

## Re-evaluation of the age of some dinosaur localities from the southern Pyrenees by means of megaloolithid oospecies

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### Abstract

Since the beginning of the 20th Century the Upper Cretaceous continental and transitional marine deposits of the southern Pyrenees have produced more than 220 dinosaur fossil localities. New discoveries and advances in magnetostratigraphy and biostratigraphy provide a robust biostratigraphical framework for the latest Cretaceous dinosaur faunas in the region, although the age of some localities has remained uncertain. Here, we re-evaluate the age of some classic and new dinosaur fossil localities on the basis of the potential dating of megaloolithid oospecies and provide parataxonomic and age data for twenty-three localities with new megaloolithid egg fossils. Further, we review the nomenclature and probable synonymies of several of the most historically significant localities in the southern Pyrenees. With the new age assignments proposed for some significant localities (Basturs, Orcau-1, Els Nerets, Figuerola-2, Suterranya-1), we claim that in the southern Pyrenees a) the ankylosaurian dinosaurs survived beyond the early Maastrichtian-late Maastrichtian boundary and coexisted with hadrosauroids; b) the theropod record is scarce in the early Maastrichtian and the taxonomic diversity (richness) of theropods is notably higher in the late Maastrichtian; and c) the megaloolithid egg record assigned to sauropods is continuous through the entire Maastrichtian but is scarce in the Upper Campanian.

*Keywords:* dinosaurs, biostratigraphy, Late Cretaceous, Pyrenees, Megaloolithus

### Resumen

Desde principio del siglo XX los depósitos continentales y de transición de los Pirineos meridionales han producido más de 220 localidades con fósiles de dinosaurios. Los nuevos descubrimientos y los avances en magnetostratigrafía y biostratigrafía han proporcionado un robusto esquema biostratigráfico de las faunas finicretácicas de dinosaurios en la región, a pesar de que la edad de algunas localidades permanecía incierta. En el presente trabajo reevaluamos la edad de algunas localidades clásicas y nuevas con fósiles de dinosaurios en base al potencial de datación de las oospecies megaloolíticas y aportamos datos parataxonómicos y de edad para veintitrés localidades con nuevos fósiles de huevos megaloolíticos. Además, revisamos la nomenclatura y las probables sinonimias de varias de las localidades históricamente más significativas de los Pirineos meridionales. Con las nuevas asignaciones de edad propuestas en algunas localidades significativas (Basturs, Orcau-1, Els Nerets, Figuerola-2, Suterranya-1) se establece que en los Pirineos meridionales a) los dinosaurios anquilosaurios sobrepasaron el límite entre el Maastrichtiense inferior y superior y coexistieron con los hadrosauroides; b) el registro de terópodos es escaso en el Maastrichtiense inferior siendo remarcablemente más elevado en el Maastrichtiense superior; y c) el registro de huevos megaloolíticos asignados a saurópodos es continuo en todo el Maastrichtiense pero escaso en el Campaniense superior.

*Palabras clave:* dinosaurios, biostratigrafía, Cretácico Superior, Pirineos, Megaloolithus

## 1. Introduction

Areas of the present-day Pyrenees (southern France and north-eastern Spain) contain localities ranging from the late Campanian to the latest Maastrichtian, providing a produc-

tive succession of dinosaur fossil remains from the latest Cretaceous (Buffetaut and Le Loeuff, 1991; López-Martínez *et al.*, 2001; Laurent *et al.*, 2002; Riera *et al.*, 2009). In the last century more than two hundred localities have been discovered in the southern Pyrenees. Mr. Bartolomé Castell made

the first isolated findings in 1927 in the vicinity of Tremp (Marín and Bataller, 1929); these were followed by further prospects and geological field characterizations that yielded additional material from localities such as “Orcau”, “Suter-raña” and “Bastús” (Lapparent and Aguirre, 1956; Lapparent, 1958). In the early 1980s and 1990s more localities were described, including significant bone, egg and track localities such as Els Nerets, Sant Romà d’Abella, Fumanya and Fontllonga (Casanovas-Cladellas and Santafé-Llopis, 1993; Casanovas-Cladellas *et al.*, 1985, 1993; Le Loeuff and Martínez, 1997; López-Martínez *et al.*, 1998). Since then, various authors have compiled the fossil localities containing dinosaurs (López-Martínez, 2003; Vila *et al.*, 2006; Suñer *et al.*, 2008; Riera *et al.*, 2009), and at present the total number of localities is about 220. The stratigraphic age for these continental dinosaur-bearing localities has traditionally been provided by stratigraphic correlation with marine series (Ardèvol *et al.*, 2000) and magnetostratigraphy (Galbrun *et al.*, 1993), together with the use of various biostratigraphic markers (charophytes, palynomorphs, rudists; Feist and Colombo, 1983; Médus *et al.*, 1992; Riveline *et al.*, 1996; Vicens *et al.*, 2004). In the last decade, the profusion of new discoveries and the advances in magnetostratigraphy and biostratigraphy in the southern Pyrenees (López-Martínez *et al.*, 2001; Oms *et al.*, 2007; Pereda-Suberbiola *et al.*, 2009; Riera *et al.*, 2009; Prieto-Márquez *et al.*, 2013; Vila *et al.*, 2012, 2013) have allowed a more precise and robust correlation for these localities. Of special interest is the calibration of the succession of megaloolithid oospecies with the magnetostratigraphic scale (García and Vianey-Liaud, 2001; Vila *et al.*, 2011).

The aim of the present work is to re-evaluate the age of 20 historically significant localities by means of the use of oospecies and other biostratigraphic criteria and to provide age and parataxonomic data for 23 localities that yield new megaloolithid egg material. Further, we provide a review of the nomenclature and probable synonymies of 18 of the dinosaur localities in the southern Pyrenees.

## 2. Geological setting

The southern Pyrenees (NE Iberian Peninsula; Fig. 1) contain a 3000-m-thick succession of sedimentary rocks encompassing the transition from shallow marine carbonate platforms to fully continental environments (Riera *et al.*, 2009 and references therein). Two main geological units of latest Cretaceous age (late Campanian to late Maastrichtian) are recognized in the area: the Arén Sandstone Fm. and the Tremp Fm. The Arén Sandstone Fm. is composed of sandstones deposited in beach, barrier-island and deltaic systems; it passes gradually to the Tremp Fm. by a diachronic interfingering of strata (Díaz-Molina, 1987). The Tremp Formation has been divided informally into four lithologic units (Rosell *et al.*, 2001): 1) the “grey unit”, 2) the “lower red unit”, 3) the “Vallcebre Limestones and laterally equivalent strata”, and 4) the “upper red unit”.

The localities discussed in the present work are situated in distinct areas of the provinces of Barcelona and Lleida; from east to west these are: the Vallcebre, Coll de Nargó, Tremp and Àger synclines. In these areas, the deposits of late Campanian to latest Maastrichtian age have yielded a diverse and abundant tetrapod fossil record that comprises dinosaurs (sauropods, theropods, ornithomorphs and ankylosaurs; López-Martínez *et al.*, 2001; Riera *et al.*, 2009; Pereda-Suberbiola *et al.*, 2009; Cruzado-Caballero *et al.*, 2010; Vila *et al.*, 2012; Prieto-Márquez *et al.*, 2013; Torices *et al.*, in press), pterosaurs (Dalla Vecchia *et al.*, 2013), crocodylians (Puértolas *et al.*, 2011; Puértolas-Pascual *et al.*, 2014), turtles (Marmi *et al.*, 2012), and amphibians and squamate reptiles (Blain *et al.*, 2010).

## 3. Methods and materials

We have reviewed the names of 18 south-Pyrenean localities and standardized with the current toponymy, correcting previous misspellings and providing name equivalences. When possible, the criterion followed for assigning the name to a locality has been its primary citation in the literature. Many localities have received different names after their first being reported and in cases where the secondary name has been cited more frequently in the literature, we have chosen to maintain the more extensively used name. If, after the review and name standardization, the locality name coincides with a previous naming we have added numerals in order to avoid misunderstandings. Regarding terminology, we used “locality” to refer a discrete area or stratigraphic section where fossils occur and which may or may not include various sites. A “site” refers to a discrete fossil-bearing level within a locality.

The new eggshell fragments described in the present study (Appendix 1) were collected from both classic and unreported localities in the southern Pyrenees (Fig. 1). These fossil remains were treated with potassium hydroxide (KOH) and/or sodium hexametaphosphate (SHMP) 30%, and cleaned in an ultrasonic bath (Val *et al.*, 2014). Samples were preliminarily analyzed using the Leica® M60 binocular, and structural characters (e.g. shell thickness, ornamental pattern, pore aperture width) were measured using Leica® Application Suite 2.8.1 software. Several samples were prepared as standard thin sections (30 µm-thick) while others were examined and photographed using the electronic microscope ESEM Quanta 200 FEI, XTE 325/D8395, in the Department of Scientific-Technical Services of the Universitat de Barcelona. Eggshells were identified in terms of parataxonomy following Mikhailov (1997).

