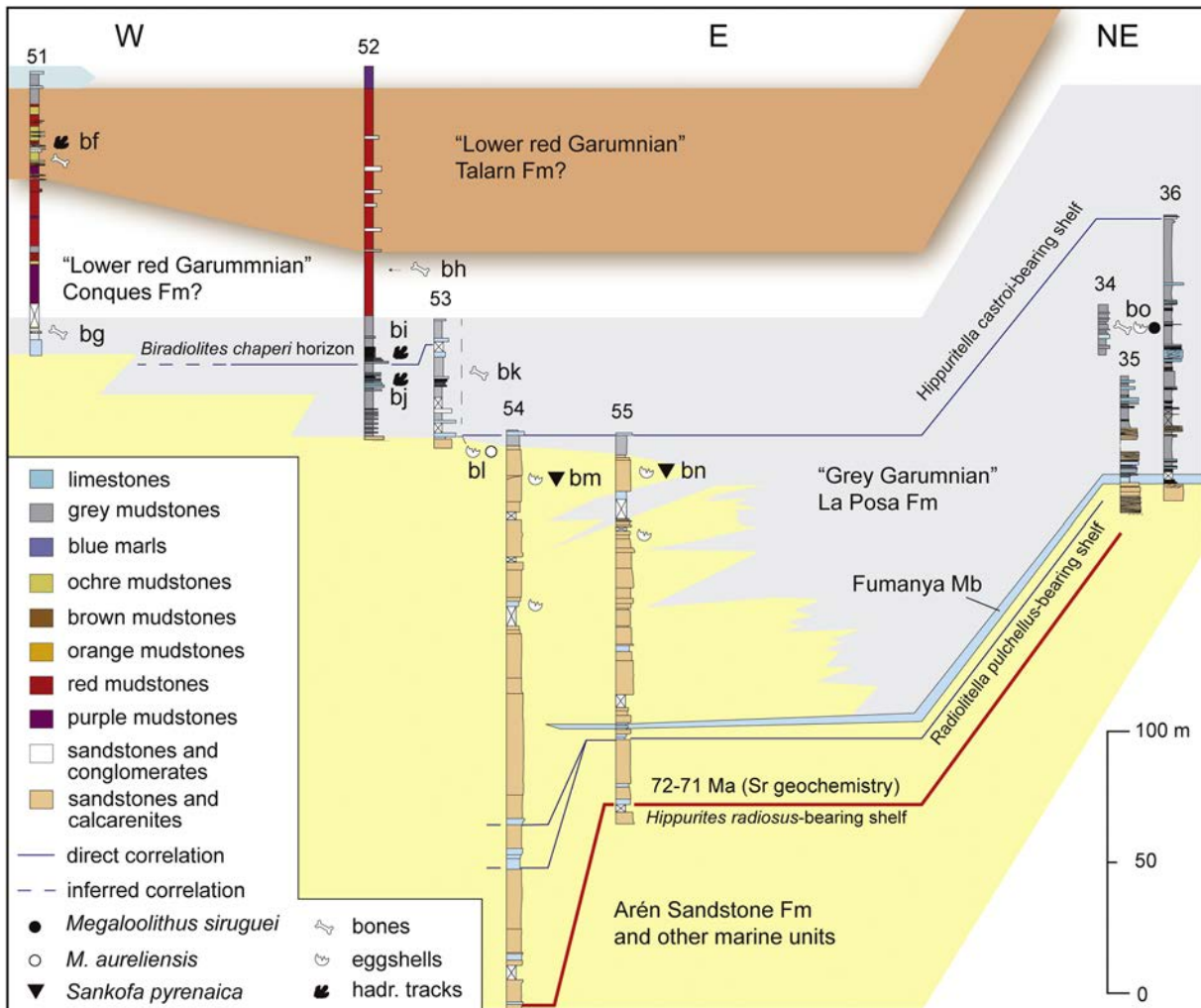


Figure 8

