Universitat Autònoma de Barcelona

Vertebrate microfossil diversity from the Tremp Formation (Maastrichtian): Contributions to evolution of the Late Cretaceous terrestrial ecosystems from the northeastern Iberian Peninsula

ALEJANDRO BLANCO

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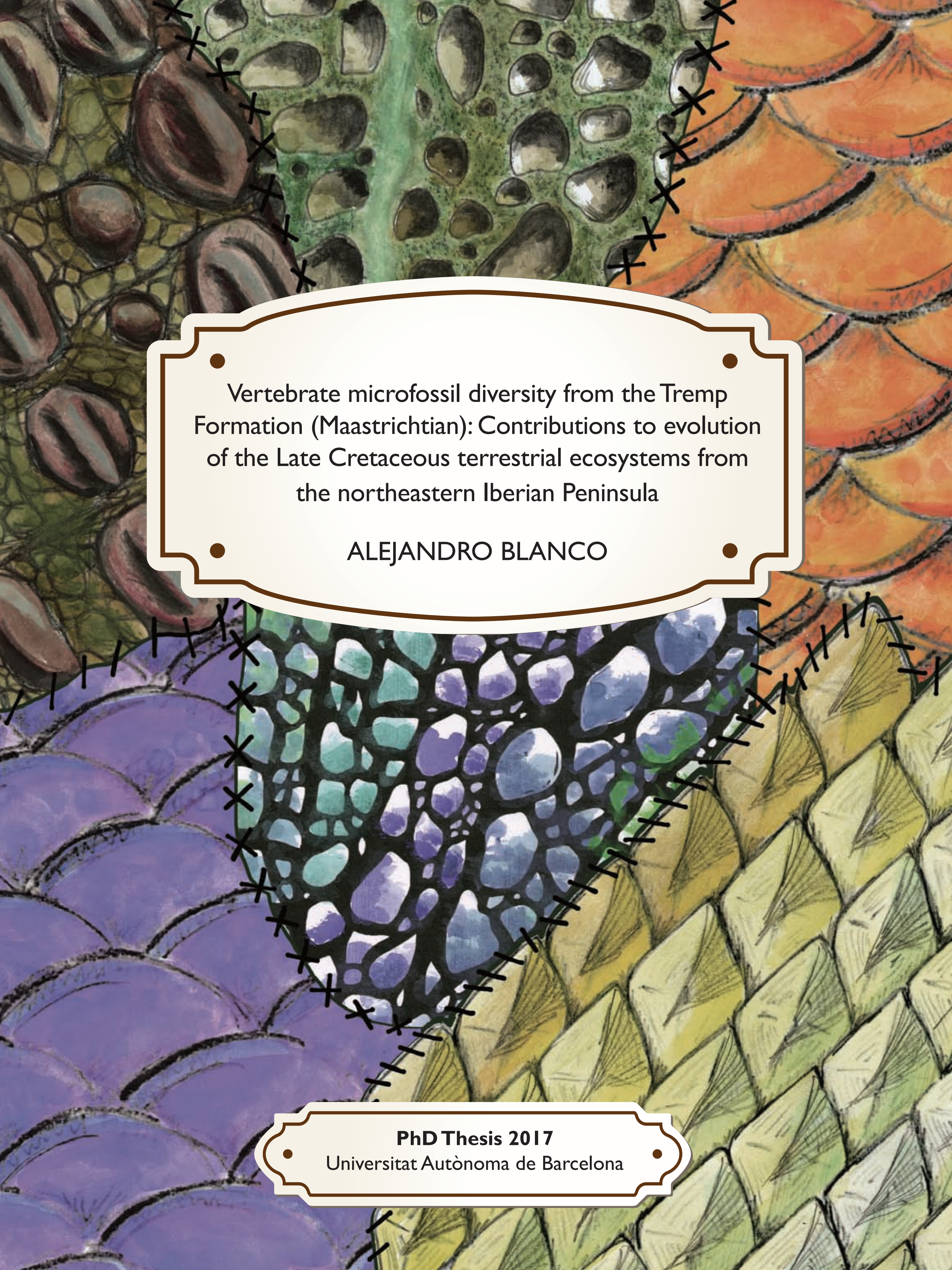

Vertebrate microfossil diversity from the Tremp Formation (Maastrichtian): Contributions to evolution of the Late Cretaceous terrestrial ecosystems from the northeastern Iberian Peninsula

ALEJANDRO BLANCO

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Diversidad de microfósiles de vertebrados en la Formación Tremp (Maastrichtiense): Aportaciones a la evolución de los ecosistemas terrestres finicretácicos del noreste de la Península Ibérica.

Alejandro Blanco Calvo
Tesis Doctoral - 2017

Memoria presentada por Alejandro Blanco Calvo para la obtención del título de Doctor en Geología. Esta tesis doctoral se encuentra enmarcada en el Programa de Doctorado en Geología de la Universitat Autònoma de Barcelona (*MEE2011-0492*), en la modalidad de compendio de publicaciones, cumpliendo los requisitos mínimos de dos artículos aceptados en revistas contenidas en los dos primeros cuartiles del *Journal Citation Reports* (Thomson Reuters), y bajo la supervisión de:

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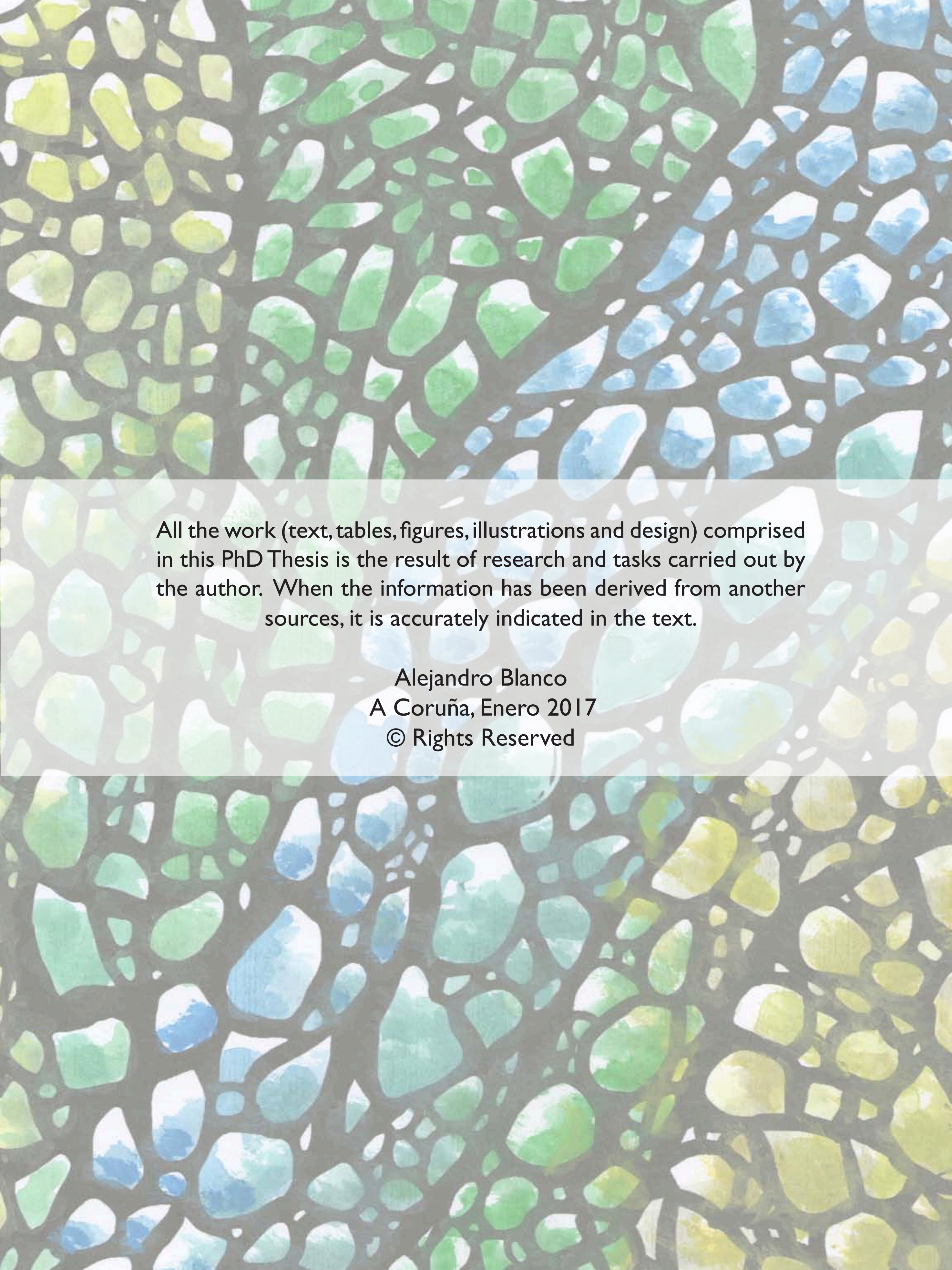

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Alejandro Blanco
A Coruña, Enero 2017

I amar prestar aen
Han mathon ne nen
Han mathon ne chae
A han noston ned 'wilith

Galadriel ~ ESdlA

Ás veces, o feito máis pequerrechiño pode ter consecuencias moi grandes e desprazadas lonxe no tempo. *Ata o máis insignificante pode cambia-lo curso do futuro.*

Un dos recordos máis vellos que teño é na sección de películas do Corte Inglés. Eu non pasaba do xeonllo dos meus pais e unha man entraba por riba no meu campo de visión cun VHS amarelo e vermello. Nese momento, miña nai dábame un agasallo do mesmo xeito que *Piecito* recibiu a súa *hoja estrella*. Aquela cinta de Don Bluth teríame entretido por moito tempo.

Outro recordo do que xa case nin podo lembrarme, é ve-lo espectáculo de *Cortylandia* dende o colo de Ma por Nadal. Segundo din, fíxenlles levarme a velo moitas veces. Inda hoxe soa aquela canción na miña cabeza. E lembro agora cómo naqueles momentos tiven mágoa por eses animais xigantes que non puideran subir ao arca de Noé.

O que tedes entre as mans é o resultado daqueles días.

A Tata e Papi,
a Ma e Pa.

Good morphology lasts forever, whereas
today's matrix and the cladograms it yields will
soon be superseded.

Colin Patterson (1998)

When confronted by a famous paleontologist
skeptical of a cataclysmic K/Pg extinction
based on selected survivals, the late Nobel
laureate Luis Alvarez responded (and then
left!): "…I'm giving you the stars and you're
giving me frogs?"

Monmaney, (1993)
(from Feduccia, 2014)

RESUMEN

La presente tesis doctoral trata sobre la diversidad de los pequeños y medianos vertebrados en los últimos ecosistemas del Cretácico Superior (Maastrichtiense) representados en el registro fósil de la Formación Tremp (Cataluña, España). Los microfósiles estudiados pertenecen a los grupos de los condrictios, osteíctios, anfibios, escamosos y cocodrilomorfos. En cuanto a peces, los resultados muestran una baja diversidad de condrictios, pero una rica asociación de osteíctios que además representa un buen ejemplo de la diversificación de los teleósteos durante el final del Cretácico. Por otra parte, el registro fósil de cypriniformes y osteoglossiformes son los más antiguos a nivel mundial y europeo respectivamente. Los resultados también revelan una diversa asociación de anfibios y reptiles escamosos, entre los cuales los restos de gecónidos son la única evidencia de este grupo en el registro mesozoico de la Península Ibérica y una de las pocas a nivel europeo. El registro fósil de cocodrilomorfos está compuesto principalmente por dientes aislados pertenecientes a diversos clados de cocodrilos notosuquios, neosuquios y eusuquios. Además, se han descrito dos especies nuevas del género *Allodaposuchus* en base a dos esqueletos parciales. Estas dos especies han sido relevantes para conocer los restos postcraneales de este grupo extinto de cocodrilos, y han permitido proponer nuevas hipótesis sobre la diversidad ecológica de los allodaposúquidos así como de la historia evolutiva de los cocodrilos actuales. A parte de las aportaciones taxonómicas y sistemáticas, los microfósiles de vertebrados estudiados han permitido entender mejor la paleoecología de los ambientes acuáticos y continentales del Maastrichtiense ibérico, así como el origen y relación biogeográfica de los vertebrados que componían estas faunas maastrichtienses. Estos nuevos datos contribuyen a reconstruir los ecosistemas del noreste ibérico durante el final del Cretácico y entender su dinámica y evolución hasta el momento de la extinción masiva del límite Cretácico-Paleógeno.

RESUMO

A presente tese doutoral trata da diversidade dos pequenos e medianos vertebrados nos derradeiros ecosistemas do Cretáceo Superior (Maastrichtiense) representados no rexistro fósil da Formación Tremp (Cataluña, España). Os microfósiles estudados pertencen ós grupos dos condrictios, osteíctios, anfibios, escamados e crocodilomorfos. No concernente ós peixes, os resultados mostran unha baixa diversidade de condrictios, pero unha rica asociación de osteictios que ademais reflexa un bo exemplo da diversificación dos teleósteos durante o final do Cretáceo. Pola outra banda, o rexistro fósil dos cypriniformes e osteoglossiformes son os máis antigos a niveis mundial e europeo respectivamente. Os resultados tamén sinalan unha diversa asociación de anfibios e réptiles escamados, entre os cales os restos de xecónidos son a única evidencia deste grupo no rexistro mesozoico da Península Ibérica e unha das poucas a nivel europeo. O rexistro fósil dos crocodilomorfos está composto maiormente por dentes illados pertencentes a diversos clados de crocodilos notosuquios, neosuquios e eusuquios. Ademais describíronse dúas novas especies do xénero *Allodaposuchus* a partires de dous esqueletos parciais. Estas dúas especies foron relevantes pra coñece-los restos post-craniais deste grupo extinto de crocodilos, e permitiron propor novas hipóteses sobre a diversidade ecolóxica dos allodaposúquidos, así como da historia evolutiva dos crocodilos actuais. A maiores das contribucións taxonómicas e sistemáticas, os microfósiles de vertebrados estudados permitiron mellora-lo coñecemento da paleoecoloxía dos ambientes acuáticos e continentais do Maastrichtiense ibérico, así coma do orixe e relación bioxeográfica dos vertebrados que compuxeran estas faunas maastrichtienses. Estes novos datos contribúen a reconstruí-los ecosistemas do nordeste ibérico durante o final do Cretáceo e entende-la súa dinámica e evolución ata o momento da extinción masiva do límite Cretáceo-Paleóxeno.

ABSTRACT

The present PhD dissertation deals on the diversity of the small- and medium-sized vertebrates from the latest ecosystems of the Late Cretaceous (Maastrichtian) represented in the fossil record of the Tremp Formation (Catalonia, Spain). The studied microfossils belong to chondrichthyan, osteichthyan, amphibian, squamate and crocodilian groups. Regarding fishes, the results show a low diversity of chondrichthyans, but a diverse assemblage of osteichthyans representing a good example of the teleost diversification during the end of the Cretaceous. Likewise, the fossil remains referred to osteoglossiforms and cypriniforms are the oldest evidence for these groups in Europe and in the world, respectively. The results of this thesis also point to a diverse assemblage of amphibians and squamates, among which the gekkotan fossil is the only occurrence of this group in the Mesozoic record of the Iberian Peninsula, and one of the little evidence in Europe. The fossil record of crocodylomorphs is mainly composed of shed teeth from different notosuchian, neosuchian and eusuchian clades. Moreover, two new species of the genus *Allodaposuchus* were erected based on two partial skeletons. These two specimens have been relevant to know the postcranial bones of this extinct crocodilian group. These species have also allowed us to propose new hypotheses about the ecological diversity of allodaposuchids and the evolutionary history of living crocodiles. Besides of systematics and taxonomic contributions, the study of the fossil microvertebrates has enabled us to assess the palaeoecology of the aquatic and continental environments from the Maastrichtian of the Iberian Peninsula, as well as the origin and biogeographical relationships of the Maastrichtian vertebrate faunas. These new data are contributing to reconstruct the ecosystems from the northeastern Iberian plate during the end of the Cretaceous; and to understand the dynamics and evolution until the massive extinction event in the Cretaceous-Palaeogene boundary.