The studied material is housed in the collection of the Institut Català de Paleontologia (IPS-58959, 58960, 58963 to 58965, 58967, 58968, 58975, 58982, 58987, 58992, 59132 to 59135, 59137, 82173 to 82180, 82182 to 82227, 82230 to 82270).

Institutional abbreviation: IPS, Institut de Paleontologia de Sabadell.

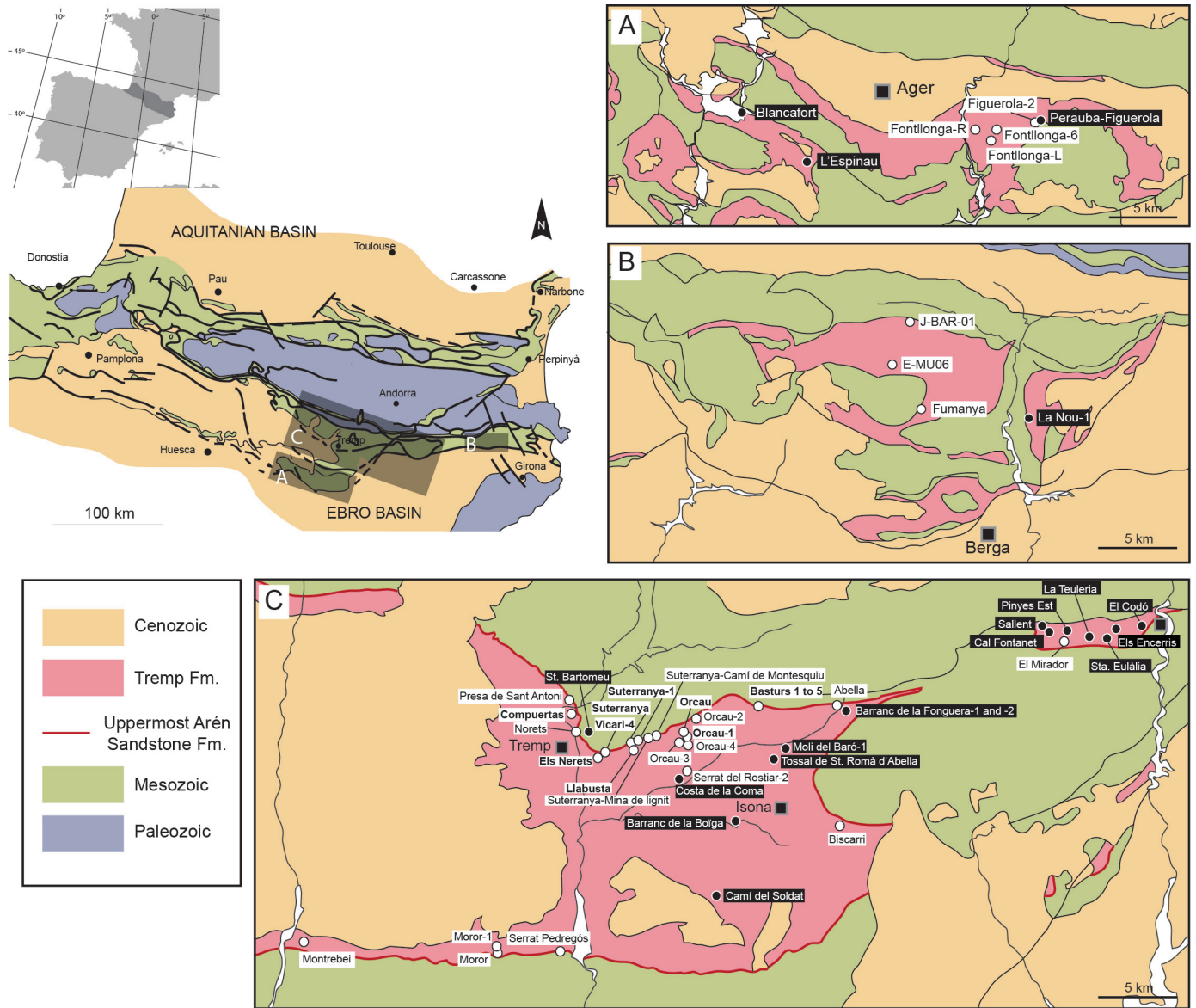


Fig. 1.- Geographical and geological location of the latest Cretaceous outcrops and localities studied or mentioned in the present work. A) Àger syncline, B) Vallcebre syncline, C) Coll de Nargó and Tremp synclines. The location of the Fontllonga L, Norets, Suterranya, and Compuertas is approximative. Names in white square: known localities. Names in black square: new eggshell localities. Names in bold: indicate localities that have changed its age after this review.

## 4. Results

### 4.1. Historical review of the nomenclature and synonymies of some dinosaur localities

Since the earliest dinosaur discoveries in the southern Pyrenees various authors have published data on particular localities, sometimes generating a number of different names or spellings for the same locality. It is out of the scope of the present work to review the nomenclature of all the southern Pyrenean localities, but in order to avoid further misunderstandings in some of the cases, we here discuss and standardize their name and synonymy (Table 1).

Several dinosaur remains were recovered in the area around the villages of Talarn, Suterranya and Orcau (Tremp Basin).

Lapparent and Aguirre (1956) reported various fossil localities in the basal levels of the “grey unit” of the Tremp Formation in this area (Pereda-Suberbiola and Ruiz-Omeñaca, 2012). The Presa de San Antonio locality reported by Lapparent and Aguirre (1956, p. 379) is situated near the village of Talarn and is probably equivalent to Sant Antoni-2 referred to Ardèvol *et al.* (1995), which was later named Presa de Tremp by Vila *et al.* (2012). The locality may correspond to that described by Bartolomé Castell in 1927 (Marín and Bataller, 1929). Southwards, the Norets locality referred to Pereda-Suberbiola *et al.* (2003) is equivalent to the Point 2 of Lapparent and Aguirre (1956, p. 380). The Els Nerets locality, originally referred to Casanovas-Cladellas *et al.* (1985), is equivalent to Vilamitjana-1 (V-1) of Ardèvol *et al.* (1995). It is also worth noting that the eggshell locality Vicari referred

Locality name	Previous names and equivalences
Presa de Sant Antoni	“Pres de San Antonio” or Point 1 of Lapparent and Aguirre (1956, p. 379), “Sant Antoni-2” of Ardèvol et al. (1995), Presa de Tremp after Vila et al. (2012).
Norets after Pereda-Suberbiola et al. (2003)	Point 2 of Lapparent and Aguirre (1956, p. 380)
Els Nerets after Casanovas-Cladellas et al. (1985)	V-1 (Vilamitjana-1) of Ardèvol et al. (1995)
Suterranya-Camí de Montesquiu	Point 3 of Lapparent and Aguirre (1956, p. 380)
Suterranya-Mina de lignit	Point 4 of Lapparent and Aguirre (1956, p. 380) , “Suterranya” of Escaso et al. (2010)
Suterranya	“Suterraña” of Moratalla (1993)
Suterranya-1 after Ardèvol et al. (1995)	“L’Abeller” of Prieto-Márquez et al. (2000), “Suterraña” of Torices et al. (in press)
Orcau-1 after Ardèvol et al. (1995)	“Orcau” of Lapparent and Aguirre (1956)
Orcau-2 after Ardèvol et al. (1995)	“Orcau” of Llompart et al. (1984)
Orcau after Moratalla (1993)	-
Moror	“Moró” of Brinkmann (1984)
Moror-1	“Moro” of Vianey-Liaud and López-Martínez (1997), López-Martínez (2000) and Bravo and Marugán-Lobón (2013)
Serrat Pedregós after López-Martínez and Vicens (2012)	Cellers-2 of López-Martínez (2000)
Montrebei after López-Martínez, (2000)	misspelled “Montrebey” in Torices Hernández (2002)
Fontllonga-6 after Vianey-Liaud and López-Martínez (1997)	“Fontllonga” of Casanovas-Cladellas and Santafé-Llopis (1993)
Fontllonga L after Moratalla (1998)	“Fontllonga” of Moratalla (1993)
Fontllonga of Casanovas et al. (1999)	“Fontllonga R” of López-Martínez (2003)
Santa Eulàlia-1 to -4	misspelled “Santa Eulària” in López-Martínez (2000)

Table 1.- Nomenclature and synonymies of some of the south-Pyrenean dinosaur localities discussed in the present work.

to by Moratalla (1993, 1998) and López-Martínez (2000) may be equivalent to the Vicari-4 locality of Torices Hernández (2002) and Torices *et al.* (2004, 2012).