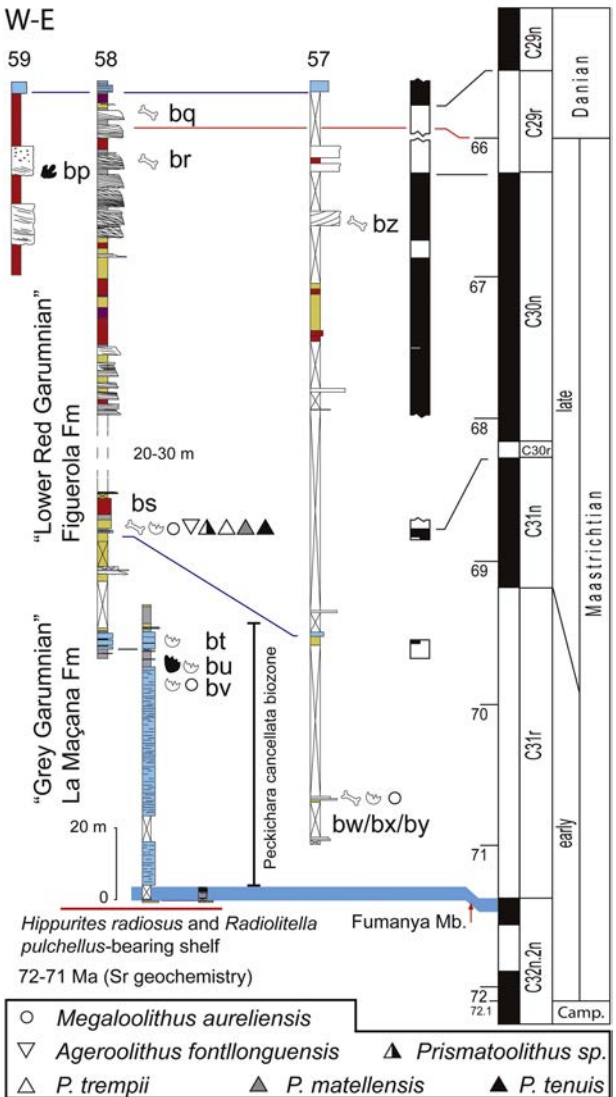


Figure 9

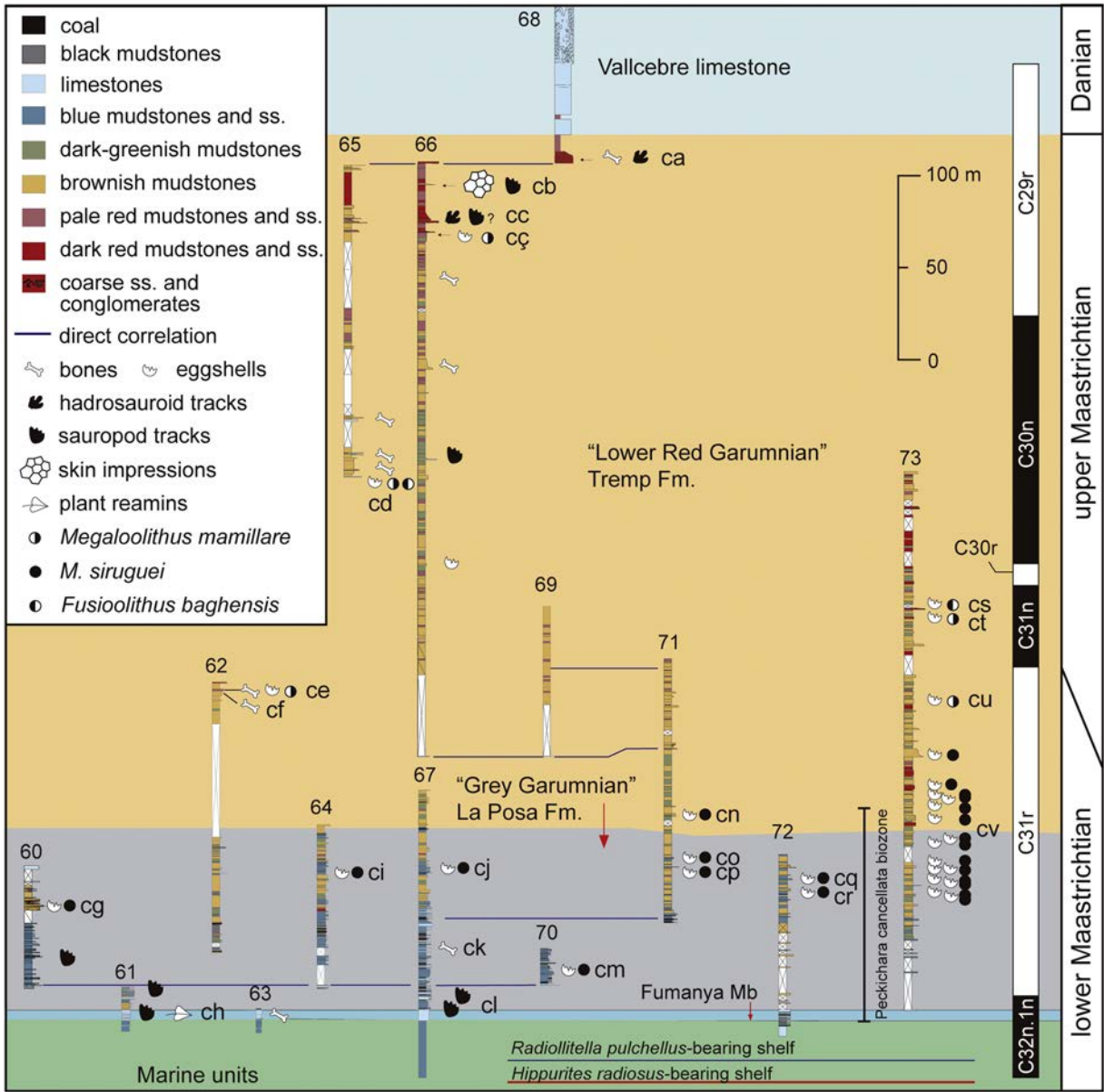