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Chapter 1. INTRODUCTION

1. INTRODUCTION

1.1 The end of an Era

During the Mesozoic Era (225 to 66 million years ago, Ma), specifically in the Jurassic and Cretaceous periods, most of the extant fish, amphibian and reptile groups appeared and diversified (Benton, 2005). Reptiles had the greatest evolutionary success in the world, dominating terrestrial and freshwater environments (dinosaurs and crocodylomorphs), shallow and deep seas (ichthyosaurs, plesiosaurs, mosasaurs, thalattosuchians and pliosaurs), and skies (birds and pterosaurs). Amongst them, dinosaurs are the most famous group for the general public; thus, the Mesozoic is commonly called the golden age of reptiles, or simply "the Age of Dinosaurs". Since the early discovery of some of their giant members most of the scientific efforts in vertebrate palaeontology have been focused on their systematics, palaeoecology and extinction.

The environment and the palaeogeography of the Earth during the Mesozoic are very well known nowadays. During the latest of the Mesozoic periods, the Cretaceous (145-66 Ma), climates were still warm. Polar regions had warm-temperate climates and the limit between the subtropical and temperate floras was displaced 15º towards the poles, compared to the present. Thus, most of North America, Europe, South America and Africa had tropical climates. At the beginnings of the Cretaceous, floras were still composed by Triassic and Jurassic relicts like low ferns, horsetails, seed ferns, tree-sized club mosses, cycads, bennettitales, ginkgos and conifers. However, the first flowering plants, *id est* the angiosperms, appeared in the Early Cretaceous and radiated rapidly after 30-40 million years of cryptic evolution, reaching the modern levels of dominance in the Late Cretaceous (Hickey & Doyle, 1977; Crane *et al.*, 1995; Nichols & Johnson, 2008; Coiffard *et al.*, 2012, Marmi *et al.*, 2016b). But at the end of the Cretaceous, a mass extinction event (the fifth in the history of the Earth) took place, killing out approximately 75% of the total species on the planet and, specifically, about 30% of the families of vertebrates (Benton, 1993; 2005; Jablonski, 1994; Sepkoski, 1996).

Our knowledge of the end-Cretaceous biotic crisis has improved considerably since Alvarez *et al.* (1980) proposed the broadly-known theory of the meteorite impact that took place 66 Ma. Although evidence for an end-Cretaceous impact in Chicxulub (northern Yucatán Peninsula, Mexico) is unequivocal (Schulte *et al.*, 2010), during these four last decades there has been intense debate about several key aspects of this theory. For instance, the synchrony of the Cretaceous-Palaeogene boundary (K/Pg) and the associated extinction event with the

Chicxulub structure has been questioned (e.g., Keller *et al*., 2007). Other researchers disagree about the real causes of the extinction because other severe changes also occurred at the end of the Cretaceous: intensive volcanism (e.g., Courtillot & Renne, 2003; Chenet *et al*., 2009), temperature oscillations (e.g., Huber *et al*., 2002; Wilf *et al*., 2003; Tobin *et al*., 2012), and sea-level fluctuations (Miller *et al*., 2005). It has been proposed that (1) each of these individual factors may be the main cause of dinosaur extinction by themselves; (2) that their combined effects triggered the extinction; or (3) that an extraterrestrial impact finished off the dinosaurs after a long period of stress due to one or more of the aforementioned factors (Archibald, 1996, 2011; Fastovsky & Bercovici, 2016). Each of these hypotheses can be tested with the fossil record: the impact hypothesis predicts an abrupt (sudden) extinction, whereas other hypotheses defending climate and sea-level changes, including those proposing the meteorite as the *coup de grâce*, imply that dinosaurs suffered a prolonged decline throughout the end of the Cretaceous. In the case of the volcanic model (Courtillot, 1999), some interpretations explain the K/Pg event by instantaneous catastrophic extinction, or alternatively, by a gradual extinction (a span of 3 Ma) caused by successive eruption episodes. After that, the association between the bolide impact and the K/Pg boundary was subsequently proved on the basis of new geochronological data which demonstrated these two facts were coeval (Renne *et al*., 2013; Richards *et al*., 2015). Renne and collaborators, however, did not rule out the fact that other factors might have played an important role in the end-Cretaceous crisis. They proposed that brief cold breaks in the latest Cretaceous were particularly stressful to ecosystems that were well adapted to the extensive preceding warmth. Global climate instability preceded the K/Pg boundary by nearly one million years, including a dramatic drop of 6ºC to 8ºC in annual continental mean temperature less than 100 thousand years (ka) before the mass extinction (Wilf *et al*., 2003). This cooling episode was consistent with a global marine regression that started in the geomagnetic polarity chron C30n (Miller *et al*., 2005). The causes of these climate perturbations are unclear, but a likely candidate was the volcanogenic emissions producing the Deccan Traps (Renne *et al*., 2013). In this sense, the Chicxulub impact might have provided the *coup de grâce* to ecosystems that were already under critical stress. On the contrary, Brusatte *et al*. (2015) did not find evidence for a global long-term decline in the biodiversity of non-avian dinosaurs, suggesting that temperature and sea-level fluctuations were not important factors in their extinction. In this sense, the Chicxulub impact was the primary cause of the event.

Regardless of the main cause(s) of the K/Pg event, some data suggest a gradual decline of tetrapods or even a “3-metre gap” between the highest dinosaur finding and the K/Pg boundary (Archibald & Bryant, 1990; Archibald, 1996; MacLeod *et al*., 1997), whereas their reinterpretation or other evidences support the catastrophic extinction (Sheehan *et al*., 1991, 2000; Sheehan & Fastovsky, 1992; Lillegraven & Eberle, 1999; Pearson *et al*., 2002; Fastovsky & Sheehan, 2005; Brusatte *et al*., 2015; Feduccia, 2014; Fastovsky & Bercovici, 2016), also refuting this “3-metre gap”. This enthralling debate is also hindered by the possibilities of sampling and taphonomic biases (Signor & Lipps, 1982). The Signor-Lipps effect postulates that artificial truncations in the stratigraphic ranges of taxa, especially uncommon taxa, make a catastrophic extinction appear as a gradual process. In other words, taphonomic biases on uncommon or poorly represented taxa, could give the wrong impression that these taxa did not reach the stratigraphic level of the extinction event. Furthermore, one of the strongest arguments supporting the catastrophic hypothesis is the "fern-spike". In several states of USA, Canada and New Zealand a thin layer (~1 cm thick) of a monospecific assemblage of ferns occurs associated with the iridium anomaly (the marker of the K/Pg boundary) at the base of the Palaeocene. It was interpreted as an indication of plant cover devastation, consequence of a global effect of the bolide impact (*i.e.*, climatic perturbations after an impact winter that was preceded by global wildfires; Vajda *et al.*, 2001), and ferns were pioneer re-colonizers in the first steps of the recovery of plant communities (Vajda *et al.*, 2001; Vadja & McLoughlin, 2004; Nichols & Johnson, 2008).

A long continuous series of exposed Upper Cretaceous beds is crucial to understand the K/Pg extinction, especially for continental biota. There are few places in the world with a good record of the latest Cretaceous continental ecosystems (late Maastrichtian, 69-66 Ma), mainly occurring in North America, northern Spain, southern France, Central Europe, Bulgaria, Romania, Crimea, Scandinavia, northeastern Russia, Siberia, China, Morocco, India, Brazil, Bolivia, Australia, New Zealand and Antarctica (Archibald & Fastovsky, 2004; LeLoeuff, 2012 and references therein). The Hell Creek Formation (Montana, Wyoming, North and South Dakota, western North America) is the area where the diversity of the latest Cretaceous biota is best-known (see the review of Fastovsky & Bercovici, 2016), with a continuous sequence of continental beds from the Cretaceous to Palaeogene, including the iridium peak marking the K/Pg boundary (Clemens & Hartman, 2014). Besides dinosaurs, the Hell Creek Formation records a large, diverse and well-known microvertebrate fossil assemblage (Estes *et al.*, 1969; Bryant, 1989; Archibald & Bryant, 1990; Pearson *et al.*, 2002; Fastovsky & Bercovici, 2016), including elasmobranchs (Cook *et al.*, 2014), actinopterygians (Brinkman *et al.*, 2014), lissamphibians (Wilson *et al.*, 2014), squamates (Longrich *et al.*, 2012), birds (Longrich *et al.*, 2011; Feduccia, 2014) and mammals (Archibald, 1996, Wilson *et al.*, 2012; Wilson, 2013). One of the best regions to study the latest Cretaceous biota is southwestern Europe. Here, Provence (southern France), the Basque-Cantabrian region (northern Spain) and the southern Pyrenees (northeastern Spain) have yielded a diverse vertebrate fossil record (Csiki-Sava *et al.*, 2015 and references therein), although Romanian beds have also provided important contributions in eastern Europe (Csiki-Sava *et al.*, 2016). Specifically, the southern Pyrenean area provides an expanded continental record from the Upper Cretaceous to the Lower Palaeogene (López-Martínez *et al.*, 1999; Oms *et al.*, 2007; Riera *et al.*, 2009) and offers an excellent opportunity to study the evolution of the latest Cretaceous continental ecosystems far away from the impact area. Here, numerous sites belonging to the Maastrichtian units of the Arén Sandstone and Tremp Formations (Mey *et al.*, 1968) have yielded a diverse fossil assemblage of vertebrates with fishes (Soler-Gijón & López-Martínez, 1998; Kriwet *et al.*, 2007), amphibians and squamates (Blain *et* al., 2010; Marmi *et al.*, 2012b), turtles (Marmi *et al.*, 2009, 2012c), crocodiles (Puértolas-Pascual *et al.*, 2011, 2014, 2016) and dinosaurs (López-Martínez *et al.*, 2001; Pereda-Suberbiola *et al.*, 2009a; Canudo *et al.*, 2016). The plant fossil record includes charophytes, sporomorphs, seeds and leaves of ferns, conifers and a diversity of angiosperms (López-Martínez *et al.*, 1999;

Vicente, 2002; Marmi *et al*., 2010a, 2012a, 2015, 2016b; Villalba-Breva *et al*., 2012; Villalba-Breva & Martín-Closas, 2013; Vicente *et al*., 2015). Invertebrates are mostly represented by molluscs (Liebau, 1973) as well as scarce remains and ichnofossils of arthropods (Mayoral & Calzada, 1998; Marmi *et al*., 2016b). However, dinosaurs have usually captured the attention of researchers generating a significant bias in the knowledge of fossil vertebrate diversity in this area (and it is the general trend in the world).

Several authors have tried to analyse the extinction/survival patterns in the Mesozoic biota, in order to assess the whole effect of the mass extinction event on the terrestrial and marine ecosystems (e.g., Canudo, 1997; MacLeod et al., 1997; Archibald & Fastovsky, 2004; Molina et al., 2006). Nevertheless, most of the studies dealing with the terrestrial realm are based on archosaurians (e.g., Sheehan et al., 1991; Fastovsky & Sheehan, 2005; Brusatte et al., 2015) and floras (e.g., Nichols & Johnson, 2002, 2008; Bercovici et al., 2009), whereas those taking into account microvertebrates are usually focused on their palaeoecological implications (e.g., Brinkman et al., 2014; Cook et al., 2014) and only a few of them test their diversity before and after the K/Pg event (Archibald & Bryant, 1990; Pearson et al., 2002; Longrich et al., 2012; Feduccia, 2014; Wilson et al., 2014). The precise knowledge of the latest Cretaceous continental biota as a whole is relevant to assess the real effects of the K/Pg mass extinction crisis. According to Benton (1993, 2005), the highest extinction rates were, of course, in non-avian dinosaurs, pterosaurs and marine reptiles (100%). Birds and marsupials also suffered high rates (75%). Medium rates were observed in crocodylomorphs (36%), turtles (27%) or even in chondrichthyans (18%). On the other hand, rates for bony fishes, amphibians, squamates, basal and placental mammals did not differ from background extinctions (<15%). However, an extended microvertebrate dataset is required to better understand the biodiversity of the Late Cretaceous ecosystems and the effect of the K/Pg event. Our perception of its magnitude could change after further efforts in microvertebrate palaeontology (e.g., Longrich et al., 2012; Feduccia, 2014).

1.2 Origins, evolution and Late Cretaceous fossil record of non-dinosaurian vertebrates

The present PhD dissertation tries to improve the current knowledge of microvertebrate fossil record in the uppermost Cretaceous of the southern Pyrenean area, describing the time-range of these taxa during the six million years before the Cretaceous-Palaeogene biotic crisis, as well as their palaeoecological and palaeobiogeographical implications for a better understanding of the last dinosaur-dominated ecosystems of northeastern Iberia. This thesis could represent one of the first insights for studying the effects of the K/Pg event on the terrestrial faunas far of the Chicxulub impact in further analyses. In order to provide an overview of the Late Cretaceous faunas, the following sections comprise a brief summary about the origins and radiation of each vertebrate group studied in this thesis, with an emphasis on the European record.

1.2.1 Fishes

The term “fishes” include a vast array of distantly related vertebrates, different in morphology, anatomy, habitats and biology, but with a phylogenetic continuity. Some people use the term “fishes” to name exclusively the bony fishes. Others also include sharks and relatives. However, this term can also include jawless craniates. In any case, the term “fishes” is paraphyletic because some of their descendants, the tetrapods, are excluded. If someone wishes to restrict this term to a monophyletic group, it should be applied to the ray-finned fishes. But here, I use this term according to Nelson (2006), in order to refer to all craniates including jawless forms and excluding tetrapods, without a taxonomic rank.

The origin of fishes dates back to the Cambrian. *Myllokunmingia* from the Chengjiang (Early Cambrian) of China is placed as the basal-most craniate (Shu *et al.*, 1999), and considered the oldest fish representative (Benton, 2005; Nelson, 2006). The first groups in the fish radiation of the Ordovician were jawless fishes. Some of them were serpent-like naked forms (Petromyzontiformes, Myxinoidea, Conodonta), but other more developed groups bore bony head shields or heavy armoured bodies (Pteraspidomorphi, Anaspida, Thelodonti, Osteostraci, Galeaspida and Pituriaspida) (Benton, 2005; Nelson, 2006). Most of these ‘agnathan’ fishes went extinct at the end of the Devonian (Fig. 1A), leaving neither Cretaceous nor extant representatives (except lampreys and hagfishes), thus I won’t discuss them any further in this thesis.

The Gnathostomata are characterized by the possession of jaws. They diverged from an ‘agnathan’ ancestor and include some fossil armoured fishes (Placodermi), but also Chondrichthyes (sharks and relatives), Acanthodii and Osteichthyes (bony fishes). Osteichthyes and acanthodians form a monophyletic group named Teleostomi. The gnathostomate lineages appeared in the Late Ordovician, but they remained scarce until the beginning of the Devonian (Benton, 2005; Nelson, 2006) (Fig. 1A). The Ordovician record belongs to possible isolated chondrichthyan scales and the first acanthodians. The oldest intact shark fossils come from the Early Devonian, such as *Doliodus problematicus* (Woodward 1892) and a *Pucapampella*-like taxon (Maisey & Anderson, 2001; Miller *et al.*, 2003). Note the important fossil gap among the gnathostomates, since the acanthodians (the sister taxon of the osteichthyans) hold the oldest fossil record and show clear Silurian representatives, before the placoderm, chondrichthyan and osteichthyan diversification (Fig. 1A). During the multiphase Late Devonian extinction event, the placoderms, most of the acanthodians, and some basal osteichthyans, together with the ‘agnathans’, disappeared, and the former dominance of seas by heavily armoured fishes gave way to modern sharks and bony fishes (Benton, 2005; Nelson, 2006).