In the vicinity of the village of Suterranya, up to four localities were distinguished. The first locality, here named “Suterranya-Camí de Montesquiu” (Point 3 of Lapparent and Aguirre, 1956, p. 380), was discovered by Walter Georg Kühne in 1954 and yielded several dinosaur bones of indeterminate affinity. The second locality, here named “Suterranya-Mina de lignit” (Point 4 of Lapparent and Aguirre, 1956, p. 380), was discovered by Josep Montané and yielded mainly fragmentary dinosaur bones currently housed in the Museo Nacional de Ciencias Naturales (MNCN) in Madrid. After conversations with Josep Montané and revision of the MNCN collections, we could claim that this latter locality probably yielded the ankylosaur bones reported by Escaso *et al.* (2010) as well as other fragmentary bones of sauropod affinity. In addition, Moratalla (1993) reported dinosaur eggshells from the Suterranya locality (originally spelled “Suterraña”); finally, Ardèvol *et al.* (1995, 1999) reported the egg locality of Suterranya-1, which is a synonym of the L’Abeller locality reported by Prieto-Márquez *et al.* (2000) and “Suterraña” of Torices *et al.* (in press); this also yielded an isolated theropod tooth.

At least five dinosaur localities have been reported in the vicinity of the village of Orcau. Lapparent and Aguirre (1956) distinguished four localities with dinosaur remains, the most important being that of “Orcau” discovered by W.G. Kühne in 1954 and containing various sauropod bones. Llompart *et*

*al.* (1984) described dinosaur tracks east of the village of Orcau. Ardèvol *et al.* (1995) renamed the bone and track localities as Orcau-1 and Orcau-2, respectively. Riera *et al.* (2009) and Vila *et al.* (2013) followed the same procedure for naming the localities of Orcau-3 (bones) and Orcau-4 (tracks), respectively. Finally, Moratalla (1993, 1998) reported dinosaur eggshells from a locality called Orcau.

At the southern margin of the Tremp Basin, Brinkmann (1984) described dinosaur remains in the Moror locality (misspelled “Moró”); some years later, Vianey-Liaud and López-Martínez (1997) and subsequent works (López-Martínez, 2000; Bravo and Marugán-Lobón, 2013) referred to an egg locality as “Moro” (we here correct the misspelling and change the name to Moror-1 for the sake of distinction). López-Martínez and Vicens (2012) also described the Serrat Pedregós egg locality, which is equivalent to the Cellers-2 locality referred to by the same authors some years before (López-Martínez, 2000). The latter author also reported the Montrebei eggshell and tooth locality (misspelled “Montrebey” by Torices Hernández, 2002).

In the Àger syncline, various authors reported dinosaur remains from at least three localities with similar names. The first locality reported in the literature was “Fontllonga” (Casanovas-Cladellas and Santafé-Llopis, 1993), which is the same locality later reported by Vianey-Liaud and López-Martínez (1997) and subsequent works as Fontllonga-6. In the same year Moratalla (1993) gave the name “Fontllonga” (later named “Fontllonga L”; Moratalla, 1998) to a locality with dinosaur eggshells. Another locality in the area, also



named “Fontllonga” (Casanovas *et al.*, 1999) and yielding a hadrosaur dentary, is a synonym of “Fontllonga R” of López-Martínez (2003).

In the Coll de Nargó syncline, López-Martínez (2000) reported “several superposed levels with scattered clutches” in the area of “Santa Eulària”, which probably correspond to the sites of Santa Eulària-1 to -4 (we have corrected the misspelling), sampled in the present work (Appendix 1).

#### 4.2. Parataxonomical study

The parataxonomical study of dinosaur eggshells collected in new and classical localities of the southern Pyrenees allows them to be attributed to four megaloolithid oospecies: *Megaloolithus aureliensis*, *M. siruguei*, *M. mamillare* and *M. baghensis* (see Appendix 2 for further data and discussion). The studied sample includes 2738 eggshell fragments from in situ complete eggs, eggshell accumulations (egg debris) and scattered eggshells (Appendix 1). Most eggshells occur in overbank deposits associated with fluvial or lagoonal systems, in grey to reddish mudstones and marls, or in limestones associated with lacustrine settings.

### 5. Discussion

#### 5.1 Review and update of the age of some dinosaur localities

Some authors have argued that dinosaur eggshells can be used as biochronological markers in continental deposits (García and Vianey-Liaud, 2001). This idea, originally proposed for the Aix Basin in Provence (France), has been successfully exported to the southern Pyrenees regions of Vallcebre and Coll de Nargó (Vila *et al.*, 2011; Sellés *et al.*, 2013). The oospecies assemblages (properly named oozones, see Sellés *et al.*, 2013) are calibrated with magnetochrons and indicate restricted temporal ranges for the megaloolithid oospecies (Fig. 2). For instance, the dominance of *M. siruguei* (together with the oospecies *M. aureliensis* and *Cairanoolithus*) mainly indicates a late Campanian to early Maastrichtian age; its replacement with *Megaloolithus mamillare* occurs around the C31r-C31n polarity change; and the appearance of *M. mamillare* and/or *M. baghensis* (formerly *M. pseudomamillare*, Vianey-Liaud *et al.*, 2003) indicates a late Maastrichtian age (García and Vianey-Liaud, 2001; Vila *et al.*, 2011; Sellés *et al.*, 2013).

In the present work, the use of oozones based on megaloolithid oospecies enables the re-evaluation of the age of several localities (Fig. 2A). In the eastern part of the Tremp Basin, the Biscarri egg locality yielded the oospecies *Megaloolithus siruguei* and was originally referred to the late Campanian (López-Martínez *et al.*, 2000). This oospecies is represented in Oozone 1, which is of late Campanian-early Maastrichtian age (García and Vianey-Liaud, 2001), but also on its own in Oozone 2, of early Maastrichtian age (García and Vianey-Liaud, 2001; Vila *et al.*, 2011). The new magnetostratigraphic

correlations of lower Tremp Formation units in the Tremp Basin (Vila *et al.*, 2012) indicate that the basal part of the formation is probably early Maastrichtian in age and thus the Biscarri locality (together with the Barranc de la Fonguera locality; Appendix 1) would be early Maastrichtian in age.

At the north-western margin of the Tremp Basin the age of the localities of Basturs, Orcau-1, Els Nerets, Orcau, Llabusta, Vicari, Compuertas, Suterranya, Suterranya-1, and Abella has been re-evaluated (Appendix 1). Basturs (originally spelled “Bastus” by Lapparent, 1958) was the first egg locality to be discovered in the southern Pyrenees. This nesting area refers to various egg levels (the egg-bearing sites of Basturs-1, Basturs-2, Basturs-4, and Basturs-5; Ardèvol *et al.*, 1999) and was considered early Danian by Lapparent (1958), Maastrichtian by Moratalla (1993), “upper Rognacian” by Vianey-Liaud and López-Martínez (1997), and late Campanian by López-Martínez (2000) and Díaz-Molina *et al.* (2007). Moratalla (1993, 1998) and Vianey-Liaud and López-Martínez (1997) reported the oospecies *M. mamillare* in the Basturs-1 and Basturs-2 sites, and therefore they are here considered late Maastrichtian in age.

At the end of 1954 W.G. Kühne discovered the bone locality of Orcau-1 (originally named “Orcau” by Lapparent and Aguirre, 1956). These authors and Casanovas *et al.* (1987) referred the age of the locality to the Maastrichtian. Casanovas-Cladellas *et al.* (1985) reported the locality of Els Nerets (Tremp, Lleida), which was considered Maastrichtian in age. López-Martínez (2000) dated it as late Campanian, and most recently Dalla Vecchia *et al.* (2014) have suggested a late Maastrichtian age on the basis of the stratigraphic correlation of Riera *et al.* (2009) but with no further biostratigraphic constraints. Recent prospects and excavations in the Orcau-1 and Els Nerets localities indicate that they bear *Megaloolithus baghensis* and *M. mamillare* eggshells, respectively (Appendices 1 and 2), hence supporting a late Maastrichtian age.

