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Late Cretaceous (Maastrichtian) Chondrichthyes and Osteichthyes from northeastern Iberia

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ABSTRACT

Intensive sampling for vertebrate microfossils has yielded abundant fish remains in the Maastrichtian units of the Tremp Formation (southern Pyrenees, Catalonia, Spain). Samples were taken from eight new sites representing different palaeoenvironments including coastal wetlands and floodplains, in order to assess the fish diversity and to gain a better understanding of the last dinosaur-dominated ecosystems of northeastern Spain. The results suggest that a diverse ichthyofauna inhabited these transitional to inland fluvial settings throughout the Maastrichtian, comprising both marine and freshwater taxa. Three different chondrichthyans, eight basal neopterygians and at least seven teleostean species were found, the latter being more diverse than in other Maastrichtian localities in Europe. Fossil evidence from the studied late Maastrichtian assemblages suggests that teleosteans were present in all the trophic guilds. In addition, the oldest records for osteoglossids and perciforms in Europe, as well as for cypriniforms worldwide, are reported here. The findings from the southern Pyrenees also reveal ichthyofaunal turnover during the Late Cretaceous, with 'holosteans' being replaced by teleosteans. Moreover, Maastrichtian ichthyofaunas from the southern Pyrenees show Asian and North American biogeographical affinities.

1. Introduction

Fish remains are commonly recovered from Upper Cretaceous marginal-marine, transitional and continental beds in Europe. These remains, which usually consist of isolated teeth and skeletal elements, have allowed diverse chondrichthyan and osteichthyan faunas to be reported (e.g., Gheerbrant et al., 1997; Cavin, 1999; Grigorescu et al., 1999; Laurent et al., 1999, 2002; Kriwet et al., 2007; Pereda-Suberbiola et al., 2015; Csiki-Sava et al., 2015, 2016; Szabó et al., 2016a, 2016b).

Neoselachian chondrichthyans arose in the Early Jurassic (Maisey et al., 2004; Nelson, 2006), and radiated broadly during the Jurassic and Cretaceous, including all modern Batoidea (rays) and Selachii (sharks). Due to the lack of ossified skeleton, complete specimens are rare in the fossil record and neoselachians are mostly recognised from isolated teeth, placoid scales (or dermal denticles), spines or caudal stings (Cappetta, 1987; Maisey et al., 2004; Nelson, 2006; Marmi et al., 2010). In the uppermost Cretaceous of Spain, chondrichthyan fossils are frequently associated with transitional, near-coastal or lagoonal environments and include members of Hybodontiformes (e.g., *Lissodus* Brough 1935), Orectolobiformes (e.g., *Hemiscyllium* Müller and Henle, 1837), Lamniformes (e.g., *Squalicorax* Whitley, 1939), Rajiformes (e.g., *Paratrygonorrhina* Kriwet et al., 2007) and Myliobatiformes (e.g., *Coupatezia* Cappetta, 1982; *Rhombodus* Dames, 1881; *Igdabatis* Cappetta, 1972) (Cappetta and Corral, 1999; Kriwet et al., 2007; Corral et al., 2016).

The European Upper Cretaceous bony fish fossil record mostly consists of teeth, scales and isolated skeletal elements of basal neopterygian groups (i.e., lepisosteiforms, amiiforms and pycnodontiforms) and some representatives of the crown-group Teleostei (i.e., phyllodontids). Lepisosteids (commonly named gars or garpikes) are known from the Early Cretaceous on, but their remains are very abundant in continental deposits from the Late Cretaceous on, when they became widespread in Europe and America (Wiley, 1976; Grande, 2010; López-Arbarello, 2012; Alvarado-Ortega et al., 2016; Brinkman et al., 2014). In Europe, fossils of lepisosteids are commonly found in the uppermost Cretaceous beds of Spain (Cavin, 1999), France (Laurent et al., 2002), Hungary (Szabó et al., 2016a) and Romania (Grigorescu et al., 1999; Csiki-Sava et al., 2016). Semionotiformes is a controversial neopterygian order, closely related to Lepisosteiformes within Ginglymodii (López-