Chondrichthyans diversified hugely during the Carboniferous, giving diverse non-neoselachian forms, but then declined. Some representatives of this radiation survived into the Mesozoic, like the Holocephali (as the living chimaeras) or the Hybodontiformes (Benton, 2005; Nelson, 2006). Neoselachian chondrichthyans, in turn, arose in the Early Jurassic (Maisey *et al.*,

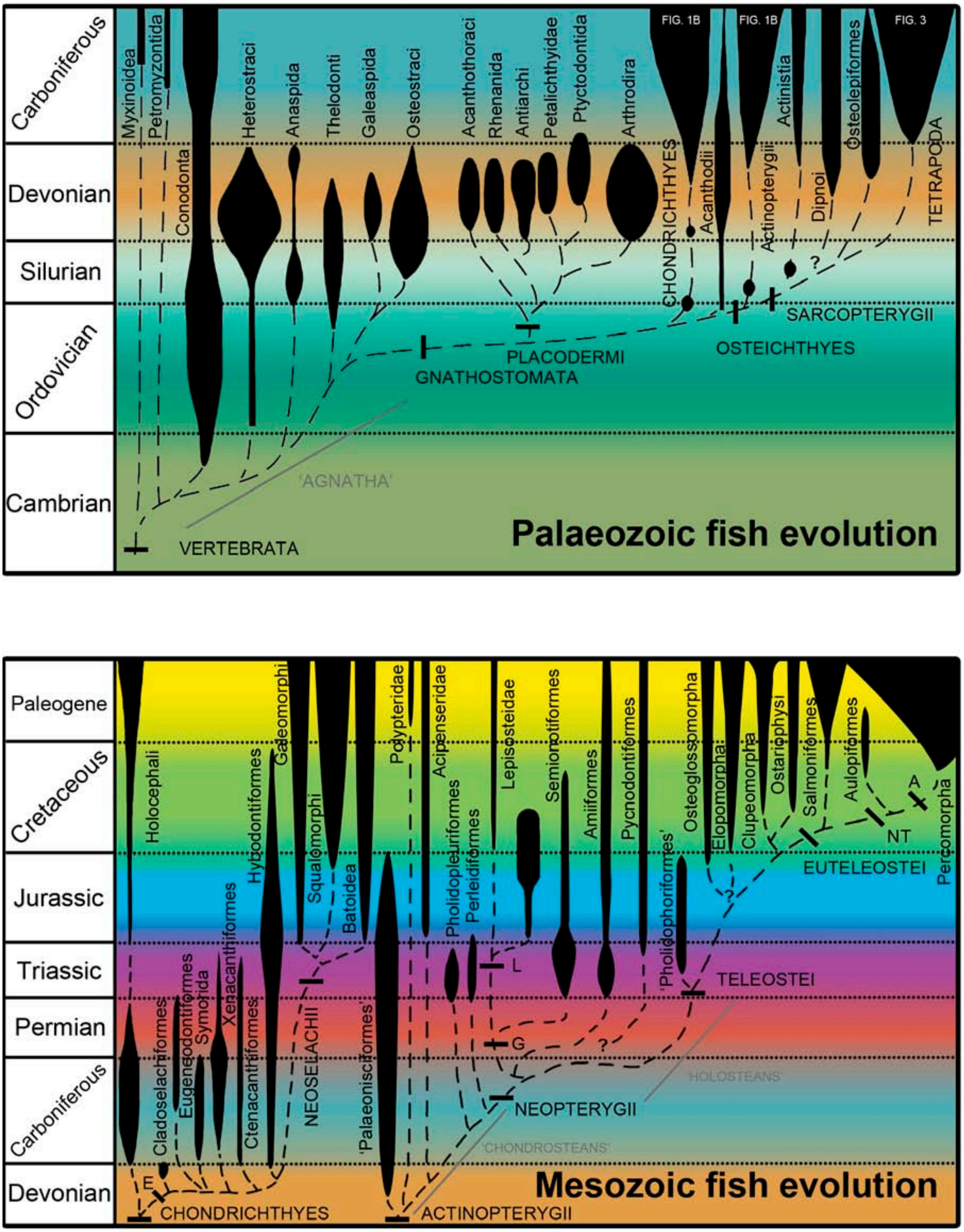


Figure 1. Fish evolution. **A)** (up), Origin and radiation of gnathostomates throughout the Paleozoic. **B)** (down), Origin and radiation of chondrichthyans and actinopterygians during the Mesozoic. *A*, Acanthomorpha; *E*, Elasmobranchii; *G*, Ginglymodi; *L*, Lepisosteiformes; *NT*, Neoteleostei. Updated from Benton (2005). Colours are from the International Chronostratigraphic Chart (v2016).

2004) and radiated broadly during the rest of the Jurassic and Cretaceous, including all living Batoidea (rays) and Selachii (sharks), as well as some fossil families (Fig. 1B). Neoselachians are characterized by several features related to a more adaptable feeding system and faster swimming compared to their precursors (see Benton, 2005 for a more detailed morphological description). The general morphology of selachians varies largely across the groups, from fusiform bodies in nektonic sharks to lined or flattened in sea-bottom and benthonic species, like Pristiophoriformes (sawsharks) or Squatiniformes (angelsharks). Batoids are the most derived group of chondrichthyans, composed by dorsoventrally flattened fishes principally adapted to a benthonic life-style (Cappetta, 1980, 1987; Nelson, 2006). Unfortunately, there is no completely agreement in the systematics and nomenclature between the living sharks and rays. Some traditional morphological studies support the hypothesis that sharks (Squalomorphi, Selachimorpha or Selachii, depending on the author) and rays (Rajiformes, Batoidea or Batomorphii, depending on the author) form a monophyletic group; thus, sharks would be paraphyletic without rays (Compagno, 1973, 1977; Cappetta, 1987; De Carvalho, 1996; Shirai, 1992, 1996). De Carvalho and Maisey (1996) proposed the Hypnosqualean hypothesys, according to which rays would be the most derived group within sharks, as the sister taxa of Pristiophoriformes. In contrast, recent cytogenetic (Schwartz & Maddock, 2002) and molecular analyses (Arnason, 2001; Douady, 2003) have suggested that selachians and batoids are sister taxa. In other words, they are monophyletic groups independent from each other. In addition, Maisey *et al.* (2004) discussed the molecular- and morphological-based phylogenies, and regarded stratigraphic data as highly congruent with molecular evidence. If the molecular hypothesis is correct, the morphological characters suggesting relationships between rays, sawsharks and angelsharks would be the result of convergence (*i.e.*, the homoplasy is stronger in the morphological than in the molecular data). Although most palaeontological works follow the traditional systematics (e.g., Benton, 2005; Marmi *et al.*, 2010b; Corral *et al.*, 2016), here I follow the second hypothesis based on molecular evidences, as Nelson (2006:50) did: "*Although I normally feel it best to accept the implications of morphological data for classifications when there is a conflict with molecular evidence, in this case with such apparently strong conflicting evidence, I prefer to recognize sharks and rays in separate taxa (as done, for example, in Berg, 1940, and Nelson, 1976, 1984), pending further work. However, the cladistic results of de Carvalho (1996) and Shirai (1996) may yet warrant changing our classification*".

According to Nelson (2006), the systematics of Neoselachia is:

- Division Neoselachii
  - Subdivision Selachii (sharks)
    - Superorder Galeomorphi
      - Order Heterodontiformes
      - Order Orectolobiformes
      - Order Lamniformes
      - Order Carcharhiniformes
    - Superorder Squalomorphi
      - Order Hexanchiformes

Order Echinorhiniformes
Order Squaliformes
Order Squatiniformes
Order Pristiophoriformes
Subdivision Batoidea (rays)
Order Torpediniformes
Order Pristiformes
Order Rajiformes
Order Myliobatiformes

Osteichthyes (bony fishes) comprises Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes). Actinopterygians and sarcopterygians are monophyletic groups which appeared in the latest Silurian (Fig. 1A). The actinopterygians have fins supported by cartilaginous or bony radials, whereas the sarcopterygians have fleshy fins supported by a basal bone and muscles (Kardong, 2007; Benton, 2005; Nelson, 2006). Sarcopterygians radiated broadly during the Devonian, including some fossil representatives as well as living lungfishes (Dipnoi), coelacanths (Actinistia), 'rhipidistians' (Porolepiformes, Osteolepiformes and relatives) and all the tetrapods. Therefore, 'sarcopterygian fishes' are paraphyletic if tetrapods are not considered. There is not complete agreement in the relationships within sarcopterygians (e.g., Romer, 1966; Panchen & Smithson, 1988; Chang, 1991, Schultze 1991, 1994; Vorobyeva & Schultze, 1991; Cloutier & Ahlberg, 1996), although the classification of Zhu & Schultze (2001) is amongst the most commonly accepted (Fig. 2). On the other hand, actinopterygians also have diverse Devonian representatives (e.g., *Dialipina* and *Cheirolepis*) but their main diversification took place during the Carboniferous and later (Benton, 2005) (Fig. 1B). This clade was traditionally subdivided in chondrosteans, holosteans and teleosteans (Müller, 1844), which are also inclusive to each other and correspond to up to three diversification events (Benton, 2005). 'Chondrosteans' and 'holosteans' are, thus, paraphyletic groups but these terms are commonly used in a grade-group sense. Basal actinopterygians (= 'chondrosteans') radiated from the Carboniferous to Triassic, and nowadays there are some living representatives (bichirs, sturgeons and paddlefishes). 'Chondrosteans' are a continuous outgroup series to Neopterygii, which acquired progressively an 'holostean' condition (Fig. 1B). Basal neopterygians (= 'holosteans') radiated during the Triassic and were typical Jurassic faunas (Arratia, 2004; López-Arbarello, 2012). Holosteans are characterized by several modifications in the feeding apparatus, bones of the tail, braincase and form of the scales (see Benton, 2005; Kardong, 2007). The term Holostei was originally erected to denominate Lepisosteidae and Amiidae in contrast to Teleostei (Müller, 1844; Huxley, 1861), but with new additions of fossil groups to the phylogeny, this term became complex (Gardiner 1960; Lehman, 1966; Arratia, 2004) and used to refer to all these non-teleostean neopterygians in a grade-sense. Patterson (1973) eliminated the name Holostei as a formal taxon and separated the neopterygians into the clades Ginglymodi and Halecostomi. Subsequently, Ginglymodi grouped Lepisosteidae, Semionotiformes and relatives, whereas Halecostomi included Halecomorphi (Amiiformes and relatives) and Teleostei. For a long time, Chondrostei and

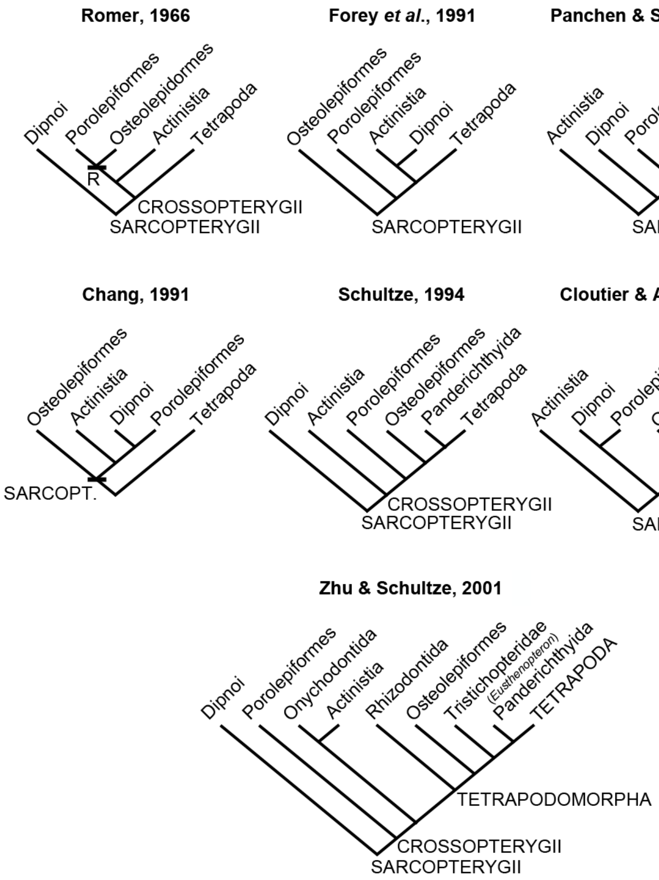


Figure 2. Sarcopterygian phylogeny, showing different hypotheses. Modified from Benton (2005).

Holostei appeared as grades, and the Teleostei as the monophyletic crown-group. However, after an exhaustive revision of lepisosteids (Grande, 2010) and amiids (Grande & Bemis, 1998), Grande (2010) re-used the term Holostei to include ginglymodians and halecomorphs restrictively, instead of Patterson's Halecostomi. In other words, Grande's revision suggests that Halecomorphi is more related to ginglymodians than to teleosteans. Regardless of these last controversial hypotheses, the term 'holosteans' still seems appropriate to refer to those non-teleost neopterygians (Nelson, 2006), which are Lepisosteiformes and Semionotiformes (both within the Ginglymodi), Halecomorphi, Pycnodontiformes, Aspidorhynchiformes and Pachycormiformes (Arratia 2004; López-Arbarello, 2012). Special mention should be made of ginglymodians: Semionotiformes was for a long time a waste-basket group to which much different Mesozoic material was referred to, especially into the genus *Lepidotes*. Nevertheless, López-Arbarello (2012) performed an exhaustive revision of ginglymodian fishes, after which the genus *Lepidotes* was restricted to the Early Jurassic and included within the lepisosteiforms. Most of the species previously referred to *Lepidotes* were relocated into the genera *Scheenstia* (Lepisosteiformes) and *Callipurbeckia* (Semionotiformes), and their phylogenetic relationships were better defined. However, many other species are still pending review (López-Arbarello, 2012). Pachycormiforms are also poorly-known fishes with uncertain phylogenetic relationships, although they have recently been considered 'holosteans' and even the sister group of teleosteans (Arratia, 2004; Nelson, 2006). Nowadays, there are few living relicts of the holostean radiation, such as the gars or *pejelagartos* (Lepisosteidae, with three extant species within the genus *Atractosteus* and four within *Lepisosteus*) and the bowfin (*Amiia calva* Linnaeus 1766) both restricted to the East of North America, but other more advanced 'holosteans' (*i.e.*, pycnodonts, aspidorhynchids) did not leave any descendants. The teleosteans probably appeared in the Late Triassic and became dominant at the end of the Cretaceous and through all the Cenozoic (Arratia, 2004). Teleost fishes are also characterized by modifications in the tail, vertebrae, jaw mechanism, scales and swim bladder (see Benton, 2005; Kardong, 2007). Within Teleostei, there is not complete agreement about its most basal clade (see discussion in Arratia, 2004), but Osteoglossomorpha, Elopomorpha, Ostariophysi and Clupeomorpha are commonly regarded as basal to all other teleost taxa (Euteleostei) (Arratia, 2004; Nelson, 2006). Teleosteans are the richest and most diverse group within vertebrates and dominate almost completely extant ichthyofaunas in rivers, lakes and oceans worldwide. They represent about 96% of all living fishes with 26,840 extant species included within 448 families (Nelson, 2006).