Figure 10

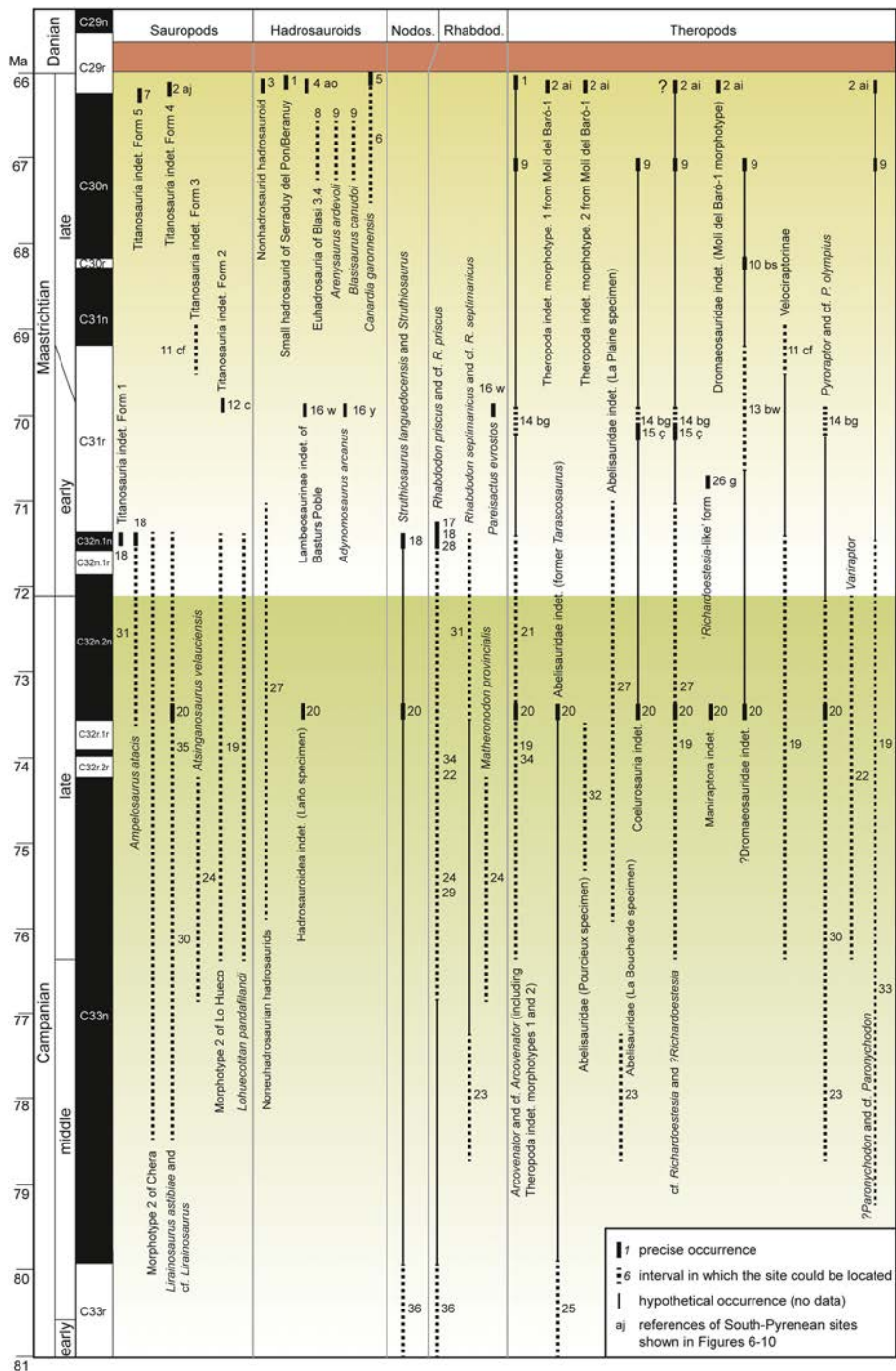