Moratalla (1993, 1998) reported the oospecies *Megaloolithus cf. mamillare* and/or *M. trempii* in the localities of Orcau, Llabusta, Vicari, Compuertas, Fontllonga L and Suterranya, and Vianey-Liaud and López-Martínez (1997) identified the oospecies *M. pseudomamillare* and *M. mamillare* oospecies in the Suterranya-1 and Abella localities, respectively. Moratalla (1993) considered the eggshell localities of Orcau, Llabusta, Vicari, Compuertas and Suterranya to be Maastrichtian in age, whereas López-Martínez (2000) suggested a latest Campanian age for these as well as for the Suterranya-1 and Abella localities. In the case of the Vicari locality, Torices *et al.* (2012) indicated that the Vicari section encompasses the latest Campanian but also the early Maastrichtian. The authors also located the Vicari-4 locality, previously referred to the late Campanian but with no further information on the parataxonomic affinity of the eggshells (Torices Hernández, 2002; Torices *et al.* 2004; in press). Vicari-4 is geographically near to where Moratalla (1993) reported the Vicari locality, being located in the same ravine, and we consider that, if not the same site, they may both have a similar strati-

graphic position and age. The present work maintains that *M. pseudomamillare* and *M. trempii* must be synonymised with *M. baghensis* and *M. cf. mamillare* with *M. mamillare* (Appendix 2); therefore, the occurrence of these oospecies in the abovementioned localities (Orcau, Llabusta, Vicari, Compuertas, Fontllonga L, Suterranya, Suterranya-1 and Abella) indicates a late Maastrichtian age. At the south-western margin of the Tremp Basin, we concur with Prieto-Márquez *et al.* (2013) that the Moror locality (the “Moró” locality reported by Brinkmann, 1984, 1988) is probably late Maastrichtian in age given the diachronous deposition of the “grey unit”, which took place in a regressive context, and given that it becomes younger westward. Likewise, the Moror-1 locality would be of similar age. However, the latter locality yielded what were purported to be *M. petralta* eggshells and was dated as “early Rognacian” (Vianey-Liaud and López-Martínez, 1997). Pending the revision of this eggshell material, the age of this locality remains controversial. The Montrebei locality, which was originally regarded as early Maastrichtian (López-Martínez, 2000) and later as late Campanian-early Maastrichtian in age (Torices *et al.*, in press), may also be of late Maastrichtian age. Unfortunately, there are no published data on the parataxonomic affinity of the dinosaurs eggshells recovered in this locality (López-Martínez, 2000), and the charophyte content (only *Clavator brachycerus*) has an ambiguous and wide stratigraphic range (Villalba-Breva and Martín-Closas, 2012).

In the Àger syncline, the Perauba-Figuerola locality represents the only south-Pyrenean locality with rhabdodontid remains (Llompert and Krauss, 1982) and yielded the oospecies *Megaloolithus aureliensis* (Appendix 1). Torices *et al.* (in press) reported dinosaur eggshells at the Figuerola-2 locality, but no further taxonomic assignment is provided by the authors. Figuerola-2 was originally regarded as early Maastrichtian (Torices Hernández, 2002) and later as late Campanian (López-Martínez, 2003; Torices *et al.* 2004; in press). The two localities are geographically adjacent to one another (about 25 m apart) and stratigraphically almost equivalent. They are located in the lower part of the “Figuerola de Meià” unit, the regional equivalent of the “lower red unit” of the Tremp Formation. This continental unit contains a charophyte assemblage of Maastrichtian age (*Septorella brachycera*, *S. ultima*, *Peckichara sertulata*, and *Maedleriella* sp.; Fig. 2B) and overlies the La Maçana Fm., which is considered late Campanian in age on the basis of its charophyte assemblages (Villalba-Breva and Martín-Closas, 2012). Thus, the recent data on charophyte biostratigraphy indicate that both localities are most probably early Maastrichtian in age. The new age assignment is consistent with the magnetostratigraphical data of Galbrun *et al.* (1993), who correlated the base of the “Figuerola de Meià” unit with the C32r magnetochron (currently early Maastrichtian in age after Gradstein *et al.*, 2012).

López-Martínez (2003) reported dinosaur eggshells from the Blancafort locality although she did not provide any further parataxonomic assignment. Recently, we have collected

several eggshells, which have been attributed to *Megaloolithus aureliensis* (Appendices 1 and 2). The samples come from a lacustrine limestone on top of the La Maçana Fm. (late Campanian in age according to charophyte assemblages; Villalba-Breva and Martín-Closas, 2012). The occurrence of the oospecies *M. aureliensis* oospecies in Blancafort is consistent with this age assignment since this oospecies ranges temporally from the late Campanian to the early Maastrichtian (García and Vianey-Liaud, 2001).

In the Coll de Nargó syncline most of the multiple egg-bearing sites (Appendix 1) in the localities of Sallent, El Codó, Pinyes Est, Santa Eulàlia, La Teuleria, Cal Fontanet, and Els Encerris yielded a single oospecies, *Megaloolithus siruguei* (Appendix 2). The occurrence of this single oospecies for more than 100 m of stratigraphic section seems to indicate that most of these localities fall within the oozone 2 (in accordance with Sellés *et al.*, 2013), which is mainly characteristic of the early Maastrichtian (Fig. 2A, B). In the same region the El Mirador locality yielded three megaloolithid oospecies (*Cairanoolithus roussetensis*, *Megaloolithus siruguei* and *M. aureliensis*; Sellés *et al.*, 2013). This co-occurrence originally seemed to be characteristic of the late Campanian Oozone 1 of García and Vianey-Liaud (2001) but with the new age calibration of Gradstein *et al.* (2012) the assemblage extends within the early Maastrichtian (C32n.1n). In the case of El Mirador locality, Sellés *et al.* (2013) assumed that it probably represents the last co-occurrence of these ootaxa in the Coll de Nargó area, and therefore the site may fall on the upper part of the C32n.1n and be early Maastrichtian in age. Finally, as noted by Vila *et al.* (2011) and Sellés *et al.* (2013), the egg-bearing sites of the upper part of the Coll Nargó and Valcebres sections contain the oospecies *M. siruguei* right in contact with *M. mamillare* or *M. baghensis* (sites of Pinyes Est-5, Santa Eulàlia-3, El Codó-41, E-MUN06, J-BAR01; Appendix 1). This probably indicates that these sites fall around the C31r-C31n reversal, which is late Maastrichtian in age according to the recent age calibrations of Gradstein *et al.* (2012).

Regarding the new eggshell-bearing localities reported in the present work (Appendices 1 and 2), some of them yielded *M. mamillare* eggshells (La Nou-1, Berguedà area, Barcelona; Tossal de Sant Romà d'Abella, and Costa de la Coma, Tremp Basin, Lleida) and *M. baghensis* eggshells (Sant Bartomeu, Barranc de la Boïga, Molí del Baró-1, Serrat del Rostiar-2, and Camí del Soldat, Tremp Basin, Lleida; L'Espinau, Àger Syncline, Lleida) and hence indicate a late Maastrichtian age. It is worth noting that some of these reports (localities of La Nou-1, Camí del Soldat and Molí del Baró-1) expand the temporal range of these two oospecies (*M. mamillare* and *M. baghensis*) into the C29r magnetochron (Fig. 2A).

### 5.2 Implications for dinosaur faunal turnover

Le Loeuff *et al.* (1994) stated that a faunal replacement occurred around the early Maastrichtian-late Maastrichtian