The Cretaceous fossil fish record comprises a few primitive 'agnathan' representatives (lampreys and hagfishes), some relicts of the early chondrichthyan radiation (chimaeras and hybodontiforms), the neoselachian crown-group, sarcopterygian relicts (coelacanths and dipnoans), a few survivors of the early chondrostean radiation, diverse 'holosteans', some basal teleosteans and the first euteleostean representatives (salmoniforms, aulopiforms and acanthomorphs). Within the crown-group Acanthomorpha most of the families belong to Percomorpha. Nevertheless, the presence and abundance of batoids, sharks, holocephalans, as well as lampreys and hagfishes in continental palaeontological sites may be strongly biased due to an environmental factor. Although there are some freshwater occurrences (e.g., Boeseman, 1964; Thorson *et al.*, 1966; Cappetta, 1987; Underwood & Rees, 2002; Martin, 2005; Pillans *et al.*, 2005; Sweetman & Underwood, 2006; Duffin & Sweetman, 2011), chondrichthyans are mainly marine faunas. For instance, batoids are linked to shallow coastal environments since they are usually neritic inhabitants, whereas continental and in-shore coastal environments might record the presence of sharks if they were connected to open-sea waters. Furthermore, holocephalans, lampreys and hagfishes, are open- and deep-seawater inhabitants at least during most of their life (Nelson, 2006). Their fossil record is scarce (e.g., Chang *et al.*, 2006), not only due to an environmental factor, but also because of a taphonomic bias accounted for the lack of an ossified skeleton. On the contrary, hybodontiforms and neoselachians are frequently reported in Cretaceous beds worldwide (e.g., Cappetta, 1987; Cuny *et al.*, 2003, 2010; Maisey *et al.*, 2004; Rees & Underwood, 2008; Bourdon *et* al., 2011; Cook *et al.*, 2014; Khosla & Verma, 2015). The fossil record of sarcopterygians is merely occasional, only represented by dipnoans and coelacanths (e.g., Sanz *et al.*, 1988; Buffetaut *et al.*, 1990; Gayet *et al.*, 2001; Cavin *et al.*, 2010). Likewise, 'chondrosteans' are poorly represented in the Cretaceous because of the few surviving families from the Triassic on. The Cretaceous fossil record is composed by few occurrences of acipenserids (sturgeons) and polyodontids (paddlefish) in North America (Brinkman, 1990, 2008; Brinkman *et al*., 2014; Neuman & Brinkman, 2005) and polypterids (bichirs) in South America (Gayet *et al*., 2001) and northern Africa (Grandstaff *et al*., 2012). On the other hand, 'holosteans' became abundant and widely dispersed during the Cretaceous: ginglymodians are commonly reported from many palaeontological sites worldwide (e.g., Wiley, 1976; Brinkman, 1990, 2008; Gayet *et al*., 2001; Cuny, 2010; Cavin *et* al., 2010, 2013, 2015; Brinkman *et al*., 2014; Csiki-Sava *et* al., 2015; Khosla & Verma, 2015, among others); amiiforms and pycnodontiforms were mainly distributed around the western Tethys in the Northern Hemisphere during the Late Cretaceous, although they have also been reported from almost all continents except Australia and Antarctica (Poyato-Ariza, 2005; Martín-Abad & Poyato-Ariza, 2013; Poyato-Ariza & Martín-Abad, 2013); and aspidorhynchids were distributed in North America, South America, Morocco and Europe (Brinkman, 1990, 2008; Bogan *et* al., 2011; Martill *et al*., 2011; Brinkman *et al*., 2014; Ebert, 2014). Several teleostean groups appeared and radiated during the Cretaceous, but their fossil record is often scattered and scarce. Osteoglossomorphs probably had an ancient cosmopolitan distribution; thus, they have been abundantly reported from North America, South America, Asia, India, Africa and Oceania (e.g., Nelson, 1969; Forey, 1997; Cavin & Forey, 2001; Gayet *et al*., 2001; Neuman & Brinkman, 2005; Brinkman, 2008; Wilson & Murray, 2008; Cavin *et al*., 2010; Taverne & Capasso, 2012; Brinkman *et al*., 2014; Khosla & Verma, 2015; Murray *et al*., 2016, among others), but they still lack a Cretaceous fossil record in Europe (Wilson & Murray, 2008). In addition, elopomorphs (especially phyllodontids) seem to have been distributed only in the Northern Hemisphere; they have occurred in North America, Europe and Morocco (Estes, 1969; Brinkman, 1990, 2008; Cavin *et al*., 2010; Brinkman *et al*., 2014; Csiki-Sava *et al*., 2015), although a recent study has suggested that some members (*i.e*., *Egertonia*) could have reached Madagascar and India through the Tethys (Halliday *et al*., 2016). Several ostarioclupeomorph groups also belonged to Cretaceous ichthyofaunas. Members of Ostarioclupeomorpha (*i.e*., clupeomorphs, gonorynchiformes, siluriformes, characiformes) have been reported from North America, South America, Morocco, Europe and India, suggesting a wide distribution during the Cretaceous (Gayet *et al*., 2001; Cavin *et al*., 2010; Brinkman *et al*., 2014; Csiki-Sava *et al*., 2015, 2016; Khosla & Verma, 2015). However, cypriniforms, one of the most basal ostariophysean groups, lack a Cretaceous fossil record (Fink & Fink, 1981, 1996; Nelson, 2006; Alves-Gomes, 2010). This might suggests that the fossil record of cypriniforms is incomplete and the information of the oldest fossil forms is missing. Regarding euteleosteans, the fossil record of salmoniforms is also scarce and was confidently reported only from several North American localities (Wilson, 1978; Brinkman, 1990, 2008; Neuman & Brinkman, 2005; Brinkman *et al*., 2014). On the other hand, aulopiforms and acanthomorphs show an abundant fossil record broadly distributed in the Cretaceous (Gayet *et al*., 2001; Neuman & Brinkman, 2005; Brinkman, 2008; Cavin *et al*., 2010; Brinkman *et al*., 2014; Csiki-Sava *et al*., 2015; Khosla & Verma, 2015), although percomorphs have not yet been found in Europe.

Concerning the European fossil record, the presence of holocephalans, hybodontiforms, neoselachian sharks and batoids is well documented in the Upper Cretaceous. For instance, a diverse assemblage of hybodontid and neoselachian sharks was reported from the lagoonal sediments of Charente-Maritime (Cenomanian of l'Aquitaine, France) (Vullo *et al.*, 2003, 2007). In contrast, a coeval lagoon from La Cabaña Formation (Cenomanian of Asturias, Spain) did not yield hybodontiform remains, but a variety of neoselachian sharks, batoids and one possible chimaerid (Vullo *et al.*, 2009). Neoselachian sharks and batoids were abundantly recovered from several coastal sites in the Campanian and Maastrichtian of Spain (Cappetta & Corral, 1999; Kriwet *et al.*, 2007; Corral *et al.*, 2012, 2016) and France (Vullo, 2005), showing a high taxonomic diversity. Similarly, the presence of 'holosteans', elopiforms, characiforms and aulopiforms in the Upper Cretaceous of Europe is well known. They have also been frequently recovered from coastal or marine-influenced localities, but they compose most of the fish fossil assemblages from continental beds. Several continental Campanian-Maastrichtian localities from Romania have yielded chondrosteans, lepisosteids and teleosteans (characiforms) (Grigorescu *et al.*, 1999; Csiki-Sava *et al.*, 2015, 2016). In the Iharkút site (Santonian of the Bakony Mountains, Hungary) freshwater lepisosteids and pycnodontiforms were reported (Szabó *et al.*, 2016a, 2016b). 'Holosteans' (lepisosteids, pycnodontiforms, pachycormiforms) and teleosteans (elopiforms, ichthyodectids, enchodontids) have been found in several marine localities in the Kristianstad Basin (Campanian of Scania, Sweden) (Bazzi, *et al.*, 2015). Specifically from Spain, several sites have yielded large and diverse osteichthyan samples: marine amiiforms, pycnodontiforms and teleosteans (elopomorphs, ichthyodectids, enchodontid aulopiforms) have been found at La Cabaña Formation (Cenomanian of Asturias) (Vullo *et al.*, 2009); the continental Laño site (uppermost Campanian of Burgos) has yielded lepisosteids, phyllodontids and probable teleosteans (*?Palaeolabrus*) (Cavin, 1999; Pereda-Suberbiola *et al.*, 2015; but see Bryant, 1989 for the possible inclusion of palaeolabrids within Amiiformes); whereas pycnodontiforms, phyllodontids, enchodontids and indeterminate acanthomorphs were also reported from the open-coastal Albaina site (upper Maastrichtian of Burgos) (Poyato-Ariza *et al.*, 1999; Pereda-Suberbiola *et al.*, 2015); additionally, the in-shore Quintanilla la Ojada locality (upper Maastrichtian of Burgos) yielded pycnodontiforms, amiids, phyllodontids, enchodontids and indeterminate acanthomorphs (Berreteaga *et al.*, 2011).

1.2.2 Amphibians

Tetrapods derive from crossopterygian (sarcopterygian) ancestors (i.e., Eusthenopteron, Panderichthys, Obruchevichthys, Tiktaalik) and stepped on to the land during the Late Devonian (Schultze, 1991, 1994; Zhu & Schultze, 2001; Benton, 2005; Carroll, 2009). Basal tetrapods are often commonly named 'amphibians', including living frogs, salamanders, newts and caecilians. This name refers to the characteristic biphasic lifestyle between water and land, and it is assumed that early fossils forms had the similar habits. In this sense, amphibians are paraphyletic because many descendant groups (i.e., reptiles, birds and mammals) are excluded.

The first amphibian forms (i.e., Metaxygnathus, Acanthostega, Ichthyostega, Tulerpeton) were still mainly aquatic, but subsequent Carboniferous representatives (i.e., Greererpeton, Crassigyrinus) became more terrestrial. These first tetrapods were progressively adapted to new problems related to a terrestrial lifestyle (i.e., new modes of locomotion, feeding, water balance, reproduction and detecting preys and predators) (see Benton, 2005 for detailed morphological descriptions). Classically, amphibians were divided into the basal Labyrinthodontia and Lepospondyli and the modern Lissamphibia (Romer, 1966). But cladistic analyses revealed a very different scenario (Fig. 3), where Late Devonian tetrapods were successive outgroups of a major Carboniferous tetrapod group which split into two lineages: the Batrachomorpha, including 'Temnospondyli', which evolved towards the extant lissamphibians; and another including the Lepospondyli and Reptiliomorpha, giving way to the Amniota (Yates & Warren, 2000; Ruta et al., 2003). All the batrachomorphs (except Lissamphibia), lepospondyls and non-amniote reptiliomorphs became extinct, at the latest, in the Triassic (except Asian brachyopids and Australian chingutisaurids; see Warren et al., 1997; Benton, 2005; Carroll, 2009). For this reason, only lissamphibians are discussed in this thesis.

Lissamphibia comprises all the living amphibians distributed in four clades: Allocaudata (the extinct salamander-like albanerpetontids), Salientia (frogs and toads), Caudata (salamanders and newts) and Gymnophiona (the limbless serpent-like caecilians). The allocaudates are represented by a few genera of amphibians grouped in a single family, the Albanerpetontidae. These amphibians show a similar anatomy to salamanders, with an elongated and flexible body, rounded head and a short tail. The limbs are robust and powerful, and the cervical vertebrae are fused and reduced in number making a stiffened neck, probably as an adaptation for burrowing.

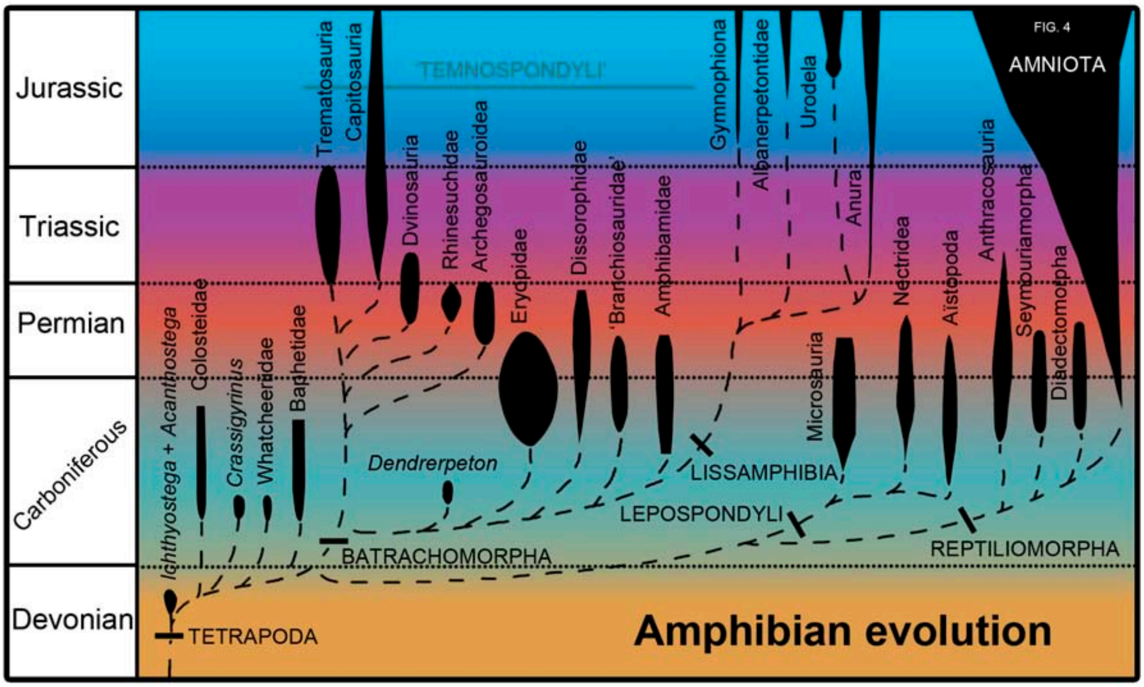


Figure 3. Amphibian evolution. Updated from Benton (2005). Colours are from the International Chronostratigraphic Chart (v2016).

Additional diagnostic characters can be found in the skull (see McGowan & Evans (1995), McGowan (2002) and Carroll (2007) for detailed anatomical features). Albanerpetontids range from the Middle Jurassic to the Miocene (Gardner, 2001; McGowan, 2002; Carroll, 2007). Frogs and toads are grouped in the clade Anura (or Salientia) characterized by an easily recognizable modified body-plan. Anurans show several anatomic adaptations related to a jumping mode of locomotion: elongated hindlimbs (especially ankle bones); a strong pelvis formed by elongated ilia fused with the posterior vertebra (urostyle); robust pectoral girdle and forelimbs to land; and a short vertebral column (reduced number of vertebrae). The tail, as commonly thought, is lost; and the head is short and flat (Carroll, 2007, 2009; Ascarrunz et al., 2016). Salientia comprises some fossil basal forms, and the living clade Anura (Carroll, 2007, 2009). The salientian fossil record goes back to the Early Triassic. Triadobatrachus from Madagascar is the oldest known salientian representative, which already shows some of the aforementioned skeletal adaptations for an unspecialized incipient jumping, despite having a vestigial tail (Rage & Roček, 1989; Ascarrunz et al., 2016). On the other hand, Prosalirus holds the oldest true anuran record, known from the Early Jurassic of Arizona (Shubin & Jenkins, 1995). Other largely modified amphibian group is Gymnophiona. This clade comprises tropical apodan amphibians that look like serpents or earthworms, commonly named caecilians. Caecilians have lost their legs and their eyes are much reduced or even buried under the skin, but in turn, they have remodelled many elements of the eye to form a tactile protruding tentacle. Caecilians also bear a solidly robust skull (which is used as a digging tool), an elongated trunk (there may be more than 200 vertebrae) and a short tail, as consequence of a burrowing lifestyle (Carroll, 2007, 2009). The caecilian fossil record goes back to the Early Jurassic. The oldest known specimens were reported from Arizona and belong to Eocaecilia, which shows typical caecilian features in the skull, elongated trunk and four reduced legs (Jenkins & Walsh, 1993). On the other hand, caudates show an elongated body with four short walking limbs and a flattened tail that allows them to swim. They seem less specialized amphibians than anurans (jumping locomotion) or albanerpetontids and caecilians (burrowing lifestyle). Extant salamander families and their sister taxa are grouped in the clade Urodela, but they are grouped together with some fossil basal forms in the more inclusive clade Caudata (Carroll, 2007, 2009). The fossil record of salamanders and newts goes back to the Middle or Late Jurassic, being Karaurus one of their oldest representatives from the Upper Jurassic of Kazakhstan (Gao & Shubin, 2003).

Phylogenetic relationships among the lissamphibians seem to be well established: anurans and caudates are grouped together in the clade Batrachia, with Gymnophiona as basal lissamphibians (Trueb & Cloutier, 1991; Ruta et al., 2003; Carroll, 2007). Although albanerpetontids could be commonly regarded as strange ('Allo'-) salamanders (-'caudata'), actually they are considered the sister taxon of Batrachia (McGowan & Evans, 1995; Gardner, 2001; McGowan, 2002; Carroll, 2007) (Fig. 3). Concerning molecular analyses, some studies based on low number of genes may disagree with this latest hypothesis (e.g., Feller & Hedges, 1998), but Zardoya & Meyer (2001) have confirmed the traditional Batrachia and the basal position of caecilians on the basis of complete mitochondrial genomes. In this case, it is interesting to remark a large fossil gap in the early lissamphibian representatives, since frogs (placed in the crown-group) hold the oldest lissamphibian record (the Lower Triassic Triadobatrachus) whereas the oldest caecilian record is younger (the Lower Jurassic Eocaecilia). Accordingly, the main lissamphibian groups should probably have differentiated in the end of the Permian (Carroll, 2007, 2009).

Cretaceous fossil record includes members of all lissamphibian clades. Anurans are the most abundant and globally widespread lissamphibians because they were present in Northern and Southern Hemispheres before the break-up of Pangaea (Carroll, 2009). The extant genera *Ascaphus* and *Leiopelma*, autochthonous from North America and New Zealand respectively, are living relicts of the early anuran radiation evidencing a wide ancestral biogeographic dispersion. However, some anuran families with presence in the Cretaceous underwent clear Laurasian (Alytidae, Pelobatidae, Palaeobatrachidae, Gobiatidae) or Gondwanan (Pipidae, Leptodactylidae) origins. All urodeles are strictly Laurasian fauna, probably with Asian origins. Their fossil record is restricted to the Northern Hemisphere even before the break-up of Pangaea, although isolated remains might testify to the presence of the family Sirenidae in the Early Cretaceous of Niger and in the Late Cretaceous of Sudan and Bolivia; additionally, some members of Bolitoglossini nowadays extend from North America across Central America and into northern South America (Carroll, 2009 and references therein). They would be the only occurrences of urodeles from the Southern Hemisphere (Evans *et al*., 1996). Albanerpetontids show clear Laurasian affinities. They were recovered from Europe, Asia and North America, although one species of *Anoualerpeton* occurred in northern Africa (Gardner *et al*., 2003; Sweetman & Gardner, 2013). The fossil record of caecilians is very poor. Besides the aforementioned Early Jurassic record of Arizona, the only other occurrences come from the Lower Cretaceous (Berriasian) of Morocco and the Upper Cretaceous (Cenomanian) of Sudan, as well as later Cenozoic record of South America (Werner, 1994; Evans *et al*., 1996; Evans & Sigogneau-Russell, 2001). Nevertheless, today caecilians are restricted to the tropics along Central and South America, Africa, Asia and India; therefore it is generally assumed that their primary dispersion preceded the break-up of Pangaea (Carroll, 2009).