Figure 11

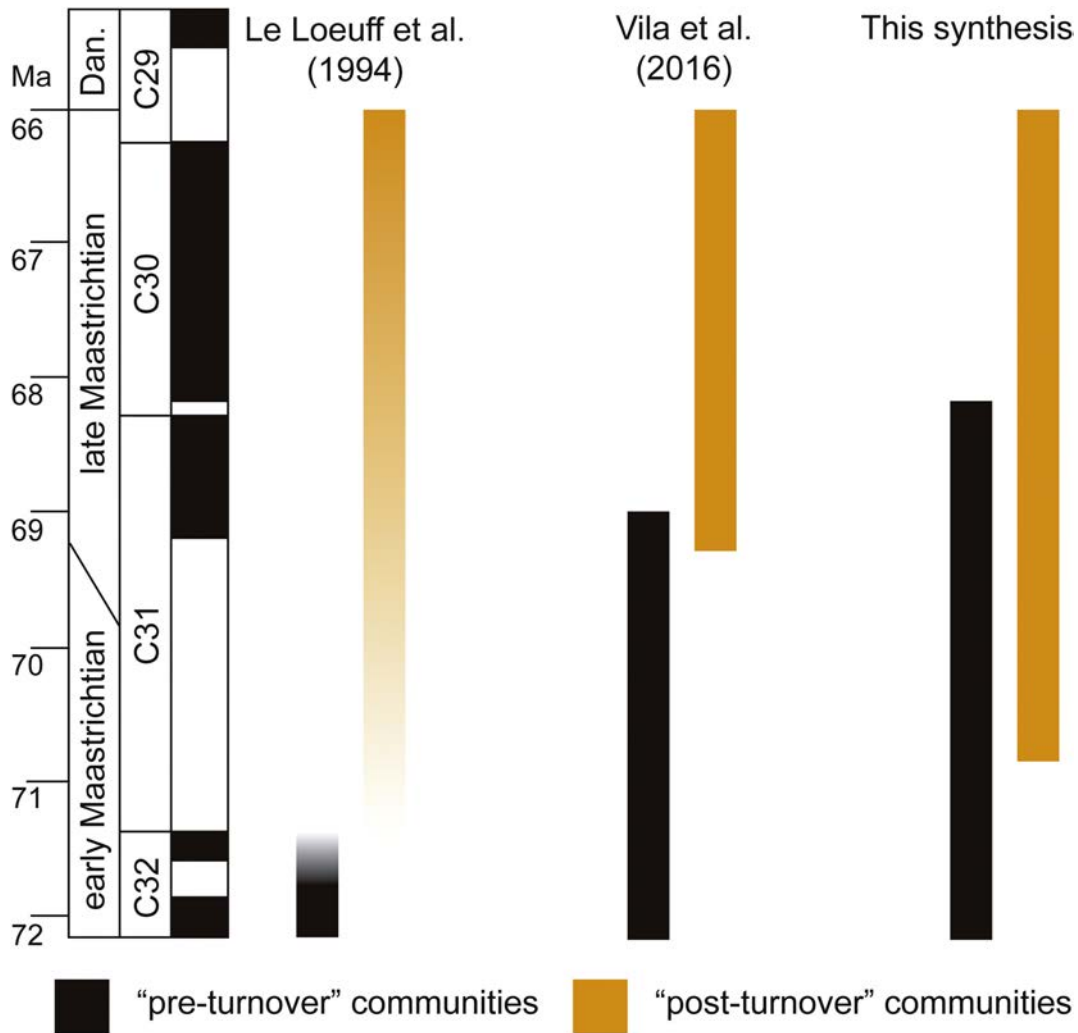


