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Late Cretaceous (Maastrichtian) amphibians and squamates from northeastern Iberia

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ABSTRACT

Maastrichtian biodiversity of medium- and large-sized terrestrial vertebrates is well known in Europe and, specifically, in the Iberian Peninsula. Regarding small-sized herpetofaunas (lissamphibians and squamates), only a few European sites have yielded a significant amount of fossils, and they are still poorly known from the Iberian Peninsula. Recent fieldwork carried out at several sites exposing the Tremp Formation (Southern Pyrenees) has revealed four new localities yielding microvertebrates. Two of them (L'Espinau and Serrat del Rostiar-1) are relatively diverse in herpetofauna, containing albanerpetontids, four different anurans (two different alytids, a pelobatid or gobiatid and a palaeobatrachid), as well as six types of squamates (including scincomorphs, iguanids, anguids and probably gekkotans). Most of these groups are shared with other Campanian-Maastrichtian localities from eastern Iberia although, in some cases, morphological differences might suggest the presence of new lower-level taxa (i.e., genera or species). Also remarkable is the presence of alytines and likely gekkotans that would represent the oldest records of these taxa in Europe and in the Iberian Peninsula, respectively. Taxa of Laurasian origin are common at the Serrat del Rostiar-1 and L'Espinau localities, while Gondwanan taxa are lacking in all cases. Evidence for Asian immigrants (i.e., alytines) is found amongst anurans. Some differences regarding the faunal composition could be explained by environmental factors (i.e., coastal wetlands vs. fluvial settings), although the possibility of taphonomic biases cannot be ruled out.

1. Introduction

The diversity of terrestrial vertebrates from the Maastrichtian of the Iberian Peninsula is mostly known for those groups containing medium-to large-bodied taxa (e.g., dinosaurs, crocodiles, pterosaurs and turtles) (Riera et al., 2009; Puértolas et al., 2011; Marmi et al., 2012a; Dalla Vecchia et al., 2013; Blanco et al., 2014, 2015). There, the dinosaur fossil record is extensive, including titanosaurid sauropods, dromaeosaurid theropods, hadrosauroid ornithopods and nodosaurid ankylosaurs; a faunal turnover is suggested within this interval, titanosaur sauropods being especially abundant in the lower Maastrichtian coastal-to-continental settings and hadrosauroid ornithopods in the upper Maastrichtian fluvial environments (Riera et al., 2009; Vila et al., 2013). Crocodiles are also common in the Maastrichtian of the Iberian Peninsula and are represented by isolated teeth, partial skulls and partial skeletons (Marmi et al., 2012b; Blanco et al., 2014, in press; Puértolas-Pascual et al., this volume). Based on skulls and postcranial bones, four species of eusuchian crocodylomorphs were described from beds assigned to the Tremp Formation (Mey et al., 1968) of the southern Pyrenees: *Arenysuchus gascabadiolorum* (Puértolas et al., 2011), *Allodaposuchus subjuniperus* (Puértolas-Pascual et al., 2013), *Allodaposuchus palustris* (Blanco et al., 2014), and *Allodaposuchus hulki* (Blanco et al., in press). Turtles comprise homogeneous and endemic faunas including pleurodires (Dortokidae and Bothremydidae) and cryptodires (Solemydidae) (de Lapparent de Broin and Murelaga, 1999; Marmi et al., 2012b).

During the Late Cretaceous, most of Europe consisted of a set of moderate-to small-sized islands separated by epicontinental seas

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(Dercourt et al., 2000). In the Maastrichtian, the Iberian Peninsula and most of western France formed the large Ibero-Armorican Island, which was between 600,000 and 1,500,000 km^2, at the westernmost edge of the southern European archipelago (Le Loeuff, 2005). Palaeobiogeographic relationships of Late Cretaceous vertebrates from Europe with faunas from other landmasses (i.e., North America, Asia and Africa) were complex and hypotheses are sometimes controversial. Pereda-Suberbiola (2009) reviewed this intriguing palaeobiogeographic scenario and concluded that, although many taxa showed biogeographical affinities with North America and Asia, the European archipelago also contained Gondwanan elements (abelisauroid dinosaurs, bothremydid turtles, madtsoiid snakes and sebecosuchian-like crocodyliforms). In addition, this author suggested that tetrapod faunas evolved isolated within emerged lands of this archipelago as a result of vicariance during the Late Cretaceous.