All lissamphibian groups are expected to be found in the Upper Cretaceous beds from Europe. As listed by Roček (2013), several anuran families were reported from different Romanian, Hungarian, French and Spanish Santonian-to-Maastrichtian localities, like Palaeobatrachidae (indeterminate palaeobatrachids), Alytidae (also named Discoglossidae; *i.e.*, *Bakonybatrachus*, *Paralatonia*, *Paradiscoglossus*, cf. *Eodiscoglossus*, and other indeterminate discoglossids) and possible Pelobatidae or Gobiatidae (Buffetaut *et al*., 1996, 1997; Duffaud & Rage, 1999; Grigorescu *et al*., 1999; Folie & Codrea, 2005; Blain *et al*., 2010; Szentesi & Venczel, 2012; Venczel & Szentesi, 2012; Company & Szentesi, 2012; Szentesi & Company, 2017), as well as other anura *incertae sedis* (*i.e.*, *Hatzegobatrachus* and *Hungarobatrachus*) (Venczel & Csiki, 2003; Szentesi & Venczel, 2010). Albanerpetontid remains are also frequently reported from the Santonian of Hungary and from Romanian, French and Spanish Campanian-Maastrichtian localities (Duffaud & Rage, 1999; Grigorescu *et al*., 1999; Laurent *et al*., 2002; Folie & Codrea, 2005; Blain *et al*., 2010; Company & Szentesi, 2012; Szentesi *et al*., 2013; Pereda-Suberbiola *et al*., 2015; Csiki-Sava *et al*., 2015; Szentesi & Company, 2017), although the incomplete nature of these specimens usually prevents a more detailed classification beyond the family level. Albanerpetontid genera (*i.e.*, *Albanerpeton, Celtedens, Wesserpeton, Anoualerpeton*; McGowan & Evans, 1995; Gardner *et al*., 2003; Sweetman & Gardner, 2013) are similar in shape, and the absence of well-preserved specimens hinders the classification. Even so, the albanerpetontid material from Blasi-2 (Huesca, Spain) revealed *A. nexuosum* (Estes 1981) affinities (Blain *et al*., 2010), whereas those of eastern Europe could be included into the genus *Albanerpeton* (Grigorescu *et al*., 1999; Folie & Codrea, 2005; Csiki-Sava *et al*., 2015). In addition, different size-classes of fossil remains suggest the coexistence of several taxa (Szentesi *et al*., 2013; Csiki-Sava *et al*., 2015). On the contrary, the European Upper Cretaceous record of caudates is rare and merely occasional (Csiki-Sava *et al*., 2015). Fossil remains of Caudata were only confidently reported from the uppermost Campanian of Laño and the Maastrichtian of La Solana in Spain (Duffaud & Rage, 1999; Pereda-Suberbiola *et al*., 2015; Szentesi & Company, 2017) and possibly from the Late Maastrichtian of southern France (Duffaud, 1997, 2000; Gheerbrant *et al*., 1997). It is interesting to remark that the fossil caudate from Laño is the oldest worldwide record of the family Salamandridae (Carroll, 2009). In turn, caecilians lack Upper Cretaceous record in Europe up to now.

1.2.3 Squamates

The amniotes are the most derived tetrapods, characterized by the development of a shelled egg which allows the embryonal development far away from water environments, and without an aquatic larval stage (Benton, 2005; Kardong, 2007; Carroll, 2009). They appeared in the Middle Carboniferous (e.g., *Hylonomus*, *Paleothyris*), evolving from a reptiliomorph-amphibian ancestor, which are sister taxa of lepospondyls. Their first split differentiates between Synapsida (towards the mammals) and Sauropsida (= Reptilia), comprising Anapsida (turtles) and Diapsida (including all living lizards, snakes, crocodiles and birds, as well as other fossil groups such as dinosaurs) (Gauthier *et al*., 1988; Benton, 1991). The reptiles radiated broadly from the Permian to the end of the Cretaceous, splitting into a large diversity of clades (Carroll & Currie, 1991; Benton, 2005). However, most of the basal reptile groups became extinct during the mass extinction event at the end of the Permian or earlier. Testudines, Rhynchocephalia, Squamata, Ichthyosauria, Plesiosauria and Archosauria were the only Cretaceous descendants of this earlier radiation. Of these aforementioned clades, this thesis is focused on squamates and crocodylomorph archosaurs.

Besides the basal-most position of Ichthyosauria (Benton, 2005), diapsids early differentiated between Lepidosauromorpha and Archosauriomorpha (Fig. 4). Subsequently, lepidosauromorphs comprise some basal fossil forms (*i.e.*, kuehneosaurids), and the living Rhynchocephalia and Squamata grouped together within Lepidosauria. In addition, some phylogenetic hypotheses place Sauropterygia (Placodontia, Nothosauria, Plesiosauria) in a

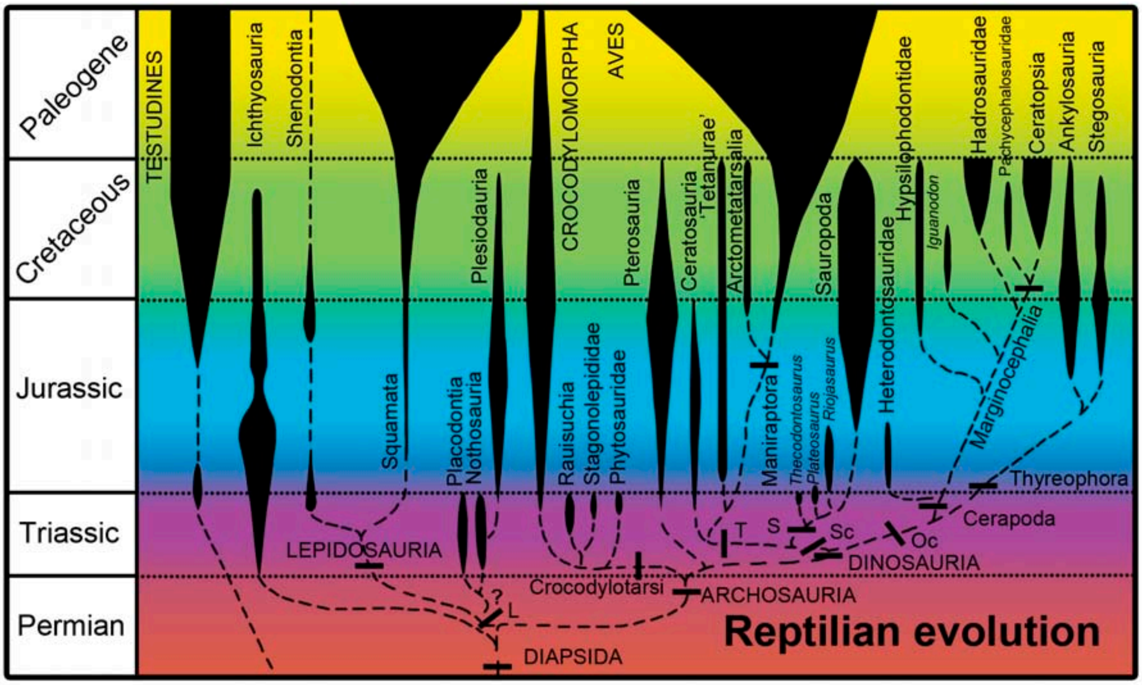


Figure 4. Reptilian evolution. *L*, Lepidosauromorpha; *Oc*, Ornitischia; *S*, Sauropodomorpha; *Sc*, Saurischia; *T*, Theropoda. Updated from Benton (2005). Colours are from the International Chronostratigraphic Chart (v2016).

basal-most position within lepidosauromorphs (e.g., Rieppel, 1993; Rieppel & Reisz, 1999; O'Keefe, 2001, 2002; Benton, 2005), but their relationships still remain controversial (Evans, 2003).

Squamates were classified by Günter (1867) in Lacertilia and Ophidia, in order to group lizards in contraposition to snakes. However, more recent studies (e.g., Estes *et al.*, 1988; Vidal & Hedges, 2005; Conrad, 2008; Wiens *et al.*, 2010, 2012; Gauthier *et al.*, 2012) have shown that 'Lacertilia' is clearly paraphyletic with the exclusion of snakes, and becomes a synonym of Squamata if these latter are included. Phylogenetic relationships between the different squamate clades are still under debate. Most of the morphological analyses (e.g., Estes *et al.*, 1988; Conrad, 2008; Gauthier *et al.*, 2012) agree in the viewpoint that Iguania (iguanids, agamids and chameleons) is the most basal group and sister taxon of all the other squamates, grouped in Scleroglossa. Among the latter, Gekkota is the basal-most group and the sister taxa of Autarchoglossa, which includes Scincomorpha and Anguimorpha. At the same time, Scincomorpha is divided in Lacertoidea (lacertids, teiids, gymnophthalmids) and Scincoidea (scincids, cordylids, xantusiids), whereas Anguimorpha includes, at last, anguids, xenosaurs, varanids and mosasaurs). There are some minor differences relative to the placement of some low-taxonomic clades between the morphological analyses, but the same main topology has been recovered (Fig. 5). There is no complete agreement in the position of Ophidia and

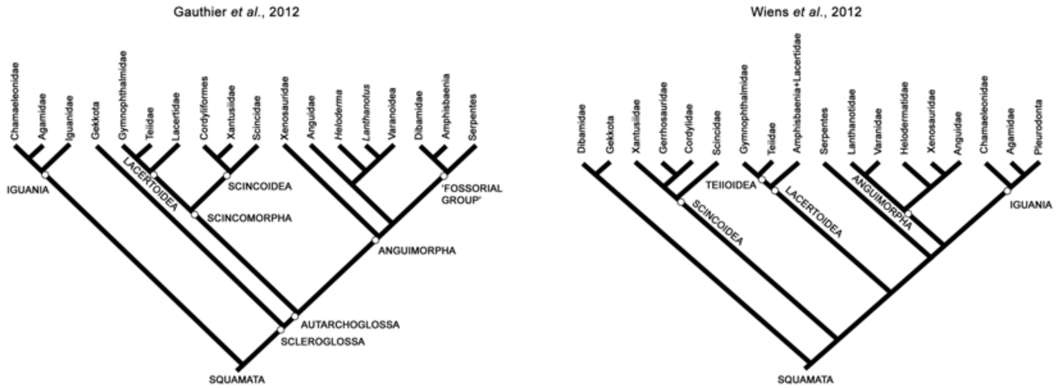


Figure 5. Squamate phylogeny, emphasizing the two main confronted hypotheses: the morphological (Gauthier *et al.*, 2012) and molecular (Wiens *et al.*, 2012) approaches. Modified from Bolet (2014).

fossorial groups such as amphisbaenians and dibamids, and when their positions are resolved (mainly within anguimorphs), it is probably due to convergence rather than ancestry (Gauthier *et al.*, 2012). Although amphisbaenians tend to be considered as lacertoids recently (Bolet, 2014). In turn, recent molecular analyses have introduced drastic modifications over the classical phylogenetic trees (e.g., Vidal & Hedges, 2005, 2009; Wiens *et al*, 2012). The greatest incongruences compared to morphological analyses are the change in the placement of Iguania from the basal-most clade to the crown-group, as the sister taxa of anguimorphs, and the split of scincomorphs into two stem-groups (Fig. 5). According to this new topology, Gekkota and/or dibamids are the most basal squamates (Vidal & Hedges, 2005; Wiens *et al.*, 2012). Thus, molecular analyses do not support the term 'Scincomorpha' because scincoids have been placed as the sister taxon of Anguimorpha+Iguania+Lacertoidea; the term 'Scleroglossa' would be then a synonym of Squamata; and 'Autarchoglossa' ("free tongue") would has no etymological sense with the inclusion of Iguania (Vidal & Hedges, 2005). A way to solve this controversy could be the use of combined morphological and molecular data (Wiens *et al.*, 2010; Martill *et al.*, 2015).

Concerning the fossil record, the earliest squamate was found in the Lower Jurassic of India (Evans *et al.*, 2002), although they might be expected in the Middle Triassic according to the origin of their sister group, the rhynchocephalians (which includes Spenodontia). Rhynchocephalians were globally dispersed in the Late Triassic, but disappeared first from Asia (Early Jurassic) and posteriorly from the rest of Laurasia (Early Cretaceous), only remaining in South America during the Late Cretaceous and in New Zealand until today (Jones *et al.*, 2009; Evans & Jones, 2010; Apesteguía & Jones, 2012). Several squamate groups were undoubtedly present in the Middle Jurassic, like Iguania (India and Mexico), 'Scincomorpha' and Anguimorpha (England) (Evans, 1998; Reynoso, 1998; Evans *et al.*, 2002). The oldest Gekkota are recorded in the Early Cretaceous of Asia but lack European record until the Eocene (Daza *et al.*, 2014), although after a reinterpretation of the material referred to *Parviraptor* some vertebrae suggest the presence of gekkotans in the Middle Jurassic of England (Caldwell *et al.*, 2015), which would be the oldest record of this group worldwide. *Purbicella* from the Late Jurassic-Early Cretaceous of England, probably represent the earliest lacertoid (Evans *et al.*, 2012). The fossil record of Amphisbaenia is more recent and abundant in the Cenozoic. The oldest unequivocal specimen comes from the Palaeocene, though they probably diverged from their supposed sister taxa, Lacertidae, during the Late Cretaceous (Kearney, 2003; Benton, 2005; Vidal & Hedges, 2005; Wiens *et al.*, 2010; Müller *et al.*, 2011; Augé, 2012; Bolet *et al.*, 2014). Recent discoveries have revealed the oldest record of Ophidia in the Middle Jurassic of England (Caldwell *et al.*, 2015). Although their origin is still obscure, snakes are believed to have evolved from a terrestrial lizard ancestor, and some hypotheses place them as the sister taxa of Mosasauria (Martill *et al.*, 2015).

The Cretaceous fossil record is strongly biased because there is a large disparity between Laurasian and Gondwanan records (Evans, 2003). Both pleurodont and acrodont iguanians were reported from several Upper Cretaceous localities in Asia, Europe, North America and South America. Anguimorphs and 'scincomorphs' were found in Europe, Asia, North America and Morocco. On the contrary, only snakes show several African occurrences besides Laurasian record. Estes (1983) proposed a first palaeobiogeographical hypothesis according to which an early Pangaean squamate lineage had undergone a vicariance process resulting in Laurasian scleroglossans and Gondwanan iguanians. However, subsequent discoveries of fossil iguanians in the mid and Late Cretaceous of Asia changed this viewpoint. In any case, any discussion of squamate palaeobiogeography or concerning the origin for major clades is hampered by the information bias towards the northern continents (Evans, 2003 and references therein).

Hence, all squamate groups, at least at high taxonomic level, are expected to be found in the Upper Cretaceous outcrops from Europe. Nevertheless, these herpetofaunas still remain quite poorly known because they are usually recognized from isolated material. For instance, Iharkút locality (Santonian, Hungary) has yielded abundant and well-preserved remains of four different scincomorphs (three of them are borioteiioids) (Makádi, 2006, 2008, 2013a, 2013b; Makádi & Nydam, 2015), but most of them consists of lower jaws. In contrast, some diverse squamate remains referred to varanids, indeterminate lizards, and ?amphisbaenians were reported from the Campanian-Maastrichtian of Southern France (Gheerbrant *et al.*, 1997; Laurent *et al.*, 2002), whereas the presence of anguimorphs and scincomorphs was pointed in the Early Maastrichtian of Romania (Grigorescu *et al.*, 1999). Unfortunately most of these remains are poorly preserved jaw fragments, isolated teeth or fragmentary vertebrae, and do not allow exact taxonomic identifications. Specifically from Spain, two localities have also yielded enough diagnostic material revealing a diverse herpetofaunal assemblage: the locality of Laño (upper Campanian, Basque-Cantabrian region) contains an iguanid, a scincomorphan, a putative amphisbaenian (probably an anguid according to Blain *et al.*, 2010), three indeterminate 'lacertilians' and two madtsoiid snakes (Rage, 1999; Pereda-Suberbiola *et al.*, 2015); and in the Blasi-2 site (upper Maastrichtian, Aragón) has yielded a probable iguanid, one indeterminate scleroglossan, an anguid and an alethinophidian snake (Blain *et al.*, 2010). In addition, this squamate diversity increased with the identification of a multicusped iguanid and a phytonomorph lizard from Lo Hueco site (upper-Campanian-lower Maastrichtian, Cuenca), together with a terrestrial mosasaur and a xenosaur-like anguimorph from Armuña locality (Maastrichtian, Segovia) (Narváez & Ortega, 2010; Houssaye *et al.*, 2013; Pérez-García *et al.*, 2016).