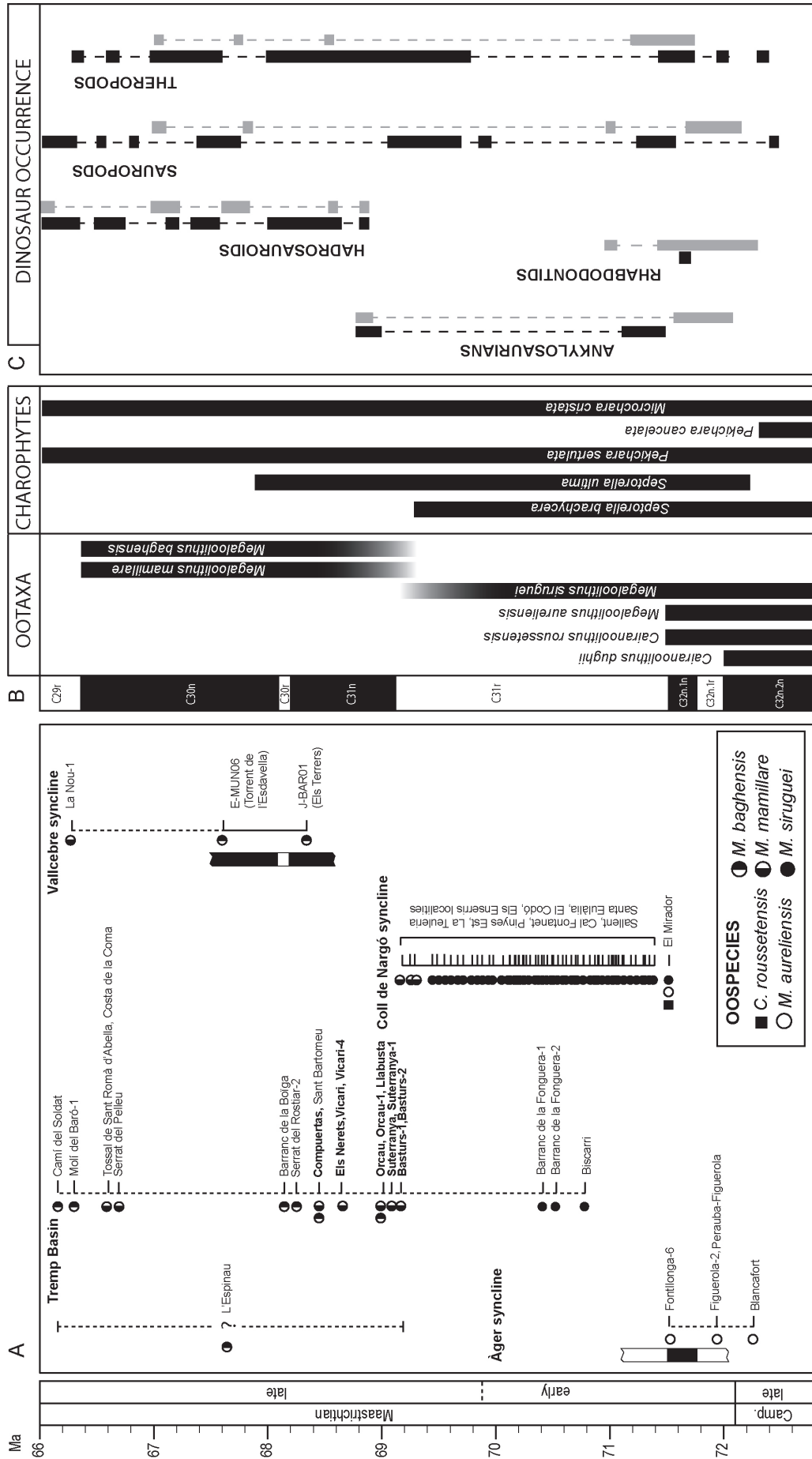


Fig. 2.- Temporal distribution of the egg-bearing localities discussed in the present work. A) Chronostratigraphy of the localities with megaloolithid oospecies within the south-Pyrenean areas. Correlation with magnetochrons in the Ager and Vallcebre synclines is after López-Martínez (2003) and Vila *et al.* (2011). The chronostratigraphic position of the egg-bearing localities in respect to the magnetochrons in the Trepmp Basin is approximative. Names in bold: indicate localities that have changed its age after this review. B) Biostratigraphic ranges of megaloolithid oospecies and charophytes biozones in south-western Europe (based on Garcia and Vianey-Liaud, 2001 and Riveline *et al.* 1996; magnetostratigraphy from Gradstein *et al.* 2012). C) Fossil occurrences of the main dinosaur groups in the southern and northern Pyrenees (black and grey bars, respectively). Bars include bones, tracks and eggs except for the sauropod dinosaurs, in which the egg record is not represented.

boundary in the so-called Ibero-Armorican Domain in south-western Europe. During this turnover a late Maastrichtian assemblage dominated by hadrosauroids replaced an early Maastrichtian fauna dominated by titanosaurian sauropods. To understand how this purported turnover took place it is pivotal to establish the age of the dinosaur-bearing localities throughout the region. The new age assignments proposed for some south-Pyrenean localities have implications mainly for the temporal distribution of certain dinosaur taxa (ankylosaurians and theropods) in the latest Cretaceous and therefore for the turnover pattern of south-western Europe (Fig. 2). In the southern basins, for example, the localities of Fontllonga-6, Biscarri, Els Nerets and Suterranya-Mina de lignit yielded ankylosaurian remains (Santafé-Llopis *et al.*, 1997; López-Martínez *et al.*, 2000; López-Martínez, 2003; Escaso *et al.*, 2010). The present revision indicates that at least two of these localities (Els Nerets and Suterranya-Mina de lignit) have a late Maastrichtian age, and this implies that the ankylosaurian dinosaurs persisted until the early late Maastrichtian (Fig. 2A). This assertion concurs with what has been reported in the northern Pyrenees (Fig. 2C), where ankylosaurian remains have been collected in deposits of late Maastrichtian age (Laurent *et al.*, 2002). As a whole, the Pyrenean record seems to indicate that the clade did not go extinct at the early Maastrichtian-late Maastrichtian boundary but they lasted beyond it and coexisted for some time with hadrosauroid faunas.

In terms of theropod distribution and fossil abundance, the new age assignments proposed for some localities modify the recent theropod successions proposed by Torices *et al.* (in press) in the southern Pyrenees. For instance, the authors situated several of the localities with theropod teeth in the late Campanian. However, the Figuerola-2 locality is here considered to be early Maastrichtian in age, whereas the localities of Vicari-4, Suterranya-1 and probably Montrebei are late Maastrichtian in age. This implies that some of the theropod taxa reported in late Campanian localities are now restricted to the late Maastrichtian (Fig. 2A). This is the case for cf. *Richardoestesia* sp. and “*Richardoestesia*-like”, which now seem to be restricted exclusively to the late Maastrichtian, at least in the southern Pyrenees. Moreover, with the new distribution the theropod record in the southern Pyrenees clearly varies through the latest Cretaceous in terms of the predominant type of evidence. That is, the oological record is more diverse than the bone record prior to the early Maastrichtian-late Maastrichtian boundary (Sellés *et al.*, 2014). By contrast, the bone record (mainly teeth) is much more highly represented in deposits of late Maastrichtian age, being scarce in the late Campanian-early Maastrichtian interval. This pattern, which is probably influenced by sampling and other biases, comes to light clearly in Fig. 2C, where the theropod record is notably more concentrated in the late Maastrichtian.

Regarding sauropods, the late Maastrichtian age of some eggshell localities (e.g. Els Nerets, Basturs, Orcau, Suterran-

ya-1) demonstrates that the egg record of this group is almost continuous and abundant throughout the entire Maastrichtian. This contradicts previous statements made by López-Martínez (2003), who postulated a major abundance of egg localities in Upper Campanian and a decrease in Maastrichtian deposits. In the light of the new temporal distribution of the localities and the integration of new sites from other areas (e.g. the Coll de Nargó and Vallcebre synclines) the egg record of sauropod dinosaurs becomes notably scarce in Upper Campanian deposits but is well represented in the Maastrichtian

The new age assignments do not have significant implications for the temporal distribution of rhabdodontid and hadrosauroid dinosaurs, since the ornithopod-bearing localities discussed in the present work (Perauba-Figuerola, and Els Nerets and L’Espinau, respectively) fall within the time interval expected for each group in the region. The present study will hopefully lay the groundwork for future studies on dinosaur biostratigraphy not only in the southern Pyrenees but also in the whole Ibero-Armorican Domain.

## 6. Conclusions

The present study updates the nomenclature and age of several classic and new dinosaur fossil localities in the uppermost Cretaceous (Campanian-Maastrichtian) continental deposits of the southern Pyrenees. The age of about 30 localities has been re-evaluated by means of an analysis and review of new and previous parataxonomic assignments, with some material re-assigned to known megaloolithid oospecies (*M. aureliensis*, *M. siruguei*, *M. mamillare*, *M. baghensis*). The new age assignment includes classical dinosaur-bearing localities such as Basturs, Orcau-1, Els Nerets, Suterranya-1 and Figuerola-2, among others, which have significant implications for the faunal turnover proposed in south-western Europe. According to the new data, the ankylosaurians would have survived until the late Maastrichtian in the southern Pyrenees, as reported in the northern basins. The new age assessment suggests that in the southern Pyrenees the fossil record of theropods is scarce prior to the early Maastrichtian and that their taxonomic diversity (richness) is much higher in the late Maastrichtian. Interestingly, the sauropod egg record becomes continuous throughout the entire Maastrichtian but is scarce in the Upper Campanian.

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### Appendix 1.- Listed samples and localities with megaloolithid oospecies discussed in the present work.