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Arbarello, 2012). Semionotiform-like fossil material has been broadly reported from many Cretaceous localities of Europe (Estes and Sanchíz, 1982; Buscalioni et al., 2008; Sweetman et al., 2014; Pouech et al., 2015) as well as Morocco (Cavin et al., 2010, 2015; Forey et al., 2011), Tunisia (Cuny et al., 2010a) and Thailand (Cuny et al., 2010b). Other plesiomorphic ray-finned fishes related to gars are Amiiformes, which were diverse and widely distributed in the northern hemisphere during the Cretaceous (Berreteaga et al., 2011; Martín-Abad and Poyato-Ariza, 2013; Poyato-Ariza and Martín-Abad, 2013; Sweetman et al., 2014; Pouech et al., 2015). However, their only extant representative, the bowfin *Amia calva* Linnaeus 1766, is restricted to the east of North America (Grande and Bemis, 1998). Pycnodontiformes is an extinct group of durophagous neopterygians that ranges from the Late Triassic to the Eocene. They are known from almost all continents with the exception of Australia and Antarctica (Poyato-Ariza and Wenz, 2002; Poyato-Ariza, 2005). In addition to all the above-mentioned basal neopterygian groups, the more derived teleosteans became more abundant during the Late Cretaceous (Arratia, 2004; Poyato-Ariza and Martín-Abad, 2013). Among them, Phyllodontidae is the most commonly identified teleostean family, which comprises extinct durophagous fishes. Phyllodonts were distributed from North America to Europe and the north of Africa, ranging from the Late Cretaceous to the Late Eocene. In Europe, they have been recovered from scarce Cretaceous outcrops in Spain and France (Cavin, 1999; Laurent et al., 1999, 2002; Berreteaga et al., 2011; Pereda-Suberbiola et al., 2015). Other teleostean taxa (e.g., osteoglossomorphs, perciforms) remain unknown in the Upper Cretaceous beds of Europe, but have been reported from other continents such as North America, South America, Asia and Africa (Brinkman, 1990, 2008; Gayet, 1991; Li, 1996; Otero and Gayet, 2001; Taverne et al., 2007; Wilson and Murray, 2008; Brinkman et al., 2014).

In recent decades, knowledge of the diversity of the Campanian-Maastrichtian vertebrates of Spain has grown significantly. However, archosaurs (crocodylomorphs and dinosaurs) have usually captured most of the attention of researchers (Pereda-Suberbiola et al., 2009; Riera et al., 2009; Puértolas-Pascual et al., 2014, 2016; Prieto-Márquez et al., 2013; Blanco et al., 2014, 2015a, 2015b; Cruzado-Caballero et al., 2015; Sellés et al., 2015; Torices et al., 2015; Canudo et al., 2016; Blanco and Brochu, in press). Our understanding of the diversity of chelonians, squamates and amphibians has also recently been upgraded (Duffaud and Rage, 1999; Rage, 1999; de Lapparent de Broin and Murelaga, 1999; Blain et al., 2010; Company and Szentesi, 2012; Marmi et al., 2012; Blanco et al., 2016; Szentesi and Company, 2016). As regards to fishes, selachians and batoids from the Maastrichtian transitional settings of the Basque Country and Catalonia (Spain), as well as coeval localities in southern France, are well known (Cappetta, 1987; Gheerbrant et al., 1997; Soler-Gijón and López-Martínez, 1998; Cappetta and Corral, 1999; Vullo, 2005; Kriwet et al., 2007; Corral et al., 2016). By contrast, less attention has been paid to the Iberian osteichthyan record in spite of the fact that their remains are abundant in several Campanian-Maastrichtian localities — e.g., Arazede (Portugal), Albaina and Laño (Basque Country, Spain) and Quintanilla la Ojada (Burgos, Spain) (Sauvage, 1897–1898; Poyato-Ariza et al., 1999; Cavin, 1999; Berreteaga et al., 2011). In most published studies, osteichthyan fish remains have only been cited together with other vertebrate fossils, lacking detailed descriptions, exhaustive systematic data and palaeoecological inferences (e.g., Torices et al., 2010; Serrano et al., 2012).

