Cretaceous Research 49 (2014) 45–54

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Diversity of theropod ootaxa and its implications for the latest Cretaceous dinosaur turnover in southwestern Europe

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ARTICLE INFO

Article history:
Received 6 November 2013
Accepted in revised form 1 February 2014
Available online 4 March 2014

Keywords:
Dinosaurs
Eggs
Theropoda
Turnover
Late Cretaceous
Diversity

ABSTRACT

The scarcity of diagnostic skeletal elements in the latest Cretaceous theropod record of the Ibero-Armorican domain (southwestern Europe) prevents to perform accurate phylogenetic, paleobiogeographic, and diversity studies. In contrast, eggs and eggshells of theropod dinosaurs are relatively abundant and well known in this region from which several ootaxa have been described. Here, we describe the first Late Maastrichtian theropod ootaxon (*Prismatoolithus trempii* oosp. nov.) from SW Europe and demonstrate that oological record can be used as a proxy for assessing diversity of egg-producers and may help to complement their scarce bone record. The performed analyses indicate that the theropod taxa and ootaxa reach their diversity maxima during the Late Campanian and start to decrease near the Campanian–Maastrichtian boundary at both global and regional scales. The oological diversity of theropods in the Ibero-Armorican domain is consistent with the theropod diversity identified at high taxonomic level. Two distinct assemblages of theropod ootaxa can be recognized in the latest Cretaceous of the Ibero-Armorican domain. Their temporal transition can be correlated with other dinosaur faunal changes recorded in the region. This faunal turnover took place around the Early–Late Maastrichtian boundary, involving ornithopods, sauropods, ankylosaurs and, according to the present results, theropods as well.

1. Introduction

Recently, several studies have focused on the global and regional diversity of dinosaurs at the end of the Cretaceous (Brusatte et al., 2012; Mannion et al., 2013). In the paleogeographic region of southwestern Europe, the so-called Ibero-Armorican domain, of particular interest are the works assessing the diversity of the most abundant latest Cretaceous dinosaur taxa: the hadrosauroids (Prieto-Marquez et al., 2006; Pereda-Suberbiola et al., 2009a,b; Cruzado-Caballero et al., 2010; Prieto-Márquez et al., 2013) and sauropods (Vila et al., 2012; Díez Díaz et al., 2013). Conversely, other contemporaneous groups of dinosaurs reported from the uppermost Cretaceous (Campanian and Maastrichtian) of this region such as rhabdodontid ornithopods, nodosaurid ankylosaurs, and theropods (Allain and Pereda-Suberbiola, 2003; Garcia and Pereda-Suberbiola, 2003; Riera et al., 2009; Torices et al., 2013) have received less attention.

Theropod dinosaurs are well recorded at the region, but frequently can only be diagnosed at high taxonomic level. Various groups including abelisauroids (Buffetaut et al., 1988; Astibia et al., 1990; Le Loeuff and Buffetaut, 1991; Tortosa et al., 2013), dromaeosaurids (Antunes and Sigogneau-Russell, 1992; Le Loeuff et al., 1992; Le Loeuff and Buffetaut, 1998; Antunes and Mateus, 2003; Torices et al., 2013), and probably ornithomimosaurs (Pereda-Suberbiola et al., 2000), have been reported on the basis of skeletal material. In addition, there is a remarkable abundance of scattered material of uncertain affinity (Casanovas-Cladellas et al., 1988; Torices et al., 2013) and multiple eggshell types (Table 1). Interestingly, the recognition of theropod oospecies may represent a good complementary tool in order to assess patterns of diversity (richness) of the clade in the Ibero-Armorican domain, as some authors have suggested for sauropod dinosaurs (Garcia and Vianey-Liaud, 2001; Garcia et al., 2006; Salgado et al., 2007; Vila et al., 2012; Sellés et al., 2013). The present study performs a comprehensive review on the systematics and diversity of the oological remains tentatively attributed to theropods from the Middle Campanian–Late Maastrichtian of southwestern Europe and their implications in the latest Cretaceous Ibero-Armorican theropod

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http://dx.doi.org/10.1016/j.cretres.2014.02.004
0195-6671/

Table 1
List of theropod oological remains reported from southwestern Europe.