1.2.4 Crocodiles

The other large branch of diapsids is the clade Archosauria, whose unique living representatives are crocodiles and birds, but also comprises some important fossil taxa such as non-avian dinosaurs and pterosaurs. Archosauria is divided in Crurotarsi and Ornithodira (Benton, 2005). The latter one comprises Pterosauria and Dinosauromorpha, including Aves as the crown-group. On the other hand, Crurotarsi is composed by some fossil stem-groups (*i.e.*, Ornithosuchia, Phytosauria, Rauisuchia) and Crocodylomorpha (Fig. 4).

Crocodiles (as the clade Crocodylomorpha) arose in the Early Triassic, being their first representatives small bipedal insectivores (e.g., *Saltoposuchus*). Since then, most of them have inhabited freshwater environments, but others were highly adapted to marine (e.g., thalattosuchians, gavialoids) and terrestrial ecosystems (e.g., *Doratodon*, *Argentinosuchus*, sebecids), always around a conservative body design (Benton, 2005). Feeding habits also have varied largely along the evolution of the crocodylomorphs. Although most of them were generalist predators, there were also herbivores (e.g., *Chimaerasuchus*, *Mariliasichus*), insectivores (e.g., *Saltoposuchus*) and durophagous malacophages (e.g., *Iharkutosuchus*) (Benton, 2005; Andrade & Bertini, 2008; Ősi & Weishampel, 2009).

According to Benton & Clark (1988), the clade Crocodylomorpha is composed by two basal-most forms (*Saltoposuchus* and *Pseudohesperosuchus*), the 'sphenosuchians' and their sister taxon, Crocodyliformes (Fig. 6). The crocodyliforms include 'Protosuchia', 'Mesosuchia' and Eusuchia, which are inclusive clades respectively, thus, being the first two paraphyletic. 'Mesosuchia', however, forms a monophyletic group with Eusuchia, named Mesoeucrocodylia (*sensu* Benton & Clark, 1988). The first crocodyliforms (Protosuchidae) appeared in the Early Jurassic, displaying some of the most striking crocodilian features (skull surface ornamented with irregular pits; skull with pneumatic and complex air passages; a square-shaped skull-roof in outline due to the developed squamosals; the presence of a fleshy "ear-lid" attached to the squamosals, etc.). 'Protosuchia' also includes several forms more related to Mesoeucrocodylia than to Protosuchidae. Subsequently, Mesoeucrocodylia is composed by two monophyletic groups, the marine Thalattosuchia and the Metasuchia. Nevertheless, the phylogenetic affinities of thalattosuchians are still unclear and other alternative hypotheses have been proposed for the origin of the clade (Fig. 6). Metasuchia includes Neosuchia and other 'mesosuchians' (*i.e.*, Notosuchia) closer to them than to thalattosuchians. Most of the basal Jurassic and Cretaceous genera were classified in 'Mesosuchia', which lacks the specializations of the more derived

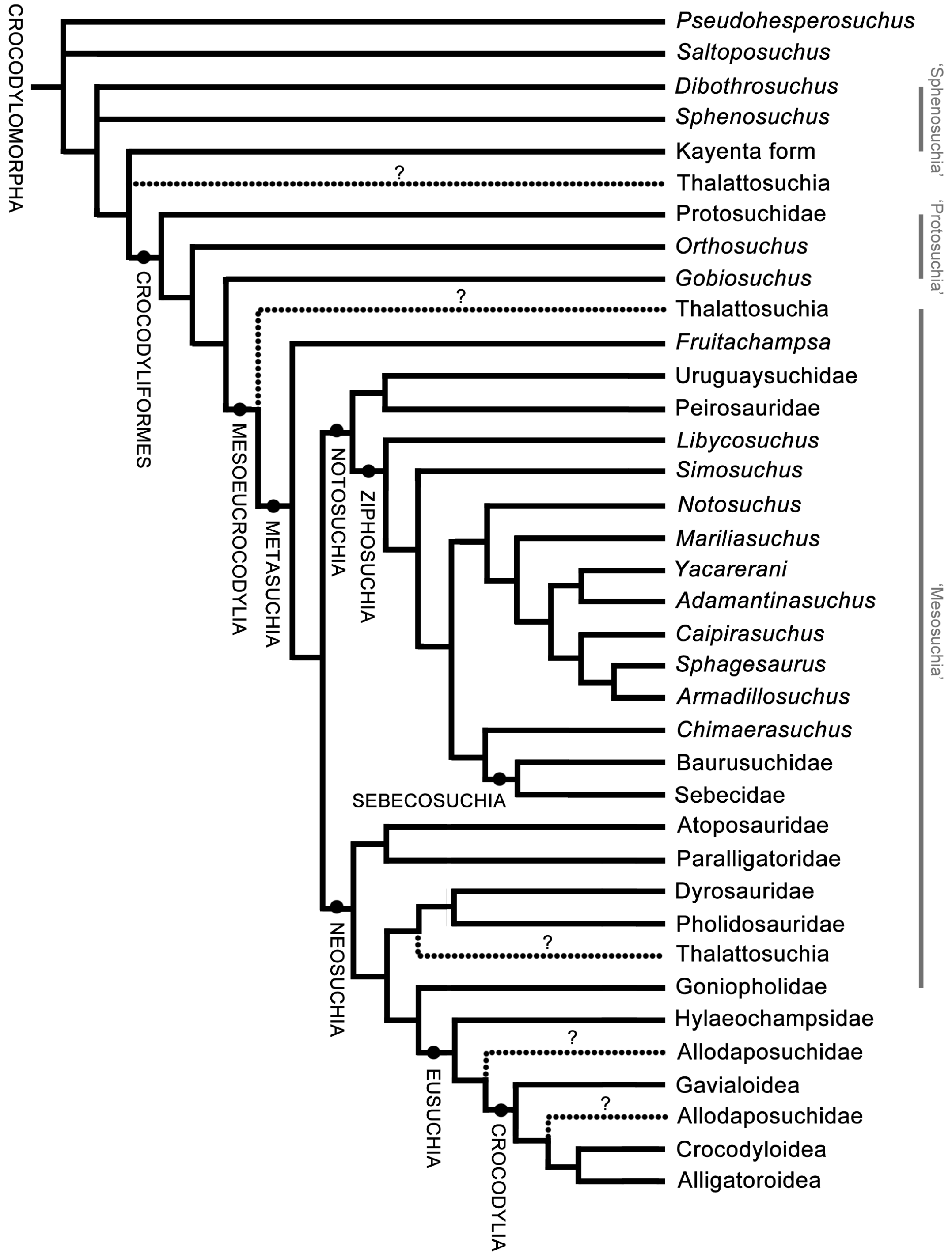


Figure 6. Phylogeny of Crocodylomorpha. Modified from Benton & Clark (1988), Wilberg (2012) and Pol *et al*. (2016).

Eusuchia (see detailed list of morphological features in Benton & Clark, 1988; Benton, 2005). On the other hand, Neosuchia is composed by Atoposauridae, Goniopholidae, Pholidosauridae, Dyrosauridae and Eusuchia, commonly named "modern crocodiles". At the same time, Eusuchia includes some fossil representatives (e.g., Hylaeochampsidae, *Allodaposuchus*) and the living crocodiles, grouped in Crocodylia.

The Cretaceous period is particularly relevant for understand the radiation of the crown-group Crocodylia, which includes the three extant crocodilian lineages (Alligatoroidea, Gavialoidea, and Crocodyloidea). The Early Cretaceous is characterized by the emergence of Eusuchia (Salisbury *et al*., 2006; Martin & Delfino, 2010). This group subsequently replaced the more basal Neosuchia, contributing substantially to the crocodilian faunas from the Cretaceous and all of the Cenozoic until the present day (Buscalioni *et al*., 2003; Salisbury *et al*., 2006; Puértolas-Pascual *et al*., 2016). However, the process of replacement is insufficiently documented in detail because the taxonomy of crocodiles composing the faunal assemblages is incomplete, as well as their fossil record during part of the Cretaceous (Martin & Delfino, 2010; Puértolas-Pascual *et al*., 2016). Anyway, the oldest members of Eusuchia were autochthonous of Europe and dominated European crocodylomorph faunas during the Late Cretaceous (Buscalioni *et al*., 1986; 1999, 2001; Ősi *et al*., 2007; Delfino *et al*., 2008a, 2008b; Puértolas-Pascual *et al*., 2014; Narváez *et al*., 2015, 2016a), although non-eusuchian mesoeucrocodylians were still present as evidenced by hundreds of remains (López-Martínez *et al*., 2001; Company *et al*., 2005; Puértolas-Pascual *et al*., 2016). Specifically, in the Late Cretaceous of Spain inhabited a diverse crocodilian fauna, composed by hylaeochampsids (e.g., *Acynodon*), allodaposuchids (*Allodaposuchus*, *Lohuecosuchus*, *Agaresuchus*), gavialoids (*Thoracosaurus*) and a possible crocodyloid (*Arenysuchus*) in addition to other non-eusuchian species (e.g., atoposaurids, paralligatorids, ?trematochampsids, *Ischyrochampsa*, *Doratodon*). Mesoeucrocodylians, in turn, clearly dominated the faunas outside Europe, including Central Asia and Gondwana (Storrs & Efimov, 2000; Buscalioni *et al*., 2003; Martin & Delfino, 2010 and references therein). Any new findings are very important to shed light on the evolution of Eusuchia and the biological turnover through the Late Cretaceous.

1.3 Palaeobiogeographic implications of the latest Cretaceous vertebrate faunas from the Iberian Peninsula.

1.3.1 The southern European Archipelago and the Ibero-Armorican domain

The configuration of the main landmasses surrounding the Tethys Sea changed from the previous scheme of the northern Laurasia and the southern Gondwana (resulting of the broken Pangaea) to a very different disposition during the Cretaceous. In the Late Cretaceous, several continental masses in both Northern and Southern Hemispheres were separated by oceans. Three palaeobiogeographical realms were defined (Russell, 1993): Palaeolaurasia

(Central Asia, North America and Europe) in the north, Neogondwana (South America, Antarctica and Australasia) and Indoafrica (Africa, India and Madagascar) in the south, with Europe working as a confluence area. At this moment, North America was divided in western and eastern regions by a Mid-Continental Seaway (Sanmartín *et al.,* 2001). In addition, Le Loeuff (1998) distinguished Europe from Mesolaurasia (western and eastern North America and Asia) and West Mesogondwana (South America, Africa, Madagascar and India) from East Mesogondwana (Antarctica and Australasia) (see Pereda-Suberbiola, 2009 and references therein).

By this time, most of Europe was an archipelago conformed by medium and small islands separated by shallow seas from each other (Dercourt *et al.*, 2000). The European Archipelago was also separated from Asia by the West Siberian Sea and the Turgai Strait, from North America by the proto-North Atlantic Ocean, and from Africa by the Tethys Sea (Le Loeuff, 1991). The main emerged European lands were a large Fenno-Scandinavian Shield, the smaller Ukrainian Shield, the Renish-Bohemian Island, the Irish Massif, Cornubia, the Anglo-Scottish Island, the Ibero-Armorican Island, the Austro-Alpine Island and the Rhodope-Moesian Island (Fig. 7). In addition, lesser emerged lands were the Apennine Platform, the Alboran Islands, the Adriatic-Dinaric Island, the Serbo-Pelagonian Island and the Crimean Island. The extant Iberian Peninsula together with southern France formed the Ibero-Armorican domain, the largest island in the archipelago after the Fenno-Scandinavian Shield (Philip & Floquet, 2000).

1.3.2 The dinosaurian faunas

Our knowledge of palaeobiogeographical affinities of the Late Cretaceous dinosaurian faunas of Spain is mainly biased to hadrosaur species although other clades are present. The presence of theropod dinosaurs is mainly testified by shed teeth, which hinders their taxonomic interpretation. However, abelisauroids were probably present (Torices *et al.*, 2015). This clade, with clear Gondwanan affinities, is known from the latest Cretaceous of South America, Africa, India and Madagascar (Pereda-Suberbiola, 2009). Sauropods are represented by titanosauriforms, a group that reached a near-global distribution by the latest Cretaceous. Thus, although Gondwanan affinities were hypothesized, their palaeobiogeographical information is not reliable (Pereda-Suberbiola, 2009). Additionally, nodosaurids, restricted to the early Maastrichtian, are considered North American immigrants (Pereda-Suberbiola, 2009). On the other hand, several hadrosaurs have been recognized in the Ibero-Armorican Island, including at least two indeterminate hadrosauroids (e.g., the Fontllonga and La Solana forms) and a minimum of four lambeosaurine hadrosaurids (*Blasisaurus*, *Arenysaurus, Pararhabdodon* and *Canardia*) in addition to other indeterminate specimens pending of revision (Company *et al.*, 1998; Pereda-Suberbiola *et al.*, 2009a, 2009b; Cruzado-Caballero *et al.*, 2010a; Prieto-Márquez *et al.*, 2013; Blanco *et al.*, 2015c). Outside of the Iberian Peninsula, *Telmatosaurus* and *Tethyshadros*

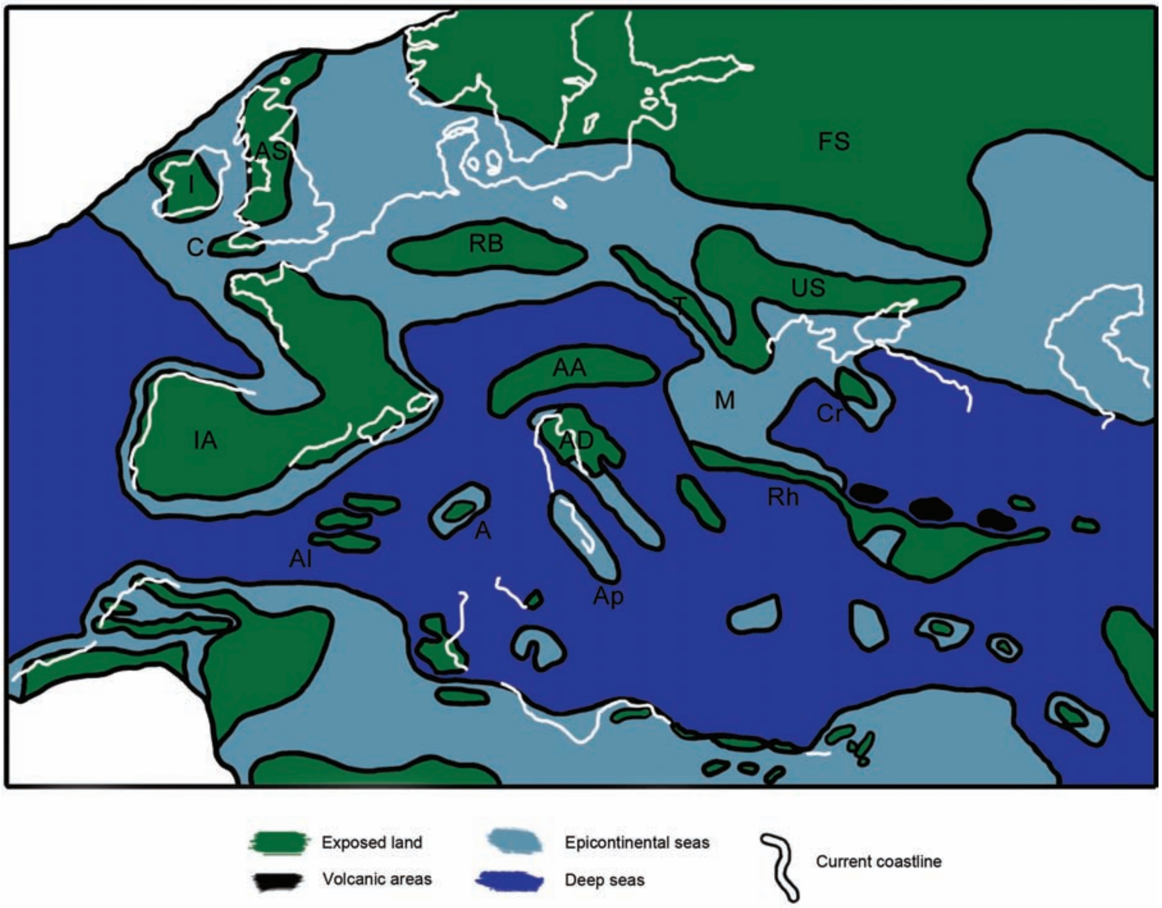


Figure 7. Palaeogeography of Europe during the Maastrichtian. Modified from Philip & Floquet (2000) and Pereda-Suberbiola (2009). ***A***, Apenine platform; ***Al***, Alboran islands; ***Ap***, Apulian platform; ***AA***, Austro-alpine island; ***AD***, Adriatic-Dinaric island; ***AS***, Anglo-Scottish island; ***C***, Cornubia; ***Cr***, Crimean island; ***FS***, Fennoscandinavian shield; ***I***, Irish island; ***IA***, Ibero-Armorican island; ***M***, Moesian platform; ***RB***, Renish-Bohemian island; ***Rh***, Rhodope; ***T***, Transylvania; ***US***, Ukrainian shield.

are known from the Maastrichtian of Romania and Italy, respectively (Nopcsa, 1900, 1903; Weishampel *et al*., 1993; Dalla Vecchia, 2009).