Regarding the small-sized herpetofaunas (lissamphibians and squamates), the southern European archipelago had a mixture of elements from different origins: Palaeolaurasian (albanerpetontids, alytid anurans, polyglyphanodontine and paramacellodid scincomorphan lizards), Euramerican (palaeobatrachid anurans and batrachosauroidid salamanders) and Gondwanan (boid and madtsoiid snakes) (Pereda-Suberbiola, 2009 and references therein). However, it is important to note that the presence of boids in the Cretaceous of Europe has been recently questioned (see Rage, 2012). Lissamphibian and squamate faunas from the Late Cretaceous of the Iberian Peninsula are still poorly known (Marmi et al., 2012b; see also Marmi et al., this volume). Besides the locality of Armuña, which has yielded a new anguimorphan with xenosaur affinities and a terrestrial mosasaur (Pérez-García et al., this volume), only three localities have provided enough diagnostic material. In the upper Campanian-lower Maastrichtian locality of Laño (Basque-Cantabrian region), the miscellaneous assemblage contained groups of essentially Laurasian distribution (albanerpetontids, alytids and palaeobatrachids) and taxa with close links with the southern continents (madtsoiid snakes) (Astibia et al., 1990; Pereda-Suberbiola et al., 2015). The affinities of lizards were not clear enough to provide palaeobiogeographic information. Of a similar age, the Chera locality (Valencia) provided a few lissamphibian remains consisting of Laurasian elements (albanerpetontids, an alytid and a likely pelobatid) as well as several mandibular and maxillary bone fragments and isolated vertebrae of indeterminate squamates (Company, 2004; Company and Szentesi, 2012). Only a single vertebra from Chera was tentatively assigned to Iguania or Borioteiioidea (Company et al., 2009). In the assemblage of Blasi-2 (upper Maastrichtian, Aragón), lissamphibians (albanerpetontids, alytids and palaeobatrachids) and squamates (an indeterminate Scleroglossa, an anguid lizard and an alethinophidian snake) were reported by Blain et al. (2010), who also suggested affinities with northern landmasses. These authors, as well as Company and Szentesi (2012), stated that the lack of clear Gondwanan elements in Chera and Blasi-2 might be due to environmental requirements. The depositional settings of these two localities were interpreted as coastal wetlands, while Laño, the only locality with Gondwanan representatives, corresponded to an inner alluvial system (Pereda-Suberbiola et al., 2000, 2015; Blain et al., 2010; Company and Szentesi, 2012).

New findings of microvertebrates in the Iberian Peninsula are crucial to elucidating the factors that promoted isolation or faunal exchanges between Europe and North Africa during the Late Cretaceous. In recent years, new localities with herpetofaunas have been discovered in the Maastrichtian beds of the Tremp Formation (southern Pyrenees). They mostly correspond to fluvial facies with some marine influence (Díez-Canseco et al., 2014) and may be very suitable to assess whether the lack of Gondwanan taxa throughout the Maastrichtian of northeastern Iberia was only due to environmental restrictions, as suggested by Blain et al. (2010) and Company and Szentesi (2012), or also to extinction processes. The potential lacustrine origin of L'Espinau makes this locality interesting in providing insights into a microvertebrate assemblage corresponding to a previously unrecorded environment.

2. Geological setting

During the Late Cretaceous, the southern Pyrenean region was an elongated basin connected to the Atlantic. As a result of the contact between the Iberian and European continental plates and the uplift of the Pyrenean range, the Upper Cretaceous Southern Pyrenean Basin was segmented into several depositional centres from the late Santonian-Campanian to the Oligocene (Puigdefàbregas et al., 1986; Muñoz, 1989; Teixell, 2004). These depocentres are from the east to west: Vallcebre, Coll de Nargó Tremp and Àger. The new microsites reported in this study were sampled in the Tremp Formation beds exposed at the Tremp syncline (Serrat del Rostiar-1, Serrat del Pelleu, Camí del Soldat) and the Serres Marginals (L'Espinau) (Fig. 1).

The Tremp Formation overlies shallow-marine sediments (Arén Sandstone or Terradets formations) and records a regressive trend that occurred in the Pyrenean region during the latest Cretaceous (Mey et al., 1968). The Tremp Formation is composed of transitional and continental strata, encompassing the Cretaceous-Paleogene boundary, and reaches up to 800 m in thickness in the eastern Tremp Basin. Four informal lithologic units were recognised by Rosell et al. (2001) from the base to the top: the grey unit (deposited in coastal wetlands), the lower red unit (fluvial to fluviodeltaic, see below), the Vallcebre Limestone and laterally equivalent strata (lacustrine) and an upper red unit (fluvial). The Cretaceous-Paleogene boundary is located at the base of the Vallcebre Limestone and laterally equivalent strata (see Riera et al., 2009 and references therein). Up to now, Blasi-2 is the only known locality in the Tremp Formation to have yielded diagnostic enough fossil remains of herpetofauna (Blain et al., 2010). This microsite occurs in a 6.5-m-thick interval of grey marls belonging to the grey unit, which is interbedded with the sandstones of the Arén Formation, at the base of the Tremp Formation (López-Martínez et al., 2001).

All the sampled microsites (Figs. 1 and 2) correspond to the lower red unit of the Tremp Formation, which was deposited in different fluvial environments (floodplain, meandering river and braided river; Rosell et al., 2001; Oms et al., 2007; Riera et al., 2009) closely connected to marine settings. Hence, the marine influence has been reported based on the meander architecture as well as the occurrence of glauconite and planktonic foraminifera (Vila et al., 2013; Díez-Canseco et al., 2014).

The Serrat del Rostiar-1 site consists of grey mudstones with pedogenic nodules that represent palaeosoils developed in a floodplain environment, close to meandering rivers (sandstone deposits). It is laterally equivalent to the Basturs Poble bonebed that corresponds to the lower part of the lower red unit (Riera et al., 2009). The Serrat del Rostiar-1 locality is correlated with an undetermined polarity interval regarded as the base of C30n, C30r or C31n magnetochrons according to the palaeomagnetic results of Vila et al. (2012) (Fig. 2B). The inferred late Maastrichtian age based on palaeomagnetic data is in conflict with early Maastrichtian age according to the planktonic biozonation by Díez-Canseco et al. (2014). Lacking additional data, the exact age of Serrat del Rostiar-1 remains uncertain within the Maastrichtian (Fig. 2B).

The Camí del Soldat site is composed of grey mudstones with abundant organic matter interbedded with fine-grained sandstones. It represents the sediments deposited during low activity periods in the non-erosive part of a meander loop. These