Locality	Egg-bearing level (site)	Source material	Number of samples	Eggshell thickness (mm)	Oospecies
Barranc de La Fonguera	Barranc de La Fonguera-1	Egg debris	7	2.67-2.73	<i>Megaloolithus siruguei</i>
	Barranc de La Fonguera-2	Egg debris	12	2.17-2.39	<i>Megaloolithus siruguei</i>
Barranc de la Boïga	-	Eggshells	95	1.33-1.53	<i>Megaloolithus baghensis</i>
Orcau-1	-	Eggshells	38	1.50-1.54	<i>Megaloolithus baghensis</i>
Els Nerets	-	Eggshells	51	1.64-1.77	<i>Megaloolithus mamillare</i>
Suterranya-1	-	Eggs	25	1.76-1.78	<i>Megaloolithus baghensis</i>
Abella	-	Eggs	5	1.85	<i>Megaloolithus mamillare</i>
Tossal de Sant Romà d'Abella	-	Eggs	84	1.54-1.62	<i>Megaloolithus mamillare</i>
Costa de la Coma	-	Eggs	110	1.56-1.64	<i>Megaloolithus mamillare</i>
Sant Bartomeu	-	Egg	6	1.47-1.88	<i>Megaloolithus baghensis</i>
Molí del Baró-1	-	Eggshells	50	1.87-1.93	<i>Megaloolithus baghensis</i>
Serrat del Rostiar-2	-	Eggshells	1	1.82	<i>Megaloolithus baghensis</i>
Camí del Soldat	-	Eggshells	50	1.12-1.32	<i>Megaloolithus baghensis</i>
Els Terrers	J-BAR01	Egg	4	0.7-0.9	<i>Megaloolithus baghensis</i>
Torrent de l'Esdavella	E-MUN06	Eggshells	1	0.75	<i>Megaloolithus baghensis</i>
La Nou-1	-	Eggshells	119	1.51-1.59	<i>Megaloolithus mamillare</i>
L'Espinau	-	Eggshells	8	1.25-1.85	<i>Megaloolithus baghensis</i>
Perauba-Figuerola	-	Eggshells	1	1.57	<i>Megaloolithus aureliensis</i>
Blancafort	-	Eggshells	17	1.50-1.61	<i>Megaloolithus aureliensis</i>
Sallent	Sallent-1	Eggs	6	2.78-2.95	<i>Megaloolithus siruguei</i>
	Sallent-2	Eggs	12	2.93-3.22	<i>Megaloolithus siruguei</i>
	Sallent-3	Egg debris	3	2.92-2.95	<i>Megaloolithus siruguei</i>
	Sallent-4	Eggs	4	2.80-3.10	<i>Megaloolithus siruguei</i>
	Sallent-5	Eggs	6	2.11-2.34	<i>Megaloolithus siruguei</i>
	Sallent-6	Eggs	3	2.79-2.93	<i>Megaloolithus siruguei</i>
	Sallent-7	Eggs	13	2.57-2.65	<i>Megaloolithus siruguei</i>
Cal Fontanet	Cal Fontanet-1	Eggs	29	3.14-3.66	<i>Megaloolithus siruguei</i>
	Cal Fontanet-2	Eggs	10	3.33-3.61	<i>Megaloolithus siruguei</i>
	Cal Fontanet-3	Eggs	9	3.34-3.76	<i>Megaloolithus siruguei</i>
	Cal Fontanet-4	Eggs	26	3.45-3.65	<i>Megaloolithus siruguei</i>
Pinyes Est	Pinyes Est-1	Eggs	77	2.51-2.59	<i>Megaloolithus siruguei</i>
	Pinyes Est-2	Eggs	11	2.73-2.87	<i>Megaloolithus siruguei</i>
	Pinyes Est-3	Egg debris	20	2.37-2.79	<i>Megaloolithus siruguei</i>
	Pinyes Est-4	Eggs	12	2.54-2.72	<i>Megaloolithus siruguei</i>
	Pinyes Est-5	Eggs	23	1.98-2.07	<i>Megaloolithus mamillare</i>



## Appendix 1.- (continuation).

Santa Eulàlia	Santa Eulàlia-1	Eggs	15	2.53-2.92	<i>Megaloolithus siruguei</i>
	Santa Eulàlia-2	Eggs	28	2.48-2.73	<i>Megaloolithus siruguei</i>
	Santa Eulàlia-3	Eggs	6	1.97-2.19	<i>Megaloolithus mamillare</i>
	Santa Eulàlia-4	Egg debris	4	2.63-2.77	<i>Megaloolithus siruguei</i>
La Teuleria	La Teuleria-1	Eggs	50	2.29-2.49	<i>Megaloolithus siruguei</i>
	La Teuleria-2	Eggs	93	3.08-3.16	<i>Megaloolithus siruguei</i>
	La Teuleria-3	Eggs	5	2.57-2.66	<i>Megaloolithus siruguei</i>
	La Teuleria-4	Eggs	152	2.86-3.01	<i>Megaloolithus siruguei</i>
	La Teuleria-5	Eggs	7	2.93-3.22	<i>Megaloolithus siruguei</i>
	La Teuleria-6	Eggs	92	2.48-2.73	<i>Megaloolithus siruguei</i>
	La Teuleria-7	Eggs	117	2.31-2.45	<i>Megaloolithus siruguei</i>
	La Teuleria-8	Eggs	96	2.78-2.95	<i>Megaloolithus siruguei</i>
	La Teuleria-9	Eggs	78	2.52-2.65	<i>Megaloolithus siruguei</i>
	La Teuleria-10	Eggs	11	2.71-2.75	<i>Megaloolithus siruguei</i>
Els Enserriis	Els Enserriis-1	Eggs	9	2.68-2.82	<i>Megaloolithus siruguei</i>
	Els Enserriis-2	Eggs	6	2.88-2.93	<i>Megaloolithus siruguei</i>
	Els Enserriis-3	Eggs	30	2.66-3.04	<i>Megaloolithus siruguei</i>
	Els Enserriis-4	Eggs	15	2.76-2.94	<i>Megaloolithus siruguei</i>
	Els Enserriis-5	Eggs	13	2.85-2.87	<i>Megaloolithus siruguei</i>
	Els Enserriis-5	Eggs	15	3.21-3.33	<i>Megaloolithus siruguei</i>
	Els Enserriis-6	Eggs	13	3.04-3.09	<i>Megaloolithus siruguei</i>
	Els Enserriis-7	Eggs	10	2.11-2.81	<i>Megaloolithus siruguei</i>
	Els Enserriis-8	Eggs	20	2.43-2.72	<i>Megaloolithus siruguei</i>
	Els Enserriis-9	Eggs	7	2.83-2.99	<i>Megaloolithus siruguei</i>
	Els Enserriis-10	Eggs	67	2.63-2.67	<i>Megaloolithus siruguei</i>
Els Enserriis-11	Eggs	32	2.78-2.92	<i>Megaloolithus siruguei</i>	
El Codó	El Codó-1	Eggs	33	2.53-2.56	<i>Megaloolithus siruguei</i>
	El Codó-2	Eggs	34	2.40-2.57	<i>Megaloolithus siruguei</i>
	El Codó-3	Eggs	11	2.57-2.66	<i>Megaloolithus siruguei</i>
	El Codó-4	Eggs	5	2.58-2.62	<i>Megaloolithus siruguei</i>
	El Codó-5	Eggs	3	2.22-2.31	<i>Megaloolithus siruguei</i>
	El Codó-6	Eggs	3	2.73-2.84	<i>Megaloolithus siruguei</i>
	El Codó-7	Eggs	29	2.82-2.88	<i>Megaloolithus siruguei</i>
	El Codó-8	Eggs	38	2.62-2.92	<i>Megaloolithus siruguei</i>
	El Codó-9	Eggs	18	2.72-2.84	<i>Megaloolithus siruguei</i>
	El Codó-10	Eggs	3	3.08-3.26	<i>Megaloolithus siruguei</i>
	El Codó-11	Eggs	5	2.38-2.52	<i>Megaloolithus siruguei</i>
	El Codó-12	Eggs	12	2.38-2.59	<i>Megaloolithus siruguei</i>
	El Codó-13	Eggs	42	2.29-2.49	<i>Megaloolithus siruguei</i>
	El Codó-14	Eggs	15	2.24-2.48	<i>Megaloolithus siruguei</i>
	El Codó-15	Eggs	2	3.07-3.13	<i>Megaloolithus siruguei</i>
	El Codó-16	Eggs	47	2.84-2.99	<i>Megaloolithus siruguei</i>
	El Codó-17	Eggs	8	2.64-2.72	<i>Megaloolithus siruguei</i>
	El Codó-18	Eggs	16	2.53-2.67	<i>Megaloolithus siruguei</i>
	El Codó-19	Eggs	26	2.77-2.86	<i>Megaloolithus siruguei</i>
	El Codó-20	Eggs	12	2.51-2.63	<i>Megaloolithus siruguei</i>
	El Codó-21	Eggs	33	3.18-3.33	<i>Megaloolithus siruguei</i>
	El Codó-22	Eggs	28	2.70-2.75	<i>Megaloolithus siruguei</i>
	El Codó-23	Eggs	10	2.16-2.35	<i>Megaloolithus siruguei</i>
	El Codó-24	Eggs	10	2.28-2.42	<i>Megaloolithus siruguei</i>
	El Codó-25	Eggs	15	2.84-2.87	<i>Megaloolithus siruguei</i>
	El Codó-26	Eggs	23	2.20-2.32	<i>Megaloolithus siruguei</i>
	El Codó-27	Eggs	15	2.86-2.92	<i>Megaloolithus siruguei</i>
	El Codó-28	Eggs	45	2.77-2.97	<i>Megaloolithus siruguei</i>
	El Codó-29	Eggs	15	2.76-2.99	<i>Megaloolithus siruguei</i>
	El Codó-30	Eggs	15	2.31-2.45	<i>Megaloolithus siruguei</i>
	El Codó-31	Eggs	10	2.71-2.79	<i>Megaloolithus siruguei</i>
	El Codó-32	Eggs	8	3.08-3.20	<i>Megaloolithus siruguei</i>
	El Codó-33	Eggs	18	2.54-2.76	<i>Megaloolithus siruguei</i>
	El Codó-34	Eggs	20	2.44-2.57	<i>Megaloolithus siruguei</i>
	El Codó-35	Eggs	35	2.47-2.56	<i>Megaloolithus siruguei</i>
	El Codó-36	Eggs	24	3.15-3.19	<i>Megaloolithus siruguei</i>
	El Codó-37	Eggs	7	2.29-2.33	<i>Megaloolithus siruguei</i>
	El Codó-38	Eggs	35	2.78-2.83	<i>Megaloolithus siruguei</i>
	El Codó-39	Eggs	53	2.28-2.34	<i>Megaloolithus siruguei</i>
	El Codó-40	Eggs	10	2.17-2.25	<i>Megaloolithus siruguei</i>
	El Codó-41	Eggs	8	1.98-2.07	<i>Megaloolithus mamillare</i>