The most reliable biogeographical hypotheses posit an Asian origin for hadrosauroids in the Early Cretaceous (and later for Hadrosauridae), with subsequent dispersal events to Europe and North America (You *et al*., 2003; Godefroit *et al*., 2003, 2005, 2008; Pereda-Suberbiola *et al*., 2009a; Prieto-Márquez *et al*., 2013). A later isolation of the European Archipelago may have preserved non-hadrosaurid hadrosauroids until the Maastrichtian (Averianov & Archibald, 2005). The finding of hadrosauroid teeth in the Cenomanian of the Aquitania Basin of France was interpreted as an evidence of a pre-hadrosaurid lineage, of which *Telmatosaurus*, *Tethyshadros*, and the hadrosauroid forms from La Solana and Fontllonga would be Maastrichtian descendants (Company *et al*., 2009; Pereda-Suberbiola *et al*., 2009a; Blanco *et al*., 2015c). The plesiomorphies present in these European relicts could be explained in terms of geographical isolation. Subsequent dispersal events during the latest Cretaceous from Asia and North America would have brought derived hadrosaurids to Europe. This scenario is consistent with (1) the contrast between the relatively basal phylogenetic position of some lambeosaurine species (*Pararhabdodon*, *Canardia*) and their late stratigraphic location; (2) the interpretation of *Pararhabdodon* and *Canardia* as basal lambeosaurines closely related to the Asian *Tsintaosaurus* and *Aralosaurus* respectively (Prieto-Márquez & Wagner, 2009, 2013; Prieto-Márquez *et al*., 2013); and (3) the coexistence of both hadrosauroids and hadrosaurids in the Maastrichtian of the Ibero-Armorican Island (Pereda-Suberbiola *et al*., 2009a; Cruzado-Caballero *et al*., 2010b; Blanco *et al*., 2015c).

It is a general observation that Ibero-Armorican dinosaurs are of significant small size compared to their Asian and North American relatives, probably due to island isolation (Company *et al*., 2013; Dalla Vecchia *et al*., 2014). The occurrence of dwarfism in different dinosaur clades that inhabited the European Archipelago was pointed by several authors (Weishampel *et al*., 1991, 1993, 2003; Grigorescu, 2003; Sander *et al*., 2006; Benton *et al*., 2006, 2010; Stein *et al*., 2010) and specifically for Spain, Company *et al*. (2013) and Blanco *et al*. (2015c) have reported small-sized hadrosauroids. If these hadrosaurs represent true island dwarves or simply small dinosaurs should still be assessed by exhaustive histological studies. An alternative point of view, suggests that differences in size might reflect sexual dimorphism (Fondevilla *et al*., 2015). However, this hypothesis is based on isolated and undiagnostic appendicular bones, and moreover histological approaches cannot differentiate between sexes.

1.3.3 The non-dinosaurian faunas

Concerning microvertebrate fossils, most of the palaeobiogeographical history of these clades remains still poorly known, mostly due to their isolated nature and the fragility of this type of fossils.

Basal neopterygians are of scarce palaeobiogeographic information because of their wide dispersion, and teleosteans are mostly unknown in the Maastrichtian of the Ibero-Armorican domain. In contrast, rays are considered good palaeobiogeographical indicators due to the restriction to the neritic shallow depths (Cappetta, 1987). The occurrence of the same species in two different landmasses points to an interconnection between continental platforms. On this basis, some rays reported from the southern Pyrenean basin (*i.e.*, *Igdabatis indicus*) show Indian affinities and suggest a connection between Ibero-Armorica and India during the Maastrichtian (Soler-Gijón & López-Martínez, 1998).

As noted above, some of the amphibian lineages (urodeles and albanerpetontids) are Laurasian fauna. In this case, their occurrence in Africa is interpreted as the result of a trans-Tethys dispersal event (Pereda-Suberbiola, 2009). Urodeles had been primarily Asian immigrants during the Triassic or Early Jurassic, but they were well established in European faunas from the Middle Jurassic on (Carroll, 2009), whereas the origin of albanerpetontids was probably in Europe according to the point of highest diversity. Similarly, alytids (or discoglossids) anurans are primarily Palaeolaurasian and extended their distribution to India during the Late Cretaceous. On the other hand, lissamphibian taxa considered Euro-American are the batrachosauroidid urodeles (reported from southern France; Duffaud, 1997) and the palaeobatrachid anurans; but their early record is still unclear to hypothesize the origin of these clades (Pereda-Suberbiola, 2009).

As evidenced by Evans (2003) in her review of the history and radiation of Mesozoic lizards, it is still premature to elucidate palaeobiogeographical implications for most of the herpetofaunal clades due to the paucity of the fossil records in the Southern Hemisphere. Even so, Madtsoiidae is regarded a Gondwanan family of snakes. The two madtsoiids found at Laño site are the only report of this family in Palaeolaurasia and represent African immigrants (Rage, 1999; Pereda-Suberbiola, 2009).

Regarding turtles, several clades with diverse origin were found in Ibero-Armorican localities: solemydids and, tentatively, chelydroids show euro-american relationships; kallokibotionids and dortokids are considered European endemisms; and bothremydids are regarded as Gondwanan fauna reaching Europe from Africa across the Tethys Sea (Pereda-Suberbiola, 2009).

Basal Eusuchians such as hylaeochampsids and allodaposuchids are European endemisms, whereas true crocodylians arose in North America or Europe (Buscalioni *et al*., 2003). Hylaeochampsids (e.g., *Acynodon*, *Iharkutosuchus*) reached a wide dispersion in the European Archipelago during the Late Cretaceous. Although its taxonomy is still controversial (see Section 9.1.3), the genus *Allodaposuchus* is only known from Romania, Hungary and Spain. On the contrary, some mesoeucrocodylians show Gondwanan affinities. For instance, *Doratodon* is closely related to (or included in) Sebecosuchia, which is a notosuchian clade well known from South America (Company *et al.,* 2005; Pereda-Suberbiola, 2009; Rabi & Sebők, 2015). Moreover, some isolated teeth point to the presence of the African trematochampsid crocodiles in several Spanish and French localities (Pereda-Suberbiola, 2009; Puértolas-Pascual *et al*., 2016).

Chapter 2. STRUCTURE & GOALS

Art by Alejandro Blanco

2. STRUCTURE & GOALS

2.1 Structure of the dissertation

This thesis deals with the record vertebrate microfossils of the Maastrichtian part of the Tremp Formation (southern Pyrenees, northeastern Spain). These transitional to continental sediments play an important role in our understanding of the last six million of years of the Mesozoic Era. This dissertation begins with the Introduction (Chapter 1), which is structured in different parts. Due to the proximity of the Tremp Formation to the K/Pg extinction event, an extended overview about the current knowledge of the end-Cretaceous extinction and its effects in the different groups of vertebrates is explained in the first paragraphs. Next, the evolutionary history of vertebrate groups studied in this research (fishes, lissamphibians, squamates and crocodylomorphs) is reviewed with special focus in the Cretaceous period, in order to provide a general overview of the diverse vertebrate faunas that might be expected to occur in the Upper Cretaceous beds of Europe. The following part of the Introduction is focused on palaeogeography of Europe during the Maastrichtian and the palaeobiogeographical origins of the vertebrate assemblage of the Ibero-Armorican Island.

After the Introduction, the main goals of this work are listed in the Structure & Goals section (Chapter 2). After that, the geological setting and the general methodology are explained (Chapter 3 and 4). Next, the main body of the dissertation groups the results, which are structured as a compendium of published papers (Chapters 5 to 8). Each paper represents the outcome of the research I have carried out during the last three years. Before each paper, a short synopsis is introduced to justify the connection with the main goals of the thesis. The papers included in these chapters are:

> *Blanco, A., Puértolas-Pascual, E., Marmi, J., Vila, B. & Sellés, A.G. 2014.* Allodaposuchus palustris *sp. nov. from the early Maastrichtian of Fumanya (south-eastern Pyrenees, Iberian Peninsula): systematics, palaeoecology and palaeobiogeography of enigmatic allodaposuchian crocodylians.* Plos One, 9(12), e115837. *doi:10.1371/journal.pone.0115837*
>
> *Blanco, A., Méndez, J.M. & Marmi, J. 2015. The fossil record of the Uppermost Maastrichtian Reptile Sandstone (Tremp Formation, northeastern Iberian Peninsula).* Spanish Journal of Palaeontology, 30 (1), 147-160.

Blanco, A., Fortuny, J., Vicente, A., Luján, A.H., García-Marçà, J.A., Sellés, A. 2015. A new species of Allodaposuchus *(Eusuchia, Crocodylia) from the Maastrichtian (Late Cretaceous) of Spain: phylogenetic and paleobiological implications.* PeerJ, 3(2), e1171. *doi: 10.7717/peerj.1171*

Blanco, A., Bolet, A., Blain, H., Fondevilla, V. & Marmi, J. 2016. Late Cretaceous (Maastrichtian) amphibians and squamates from northeastern Iberia. Cretaceous Research, 57, 624-638. *doi: 10.1016/j.cretres.2015.07.005*

Marmi, J., Blanco, A., Fondevilla, V., Dalla Vecchia, F.M., Sellés, A.G., Vicente, A., Martín-Closas, C., Oms, O. & Galobart, À. 2016. The Molí del Baró-1 site, a diverse fossil assemblage from the uppermost Maastrichtian of the southern Pyrenees (north-eastern Iberia). Cretaceous Research, 57, 519-539. *doi: 10.1016/j.cretres.2015.06.016*

Blanco, A., Szabó, M., Blanco-Lapaz, À. & Marmi, J. 2017. Late Cretaceous (Maastrichtian) Chondrichthyes and Osteichthyes from northeastern Iberia. Palaeogeography, Palaeoclimatology, Palaeoecology, 465, 278-294. *doi: 10.1016/j.palaeo.2016.10.039*

On the other hand, Chapter 9 comprises a global Discussion of the results provided by this thesis as a whole, specially focusing on the improvement of the knowledge of the Maastrichtian vertebrate faunas of this area from different viewpoints (temporal distribution, palaeobiogeography and paleoecology). After the Discussion, the dissertation ends with the main Conclusions of this work (Chapter 10). A paper authored by myself and another collaborator, which is complementary to the main research carried out in this thesis, is included in the Appendix. After that, the Bibliography lists the references cited in the Chapters 1-4 and 9. References cited in each article are listed at the end of itself.

The Appendix includes:

Blanco, A. & Brochu, C.A. (in press). Intra- and interspecific variability in allodaposuchid crocodylomorphs and the status of western European allodaposuchids. Historical Biology. *doi: 10.1080/08912963.2016.1201081*

2.2 Goals of the dissertation

- To improve the knowledge of the fossil record of fishes, amphibians, squamates and crocodiles from the uppermost Cretaceous of the southern Pyrenean area.

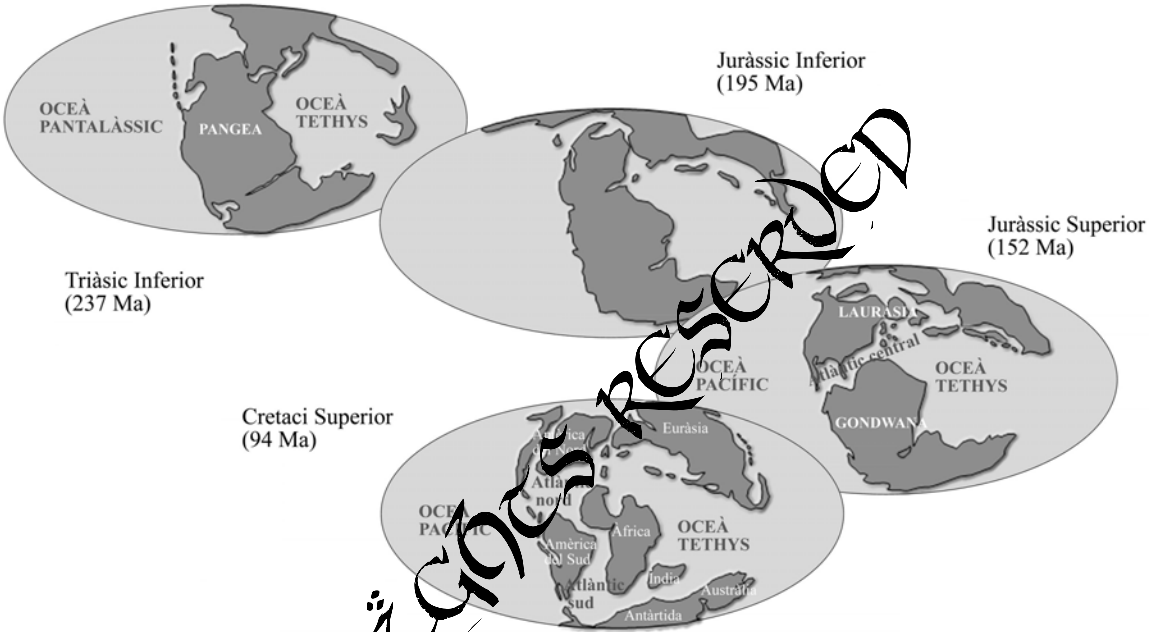
- To describe the time-range of these taxa in this area during the six million years before the Cretaceous-Paleogene mass extinction.

- To assess their palaeoecological implications for a better understanding of the last dinosaur-dominated ecosystems of northeastern Iberia.

- To discuss the paleobiogeographical implications of Maastrichtian vertebrate faunas from northeastern Iberia.

- Try to elucidate possible faunal turnovers between the early and late Maastrichtian.

Chapter 3. THE STUDIED AREA: THE TREMP FORMATION (CATALONIA SPAIN)



Art by Josep Marmi

3. THE STUDIED AREA: THE TREMP FORMATION (CATALONIA, SPAIN)

3.1 Geological setting

The localities studied in this thesis are placed in the north of Lleida and Barcelona provinces (Catalonia, northeastern Spain). They belong to the eastern part of the southern slope of the Pyrenean range (Fig. 8). This mountain belt is orientated east to west and conform a natural frontier between France and Spain.