Figure 12

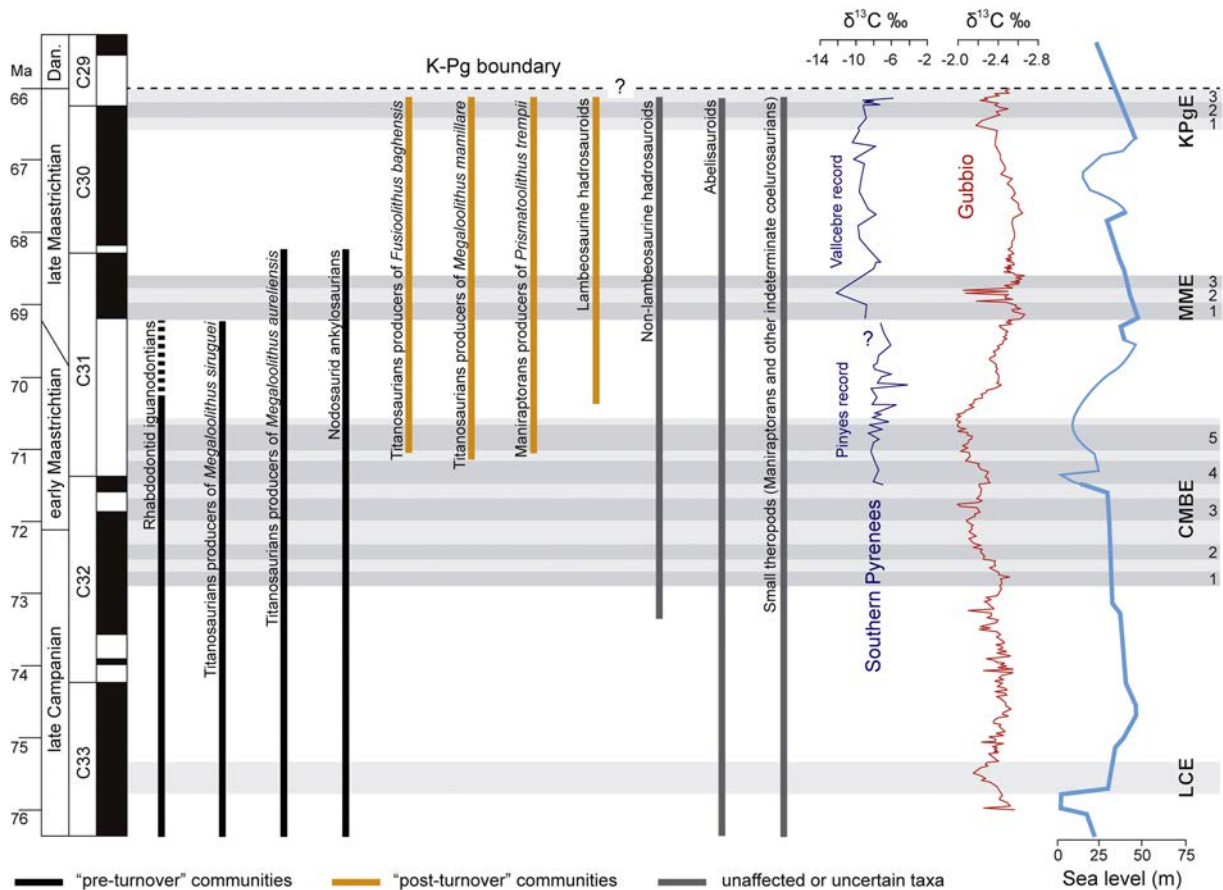


Figure 13