## Appendix 2.- Systematic palaeontology

Basic organizational group: Dinosauroid

Oofamily: Megaloolithidae Zhao, 1979

Oogenus: *Megaloolithus* Vianey-Liaud, Mallan, Buscail, and Montgelard, 1994

*Megaloolithus aureliensis* Vianey-Liaud, Mallan, Buscail, and Montgelard, 1994

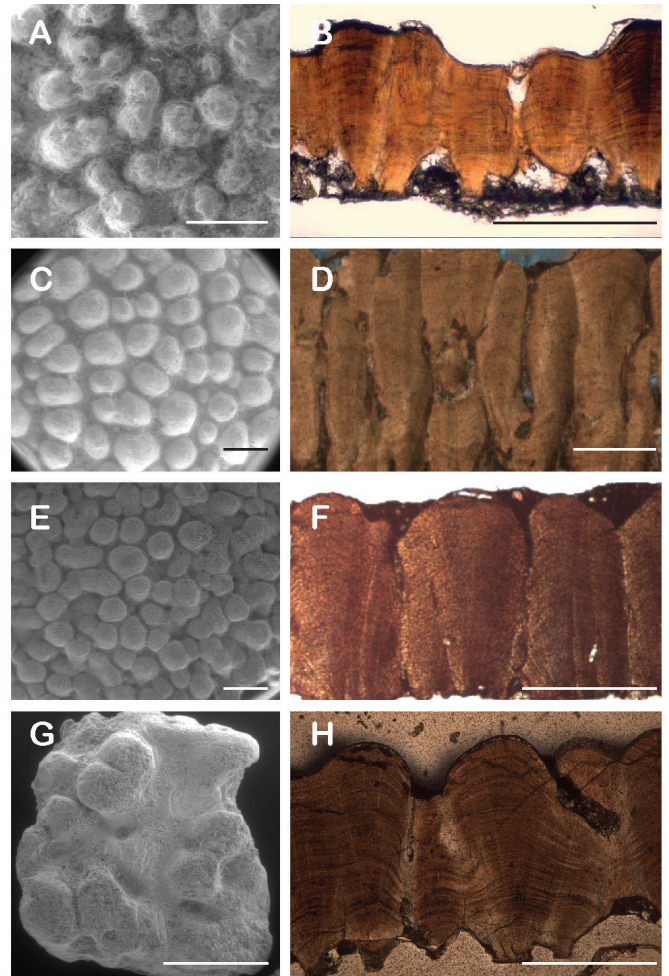
Diagnosis according to Garcia and Vianey-Liaud (2001): *Megaloolithus* with short fan-shaped units; arched growth lines can be horizontal in the small area with flat outer surface; thickness ranges from 0.75 to 1.52 mm; average node diameter about 0.5 mm; pore diameters between 10 and 50  $\mu\text{m}$ ; spherical eggs (until 20–22 cm).

Localities, stratigraphic range, and age: This *Megaloolithus* oospecies is represented by scattered eggshells at the Blancafort and Perauba-Figuerola localities. The former locality falls on top of the La Maçana unit, the regional equivalent of the “grey unit” of the Tremp Formation, late Campanian (Villalba-Breva and Martín-Closas, 2012). The Perauba-Figuerola locality locates at the lower part of the “Figuerola de Meià” unit, the regional equivalent of the “lower red unit” of the Tremp Formation, early Maastrichtian (Villalba-Breva and Martín-Closas, 2012).

Material: see Appendix 1.

Description: The outer surface of the eggshell is covered with scattered rounded nodes (0.5 mm in diameter), sometimes coalescent, with flat areas between them (Fig. 1A). Circular-shaped pore apertures (80–120  $\mu\text{m}$  in diameter) are located at the base of nodes, and less frequently in the middle of flatted areas. Eggshell ranges from 0.8 mm to 1.2 mm in thickness. In radial view, short fan-shaped shell units (H/W ratio of 1.8) are interlocked with adjacent ones (Fig. 1B). Growth lines are mainly arched at the base of those shell units, whereas they are undulating when crossing fused units. Some tubocanalliculate pore channels have been also observed in radial section, which are 95–120  $\mu\text{m}$  in width.

Comparisons and Discussion: Coalescent-nodular ornamentation like that of eggshells from the Blancafort and Perauba-Figuerola localities has been described in four megaloolithid oospecies: *M. baghensis*, *Pseudomegaloolithus atlasis*, *Patagoolithus salitraensis* and *M. aureliensis* (Vianey-Liaud et al., 2003; Vianey-Liaud and Garcia, 2003). All these oospecies exhibit similar structural features, such as shell-thickness, shape of shell units, and node and pore dimension; being the high/width ratio (H/W ratio) of the shell units the most notable differences between them. This value is about 2.33 in *M. baghensis* (Khosla and Sahni, 1995), less than 3 in *P. atlasis* (Vianey-Liaud and Garcia, 2003), 2.28 in *P. salitralensis* (Simón, 2006) and 1.75 in *M. aureliensis* (Sellés et al., 2013). Given that H/W ratio established for the studied material is 1.8, this value is more similar to that of *M. aureliensis* than any other oospecies. Although eggshell thickness can be highly variable within a certain oospecies, and that eggshell-thickness-range may overlap between several oospecies, it is worthy comment that the thickness of the oological material from the studied localities is more similar to *M. aureliensis* (0.9 mm and 0.98mm, respectively) than any other of the previously referred oospecies (0.7 mm-thick in *P. atlasis*, 1.5 mm-thick in *M. baghensis*, and 1.4 mm-thick in *P. salitralensis*). Although the size of pore apertures of the studied material is somewhat larger than that reported by Garcia and Vianey-Liaud (2001), Sellés et al. (2013) described some specimens of *M. aureliensis* from Coll de Nargó syncline with similar values of pore apertures size than those of the present work. Therefore, eggshells from the



Appendix 2 Fig. 1 (suppl.) - Megaloolithid oospecies from the studied localities (southern Pyrenees). A, B) *Megaloolithus aureliensis* (IPS-58959) from the Blancafort locality, outer surface and radial section, respectively; C, D) *Megaloolithus siruguei* from the Pinyes Est-1 (IPS-82192) site, outer surface and radial section, respectively; E, F) *Megaloolithus mamillare* from the Tossal de Sant Romà d'Abella (IPS-58963) and Costa de la Coma (IPS-58964) localities, outer surface and radial section, respectively; G, H) *Megaloolithus baghensis* from the Barranc de la Boïga (IPS-58960) and Orcau-1 (IPS-9133) localities, outer surface and radial section, respectively. Scale bar: 1 mm.

Blancafort and Perauba-Figuerola localities are attributed to the oospecies *M. aureliensis*.

*Megaloolithus siruguei* Vianey-Liaud, Mallan, Buscail, and Montgelard, 1994

Diagnosis: According to Vianey-Liaud et al (1994) and after Elez and López-Martínez (2000), and Vianey-Liaud and Zelenitsky (2003), *Megaloolithus* with shell units taller than in *M. mamillare*; thickness range 2.65 to 2.70 mm; pore diameter range 50 to 80  $\mu\text{m}$ ; reticulate pore system.

Localities, stratigraphic range, and age: This *Megaloolithus* oospecies is represented by eggs and/or scattered eggshells at the sites of Barranc de la Fonguera-1, and -2, Sallent-1 to -7, Cal Fontanet-1 to -4, Pinyes Est-1 to -4, La Teuleria-1 to -10, Santa Eulàlia-1, -2, and -4, El Codó-1 to -40, and Els Enserri-1 to -11. They all fall in the “lower red unit” of the Tremp Formation. Early Maastrichtian - ?early late Maastrichtian.

Material: see appendix 1.

Description: Relatively thick eggshells (1.75 mm to 3.6 mm), fully covered by well-delimited rounded nodes (0.51 – 1.23 mm in diameter, Fig. 1C). Circular to sub-circular pore apertures (130  $\mu\text{m}$ -width), which are located near the base of the nodes. In radial section, the edge of the elongate fan-shaped shell units (H/W ratio = 4) can be easily traceable throughout whole eggshell. Nevertheless, some of them are partially interlocked with their neighbouring ones (Fig. 1D). Growth lines are clearly arched from the base to the top of the shell units. The respiratory channel system is composed of vertical funnel-shaped channels interconnected by transversal channels, altogether forming a reticulate network of channels.

Comparisons and Discussion: Only two oospecies of *Megaloolithus* exhibit a clear reticulate channel system: *M. siruguei* and *M. microtuberculata*. The surface of *M. microtuberculata* is covered of pronounced small nodes, sometimes with irregular shape (García and Vianey-Liaud, 2001), while *M. siruguei* is covered of large rounded nodes, as in eggshells described above. In fact, the ornamental pattern is the only difference observed between these oospecies. Given that all the oological remains examined here exhibit large rounded nodes in their outer surface and reticulate pore system, they are classified as *Megaloolithus siruguei*.