Oofamily	Ootaxa	Total known material	Localities	Age	References
Prismatoolithidae	*Prismatoolithus tenuis*	57 eggshell fragments	Pioch Heraut, Coudoux-La Bastide Blanche, Puylobier, Les Pennes Mirabeau, Trets (France); Fontllonga-6 (Spain)	Late Campanian to Early Maastrichtian	Vianey-Liaud and Crochet, 1993. Vianey-Liaud and López-Martínez, 1997
	Prismatoolithus matellensis	3 eggshell fragments	Pioch Heraut (France)	Late Campanian to Early Maastrichtian	Vianey-Liaud and Crochet, 1993
	Prismatoolithus n. oosp. aff. *P. matellensis*	2 eggshell fragments	Fontllonga-6 (Spain)	Early Maastrichtian	Vianey-Liaud and López-Martínez, 1997
	? Prismatoolithidae n. oogen. et oosp. (as *P. trempii* oosp. nov. in this work)	1 eggshell fragment	Fontllonga-6 (Spain)	Early Maastrichtian	Vianey-Liaud and López-Martínez, 1997
	Prismatoolithus caboti	1 partial and cracked egg and 19 eggshell fragments	Grande Marquise, La Neuve (France)	Late Campanian to Early Maastrichtian	Garcia et al., 2000
	cf. *Prismatoolithus*	30 eggshell fragments	Cruzy, Vitrolles-Couperigne (France)	Late Campanian	Garcia, 2000
	Sankofa pyrenaica	Abundant samples of partial eggs (? 3) and eggshell fragments	Serràt Pedregós, Urbanisación Montsec (Spain)	Early Maastrichtian	López-Martínez and Vicens, 2012
Elongathoolithidae	Oogenera indet.	50 eggshell fragments	Les Labadous (France)	Early Maastrichtian	Beetschen et al., 1977; Garcia, 1999; Garcia and Vianey-Liaud, 2001
Laevisoolithidae	Oogenera indet.	4 thin sections	Cruzy, La Neuve, Vitrolles-Couperigne (France)	Late Campanian	Garcia, 2000
Incerta sedis	*Ageroolithus fontllongensis*	9 eggshell fragments	Fontllonga-6 (Spain)	Early Maastrichtian	Vianey-Liaud and López-Martínez, 1997
	cf. *Ageroolithus*	6 eggshell fragments	Vitrolles-Couperigne (France)	Late Campanian	Garcia, 2000

fauna. The first Late Maastrichtian theropod ootaxon from Europe is described. Comparisons with theropod diversity trends in other regions of the world are also provided.

2. Geological setting and age of the studied egg sites

In the southern Pyrenees (NE Iberian Peninsula), deposits of shallow marine carbonate platforms to fully continental environments are exposed along an 800 m thick section encompassing Upper Cretaceous–Lower Paleogene deposits (Riera et al., 2009 and references therein). The oological material described in the present study was recovered from ten new localities in the Àger and Tremp basins. One locality represents the top of the Arén Sandstone Formation and nine localities represent the Tremp Formation. The former formation is composed of well-sorted sandstones exhibiting medium to large-scale cross bedding, which were deposited in beach, barrier-island and deltaic systems during the Late Campanian and Maastrichtian (Díaz-Molina, 1987). The Arén Sandstone Formation passes gradually to the Tremp Formation by diachronic interfingering strata. The Tremp Formation can be divided in four informal lithological units, which produce abundant dinosaur remains (Rosell et al., 2001; Riera et al., 2009). In ascendant order, these units are: 1) a gray unit composed of gray marls and limestones representing marine to continental and transitional environments, 2) a lower red unit formed by red mudstones and line sandstones interpreted as fluvial systems, 3) the Vallcebre Limestones and laterally equivalent strata, which represent mainly lacustrine environments, and 4) an upper red unit composed of red mudstones and coarse sandstones recording alluvial and fluvial deposits. The Cretaceous–Paleogene boundary has been established at the base of the Vallcebre Limestones and lateral equivalent strata (Riera et al., 2009 and references therein).

Given the diachronic character of the Arén Sandstone and Tremp formations, the age of fossiliferous localities in southern Pyrenees is younger to the west (Oms and Canudo, 2004; Riera et al., 2009). Local dating can be achieved on the basis of correlation with marine series (López-Martínez et al., 2001), rudist (Vicens et al., 2004), charophytes (Feist and Colombo, 1983; Riveline et al., 1996) and dinosaur (megaloolithid) eggshell biostratigraphy (Vila et al., 2011; Sellés et al., 2013), and magnetostratigraphy (Galbrun et al., 1993; Oms and Canudo, 2004; Vila et al., 2012).

One of the new localities exposes strata of the Lower Maastrichtian (Isona Sud) whereas the others fall in the Upper Maastrichtian (these are Serrat del Pelleu, L'Espinau, Serrat del Rostiar-2, BastursPoble, Molí del Baró-2, Porrit-6, Barranc de la Boïga, Camí del Soldat, Les Torres-2), based on correlation with charophyte biostratigraphy, magnetostratigraphy and co-occurrence with *Megaloolithus mamillare* and/or *Megaloolithus baghensis* oospecies (Fig. 1C). Other previously published localities containing prismatoolithid eggshells and discussed in this work are summarized as follows: Fontllonga-6 (Lower Maastrichtian, after Vianey-Liaud and López-Martínez, 1997), La Maçana (Lower Campanian, after Villalba-Breva and Martin-Closes, 2012), Serrat Pedregós and Urbanización Montsec (Lower Maastrichtian, after López-Martínez and Vicens, 2012).

In Southern France, the theropod oological remains have been reported from several localities distributed in Hérault, Bouch-du-Rhône, and Aude departments (Vianey-Liaud and Crochet, 1993; Garcia, 2000; Garcia et al., 2000). The fossil sites occur within Fuvelian and Rognacian facies, and their age ranges from the Late Campanian to the Early Maastrichtian (Garcia and Vianey-Liaud, 2001; Table 1).

3. Material and methods

During 2009 and 2011 abundant eggshell fragments were recovered in the Upper Maastrichtian continental deposits of the