In recent years, intensive sampling for vertebrate microfossils in the Maastrichtian transitional to continental beds of the Tremp Formation (southern Pyrenees, Catalonia, Spain) has yielded abundant fish microfossils (Blanco and Bolet, 2014). These beds represent a variety of environments, including brackish mudflats, coastal wetlands and fluvial settings with some marine influence (Oms et al., 2007; Riera et al., 2009; Díez-Canseco et al., 2014; Fondevilla et al., 2015; Blanco et al., 2016; Gómez-Gras et al., 2016). The aims of the present paper are: I) to augment what is known of fish diversity, especially regarding osteichthyans, in the uppermost Cretaceous of the Iberian Peninsula; II) to explore the relationships between ichthyofaunas and environment; III) to describe the time-range of fish taxa in this area during the six million years before the Cretaceous-Paleogene mass extinction; and IV) to provide new palaeoecological data for a better understanding the last dinosaur-dominated ecosystems of northeastern Iberia.

2. Geological setting

The studied localities crop out on the southern slope of the Pyrenees in Catalonia (northeastern Spain). During the Campanian and part of the Maastrichtian, sedimentation in the area occurred in marine settings, from open-shelf to nearshore and coastal environments. In the latter, calcarenites, marls, limestones and sandstones belonging to the Les Serres, Terradets and Areny Sandstone Formations consolidated (Caus et al., 2016; Oms et al., 2016). At the Campanian-Maastrichtian boundary, a marine regression began in the southern Pyrenean basin, leading to the formation of an east-to-west elongated tidal flat of about 2500 km^2 (Oms et al., 2016). The marls and marly limestones that accumulated on this tidal flat form the Fumanya Member, the base of the so-called Tremp Formation (Mey et al., 1968). Tectonic activity in the Pyrenees region led to the uplift of the Boixols and Montsech Heights, the latter splitting the flat area up into the Àger and Tremp-Vallcebre basins from the early Maastrichtian on (Gómez-Gras et al., 2016). As a result of subsequent tectonic activity which continued up to the Paleogene, Cretaceous and Cenozoic materials from the south-central and southeastern Pyrenean basin thrust upwards to form a number of allochthonous units that were displaced tens of kilometers to the south (Boixols-Sant Corneli, Serres Marginals, Montsech, Pedraforca and Cadí thrust sheets). As a consequence, materials from the Tremp Formation nowadays crop out in four synclines. From east to west, these are the Vallcebre, Coll de Nargó, Tremp and Àger synclines.

The Tremp Formation was divided by Rosell et al. (2001) into four informal units which are from the base to the top: 1) the 'grey' unit (including the afore-mentioned Fumanya Mb), comprising mudstones, limestones and coals interpreted as coastal wetlands; 2) the 'lower red' unit, comprising mudstones and sandstones interpreted as floodplains and related fluvial settings; 3) the Vallcebre limestone and laterally equivalent strata, made up of limestones suggesting the development of extensive lacustrine areas; 4) the 'upper red' unit, consisting of mudstones, sandstones, conglomerates and limestones of fluvial, alluvial, lacustrine and palustrine origin.

The fish material reported in this study was collected from the following localities: Fumanya in the Vallcebre syncline; Els Nerets, Serrat del Rostiar-1, Serrat del Pelleu, Camí del Soldat and Molí del Baró-1 in the Tremp syncline; and l'Espinau and Fontllonga-6 in the Àger syncline (Fig. 1A–B). The samples from Fumanya were collected at the top of the Fumanya Mb, which is interpreted as a tidal flat (Oms et al., 2016). The Fumanya Mb falls within the C32n.1n magnetochron, which corresponds to an early Maastrichtian age (Oms et al., 2007; Fondevilla et al., 2016) (Fig. 1C). The locality of Els Nerets also belongs to the 'grey' unit and consists of grey lutites of variable thickness sandwiched between two units of the Areny Sandstone Formation (Torices et al., 2012). It is interpreted as a marginal-marine to coastal lagoon setting and, according to recent magnetostratigraphic data, it is included within the C31r magnetochron, giving an early Maastrichtian age (Fondevilla et al., 2016) (Fig. 1C). The localities of Serrat del Rostiar-1, Serrat del Pelleu, Camí del Soldat and Molí del Baró-1 correspond to the 'lower red' unit of the Tremp Formation and are interpreted as floodplain and meandering river environments with some marine influence (see details in Blanco et al., 2016 and Marmi et al., 2016). The age of Serrat del Rostiar-1 is early Maastrichtian (Blanco et al., 2016). By contrast, the sites of Serrat del Pelleu, Molí del Baró-1 and Camí del Soldat are correlated with the C29r magnetochron, giving them a late Maastrichtian age (Blanco et al., 2016; Marmi et al., 2016; Fondevilla et al., 2016) (Fig. 1C).