*Megaloolithus mamillare* Vianey-Liaud, Mallan, Buscail, and Montgelard, 1994

Diagnosis according to Vianey-Liaud et al. (1994): *Megaloolithus* with short fan-shaped units; thickness in the main part of the eggshells from 1.2 to 2.1 mm; average node diameter about 1 mm; pore diameters range from 75 to 120  $\mu\text{m}$ .

Synonymy: *Megaloolithus* cf. *mamillare* from the Compuertas locality of Moratalla (1993)

Localities, stratigraphic range, and age: This *Megaloolithus* oospecies is represented by eggs and scattered eggshells at the Basturs-1, Basturs-2, Abella and Sant Bartomeu localities, on top of the Arén Sandstone Formation; eggshell fragments in the Els Nerets and Compuertas localities, in the “grey unit” of the Tremp Formation; and eggs and/or eggshell fragments from the Santa Eulàlia-3, El Codó-41, Pinyes Est-5, Tossal de Sant Romà d’Abella, Costa de la Coma, and La Nou-1 localities, in the upper part of the “lower red unit” of the Tremp Formation. Late Maastrichtian.

Material: see Appendix 1.

Description: Some nearly complete sub-spherical eggs (19–20 cm in diameter) have been discovered in Tossal de Sant Romà d’Abella locality. Eggshell ranges from 1.39 mm to 2.3 mm in thickness (average of 1.9 mm) with the outer surface covered of small rounded nodes (0.73 mm in diameter). Sometimes, nodes are coalesced between two or five nodes, forming short and irregular chains (Fig. 1E). Circular-shaped pore apertures (90 – 110  $\mu\text{m}$  in diameter) are located between ornamental nodes. In radial thin section, fan-shaped shell units (H/W ratio of 2) are clearly traceable; showing well curved growth lines from the base to the top of the crystalline units (Fig. 1F). The respiratory system is tubocanalicate, with narrow and slender canals, ranging from 50 to 80  $\mu\text{m}$  in wide.

Comparisons and Discussion: Structural characters exhibited by eggshells described above are consistent with three oospecies of *Megaloolithus*: *M. jabalpurensis*, *M. dhoridungriensis* and *M. mamillare*. The Indian oospecies *M. dhoridungriensis* differs from our specimens by showing cylindrical-shape shell units, with a H/W ratio of 2.7 (Mohabey, 1998). *M. jabalpurensis* and *M. mamillare* share several structural characters (Vianey-Liaud et al., 1994, 2003), only differing in the size of the egg (15 cm and 20 cm in diameter, respectively), the eggshell thickness (2.3 mm in *M. jabalpu-*

*rens* and 2.1 mm in *M. mamillare*) and the H/W ratio (2.45 in *M. jabalpurensis* and 2.1 to 2.2 in *M. mamillare*). Given that the studied oological material exhibits sub-spherical eggs of 20 cm in diameter, 1.9 mm-thick eggshell, and H/W ratio of 2, it is attributed to the oospecies *M. mamillare*.

Moratalla (1993, 1998) described very scarce remains attributed to *M. cf. mamillare* in the Compuertas locality. The author stated that the recovered eggshells were badly preserved, obscuring several features. However, he noted that the thin eggshells collected in the locality exhibited compact and nodular ornamentation and non-fused shell units. Although we had not the chance to analyze this egg material directly on first-hand examination, all evidence point that the abovementioned characters described in the eggshells from the Compuertas locality fit with those of the oospecies *M. mamillare*. Accordingly, we tentatively assign the oological remains of this locality to *M. mamillare*.

*Megaloolithus baghensis* Khosla and Sahni 1995

Diagnosis according to Fernández and Khosla (in press): Spherical eggs 140–200 mm in diameter; nodes ornamentation, eggshell 1.0–1.70 mm thick; average node diameter about 0.60 mm; fan-shaped spheroliths distinct or even partially fused; height/width ratio 2.32:1; pore subcircular to elliptical; swollen-ended, variably spaced basal caps (0.2–0.3 mm in diameter).

Synonymies: *Megaloolithus pseudomamillare* from Suterranya-1 locality; Vianey-Liaud and López-Martínez (1997)

*Megaloolithus trempii* from Orcau, Suterranya, Vicari, Llabusta, and Fontllonga L localities; Moratalla (1998)

*Megaloolithus* cf. *mamillare* from the Suterranya and Orcau localities; Moratalla (1993, 1998)

*Megaloolithus* sp.; Vila et al. (2011)

Localities, stratigraphic range, and age: This *Megaloolithus* oospecies is represented by eggs at Suterranya-1 and by scattered eggshells at the Orcau-1, Orcau, Llabusta, Vicari, Suterranya, Fontllonga L, Barranc de la Boïga, Molí del Baró-1, Serrat del Rostiar-2, Camí del Soldat and L’Espinau localities. The Suterranya-1 locality is found on top of the Arén Sandstone Formation; the Orcau, Llabusta, Vicari, and Suterranya are found in the “grey unit” of the Tremp Formation; the Fontllonga L, Barranc de la Boïga, Molí del Baró-2, Serrat del Rostiar-2, Camí del Soldat and L’Espinau localities are located in the “lower red unit” of the Tremp Formation. Late Maastrichtian.

Material: see Appendix 1.

Description: complete eggs from Suterranya-1 and Suterranya localities are sub-spherical in shape. The smallest egg is 15–18 cm in diameter, while the largest is 21 – 23 cm, and the eggs of Suterranya are about 21 cm in diameter (Moratalla, 1993). The outer surface of the shell is covered of coalescent rounded nodes ranging from 0.2 to 0.6 mm in diameter. Nevertheless, most part of the shell surface consists in flat areas and isolate nodes (Fig. 1G). Pore opening are 0.1–0.2 mm in diameter frequently located at the flattered surfaces. The eggshell thickness ranges from 1.12 to 1.85 mm, with an average of 1.39 mm. Eggshell units are broad fan-shaped (H/W ratio about 1.9), frequently fused with adjacent ones, and showing irregular morphology in their upper part (Fig. 1G). In radial thin section, the pore channels are narrow and straight (75–90  $\mu\text{m}$ -width), corresponding to tubocanalicate pore system. Growth lines appear slightly arched from the base to the top of the shell units.

Comparisons and Discussion: The oological material described above resembles *M. aureliensis* oospecies in the ornamental patterns, and H/W ratio. However, this material is somewhat thicker



than *M. aureliensis* (1.1–1.9 mm and 0.8–1.4 mm, respectively). In addition, they differ in the shape of shell units, being more irregular in the studied material than that of *M. aureliensis*. *M. baghensis* also share several features with the studied material. For instance, the range of shell thickness of *M. baghensis* (1–1.7 mm; Mohabey, 1998) is similar to that of our specimens (1.1–1.9 mm-thick). Both ootaxa exhibit similar size of node (0.65 mm in diameter in *M. baghensis* and 0.5 mm in studied material) and pore apertures (0.15 mm in diameter in *M. baghensis* and 0.1–0.2 mm in studied material). Therefore, the oological remains described in the above-mentioned localities are attributed to the oospecies *M. baghensis*.

Moratalla (1993, 1998) reported a new oospecies named *Megaloolithus trempii* in the Orcau, Suterranya-1, Vicari, Llabusta, and Fontllonga L localities of the Tremp and Àger basins. A recent revision of this ootaxon reveals identical microstructural characters (e.g. shell thickness, ornamental pattern, shape of shell units) than those of *Megaloolithus baghensis*, and hence both oospecies should be synonymised. The eggs sizes reported by Moratalla (1993, 1998) are slightly larger than those described in the diagnosis, albeit this can be explained as the result of a tangential-view section of the eggs or even due to regional tectonic deformation of the eggs (see Vila et al. 2010). Thus, the occurrence of *M. baghensis* in the Moratalla's (1993, 1998) localities is here stated. Moratalla (1993, 1998) also reported the presence of *M. cf. mamillare* in the Orcau and Suterranya localities. On the base of descriptions given by the author, we note that all characters (such as the ornamentation composed of rounded nodes and flatted surfaces, irregular shell units, and partially fused shell unit) fit with the oospecies *M. baghensis*. Therefore, we propose to synonymize the material referred to *M. cf. mamillare* in these localities with *M. baghensis*. Similarly, Vila et al. (2011) reported an egg and eggshell fragments attributed to *Megaloolithus* sp. from the J-BAR01 and E-MUN06 localities, respectively, in the Vallcebre Syncline. We re-examined the material concluding that they can also be attributed to *M. baghensis* because they show a surface covered with coalescent nodes, partially fused short fan-shaped shell units, undulating growth lines, and relatively thin eggshells (0.7–0.9 mm-thick).

## Appendix 2 references

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