The Pyrenees were formed by the collision of the Iberian and European plates from the end of the Cretaceous until the Oligocene. The structure of this belt consists of a Palaeozoic basement and a Mesozoic and Cenozoic sedimentary cover. Two foreland basins developed on both north and south Pyrenean slopes and nowadays are located in France and Spain, respectively. During the Campanian and part of the Maastrichtian (Upper Cretaceous), the Pyrenean foreland basin was an extension of the Atlantic Ocean. Marine settings ranged from open-shelf to near-shore and coastal environments. This latter originated the calcarenites, marls, limestones and sandstones composing the Arén Sandstone Formation (Mey *et al.*, 1968) and the laterally equivalents (Les Serres and Terradets Limestone Formations) (Caus *et al.*, 2016 and references therein). 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) and progressively left the whole basin under continental sedimentary conditions. The continental beds recording this regression are called the Tremp Formation (Mey *et al.*, 1968), also named 'Garumnian' by Leymerie (1862), who described the stratigraphy in the Haute-Garonne (France). The boundary between the Tremp and the underlying Arén Sandstone is, thus, asynchronous as consequence of the marine recession towards the east (Fig. 9). The marls and marly limestones that accumulated on the afore-mentioned tidal flat form the Fumanya Member, at the base of the Tremp Fm (Oms *et al.*, 2016). Tectonic activity in the Pyrenees region led to the uplift of the Boixols and Montsec 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). Therefore, the Tremp Fm was deposited in several sub-basins that record different palaeoenvironments and sediment routing. This triggered an early disconnection and a change in the sedimentation in the Àger basin. 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 displaced tens of kilometres to the south (Boixols-Sant Corneli, Serres Marginals, Montsec, Pedraforca and Cadí thrust sheets). As a consequence, materials from the Tremp Fm nowadays crop out in four main synclines. From east to west, these are the Vallcebre, Coll de Nargó, Tremp and Àger synclines (Fig. 8).

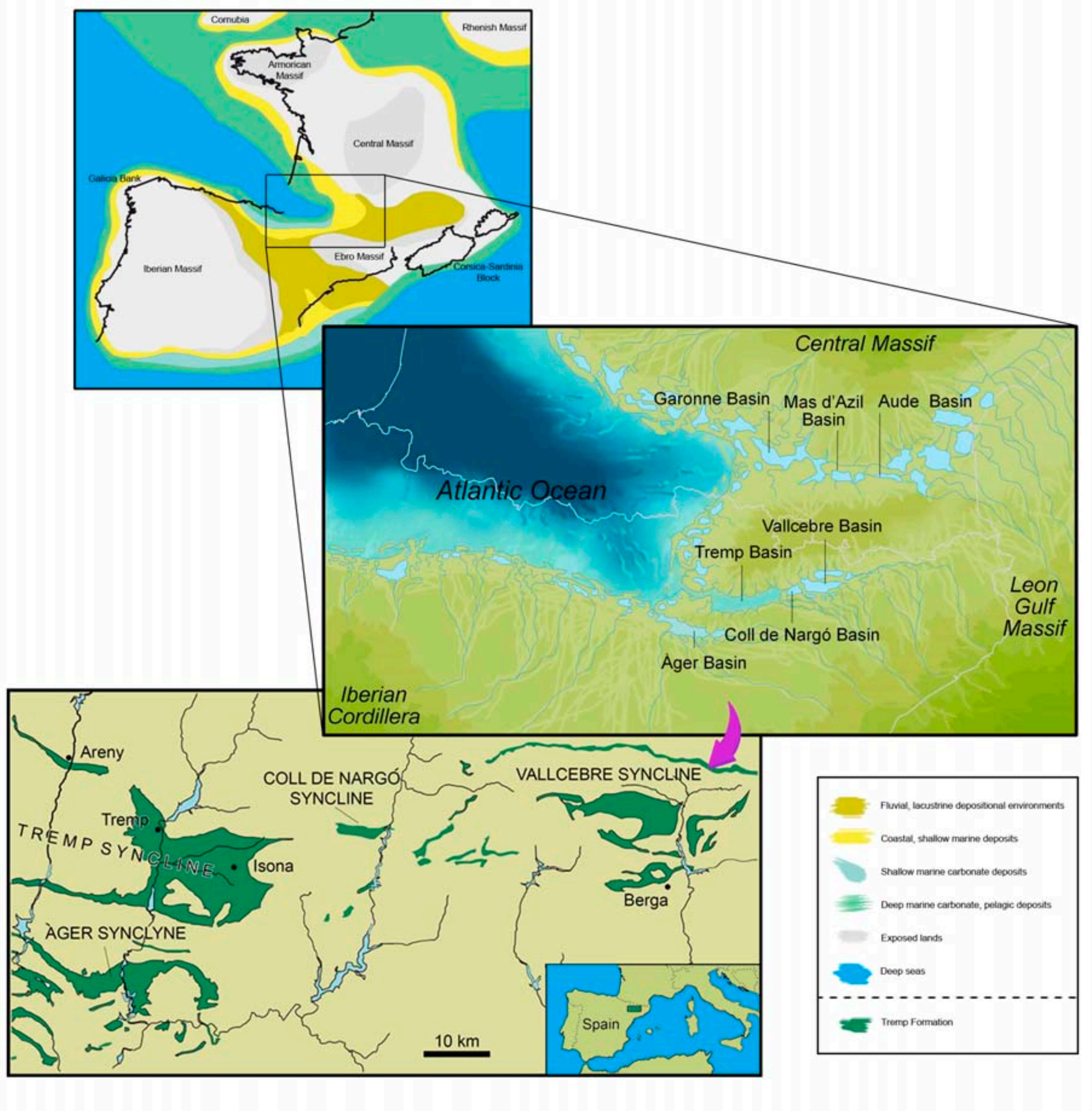


Figure 8. Palaeogeography of the Ibero-Armorican Island (up) with detail of the southern Pyrenean area (middle) during the Maastrichtian and current geographic situation of the Tremp Formation (down). Modified from Philip & Floquet (2000).

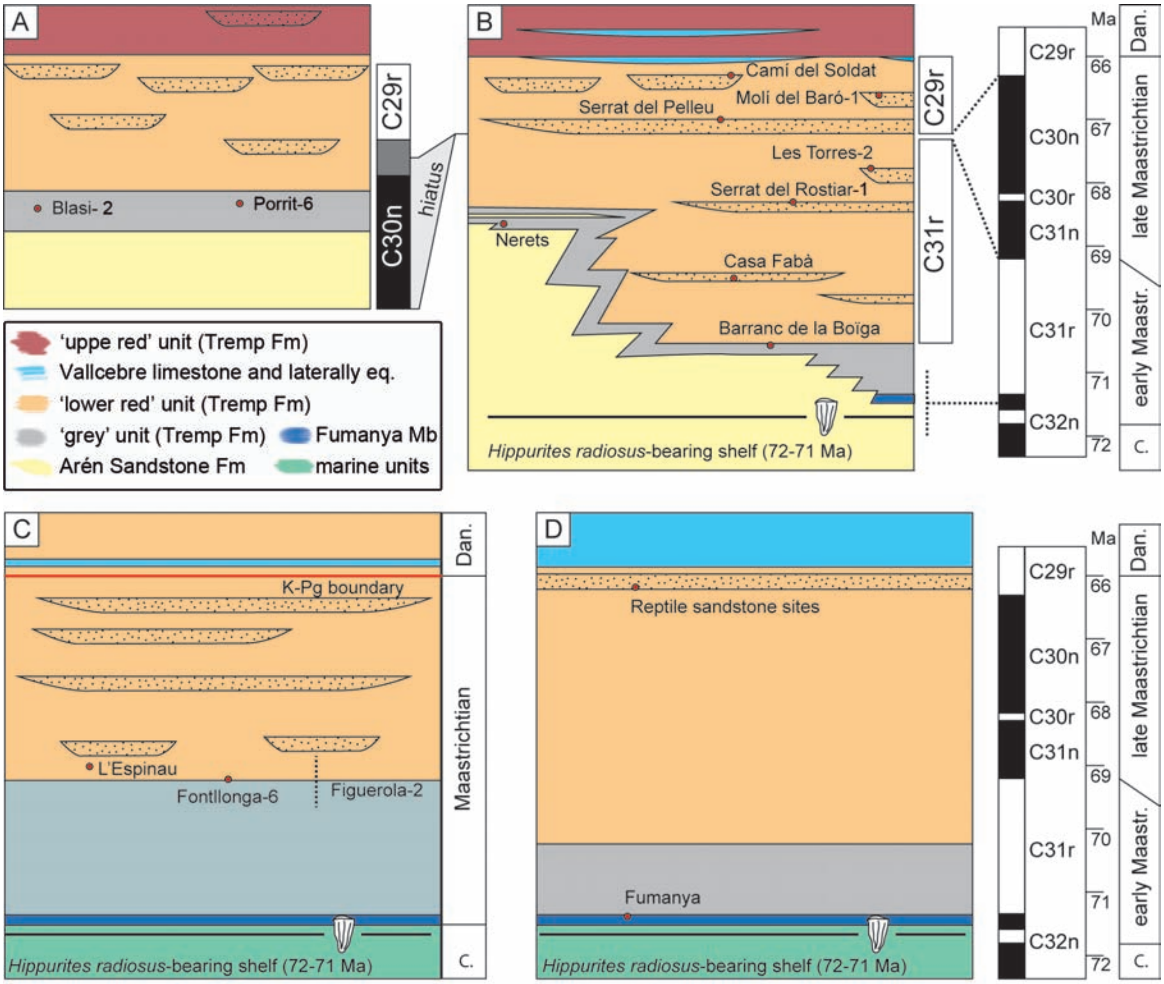


Figure 9. Geological framework for the microvertebrate sites of the Tremp Formation. **A)** western sector of the Tremp Basin. Magnetostratigraphy from Pereda-Suberbiola *et al.* (2009b). **B)** eastern sector of the Tremp Basin. Magnetostratigraphy from Fondevilla *et al.* (2016). **C)** Àger Basin. Sites are correlated by lithology. **D)** Vallcebre Basin. Magnetostratigraphy from Oms *et al.* (2007). Art by V. Fondevilla.

The Tremp Formation (Fig. 9) 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), composed of grey lutites, limestones and coals, is interpreted as coastal wetlands, estuaries and some swampy areas where abundant plant remains were deposited; 2) the 'lower red' unit, composed of mudstones and sandstones, interpreted as a period in which the regressive tendency was accentuated conforming 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, records a period of a reactivated tectonic stage.

However, isolation of different sub-basins from the early Maastrichtian on, promoted different sedimentary features among synclines. For instance, in the uppermost part of the 'lower red' unit, a thick layer composed of sandstones and/or conglomerates with oncolites is called the Reptile Sandstone (Masriera & Ullastre, 1982). This layer appears 7-10 metres below the overlying Danian Vallcebre Limestone in the Vallcebre and Àger synclines, but it is absent in the Tremp syncline (Fig. 9D). According to Oms *et al.*, (2007) this layer was deposited on braided streams under high-energy hydric regime. Its absence in the Tremp basin posits disconnected sedimentary events.

Alternatively, Cuevas (1992) and Pujalte & Schmitz (2005) revised the Tremp Fm and proposed an improved and complementary nomenclature. From their point of view, the Tremp Fm was regarded as a Group, and the four informal units were described on the basis of several formations restricted originally to the Tremp syncline. Therefore, the 'grey' unit was referred as La Posa Fm; the 'lower red' was subdivided in the Conques and the Talarn Fms; the lateral equivalents of the Vallcebre Limestone were named as Suterranya and the Sant Salvador de Toló Fms; and the 'upper red' unit was split in the Esplugafreda and the Claret Fms. Although both classifications are largely compatible, in this thesis I follow the division proposed by Rosell *et al.* (2001) because it is more widely used among the studies focused in this area.

The Maastrichtian age of the 'grey' and 'lower red' units of the Tremp Fm has been suggested by charophyte biochronology (Feist & Colombo, 1983; Ullastre & Masriera, 1983; Médus *et al.*, 1988; Villalba-Breva & Martín-Closas, 2013; Vicente *et al.*, 2015), foraminifera (Díez-Canseco *et al.*, 2014) and magnetostratigraphic evidences (Galbrun *et al.*, 1993, Oms *et al.*, 2007; Vila *et al.*, 2012; Fondevilla *et al.*, 2016), but there are some disagreements placing the limit between the early and late Maastrichtian and the K/Pg boundary. While some studies obtained excellent palaeomagnetic results in the Àger (Galbrun *et al.*, 1993) and Vallcebre synclines (Oms *et al.*, 2007) (Fig. 9C, D) as well as in some localities from Huesca province (Pereda-Suberbiola *et al.*, 2009b; Canudo *et al.*, 2016) (Fig. 9A), data from the Tremp syncline showed some ambiguities. Here, a long undetermined polarity interval was regarded as belonging to the late Maastrichtian following the magnetostratigraphic pattern of other areas of the south-Pyrenean basin (Vila *et al.*, 2012). Subsequently, Sellés & Vila (2015) attempted to provide precise chronological data for the vertebrate palaeontological sites (most of them placed in the 'lower red' unit) based on dinosaur eggshell oospecies as biochronological indicators. However, the late Maastrichtian age they proposed for most of the 'lower red' unit is at odds with those age constraints based on non-reworked planktonic foraminifera of the same area (Díez-Canseco *et al.*, 2014). In turn, Díez-Canseco *et al.* (2014) argued that most of the 'lower red' unit belongs to the early Maastrichtian. This hypothesis is in concordance with more recent magnetostratigraphic data reported by Fondevilla *et al.* (2016) which support an early Maastrichtian age for most of the Tremp Fm cropping out in the Tremp syncline (including most of the 'lower red' unit or, alternatively, the Conques Fm; Fig. 9B). According to these authors, the Fumanya Mb falls within the C32n.1n magnetochron; the 'grey' and most of the 'lower red' unit falls within the C31r, which also corresponds to an early Maastrichtian age; a following hiatus overlaps the C31n, C30r and C30n; and finally a small portion of the 'lower red' unit (coinciding with the Talarn Fm) is included in the magnetochron C29r (late Maastrichtian).

Another important chronostratigraphic challenge in the Tremp Fm is the precise location of the K/Pg boundary. Unfortunately, no iridium anomaly has been found (Médus *et al.*, 1988; Galbrun *et al.*, 1993). Traditionally, the K/Pg boundary was supposed to be located in the uppermost part of the 'lower red' unit and below the Vallcebre Limestone, based on the last non-reworked occurrence of the charophyte *Peckichara sertulata* (Feist & Colombo, 1983) and the absence of dinosaur remains coinciding with the expanse of *Microcodium*. The stratigraphically highest dinosaur remains have been found in the Reptile Sandstone (Pereda-Suberbiola *et al.*, 2003; Sellés *et al.*, 2015). However, a recent biostratigraphic approach (Díez-Canseco *et al.*, 2014) suggested that the boundary may not have been registered in the Tremp syncline as a consequence of a hiatus in the sedimentation.

3.2 Depositional settings of the microvertebrate localities

3.2.1 Localities of the Vallcebre syncline and the remaining Berguedà shire.

Fumanya

The Fumanya dinosaur megatrack site is located between Fígols and Vallcebre villages, at the north of Barcelona province. The fish material and isolated crocodilian teeth from Fumanya were collected at the top of the Fumanya Mb (C32n.1n magnetochron, early Maastrichtian), which is interpreted as a tidal flat (Oms *et al.*, 2007, 2016). The studied crocodilian skeleton from the Fumanya Sud locality was found approximately 30 meters above the base of the Tremp Formation within a 45-metre thick sequence of alternating dark mudstones, limestones and lignites. The sequence is included in the 'grey unit' of Rosell *et al.* (2001). The sedimentological analysis and the palaeontological content (charophytes, coals, rooting structures and brackish to freshwater mollusks) of this part of the sequence suggest a lacustrine-palustrine environment (Villalba-Breva *et al.*, 2012), as part of a more extensive lagoon. Magnetostratigraphy indicates an early Maastrichtian age for the site, within the C31r.

Cingles de Cal Ros, Cingles de la Creueta and Torrent del Jou

Other palaeontological localities belonging to the Vallcebre syncline (Torrent del Jou) and other places within the same lower Pedraforca thrust shed in the Catllaràs Massif (Cingles de la Creueta) and north to the town of Berga (Cingles de Cal Ros) have yielded vertebrate fossil remains. All of them belong to the aforementioned Reptile Sandstone (C29r, late Maastrichtian).

3.2.2 Localities of the Tremp syncline

Barranc de la Boiga

The site is placed in the eastern part of the Tremp Basin, near to the Orcau village. It belongs to the uppermost section of the 'grey' unit and correlates with the chron C31r. This site has not been previously published in other scientific papers.

Casa Fabà

The Casa Fabà site is located about 500 m east of the village of Orcau (Pallars Jussà shire, Lleida), in a ravine area known as Les Olives. This site consists of a surface of about 4 m^2 of a sandstone layer with carbonate matrix inter-bedded between grey marl strata. These sediments are characteristic of the 'lower red unit'. The biostratigraphic data of the site indicate an early Maastrichtian age within the chron C31r (Díez-Canseco *et al.*, 2014; Vicente *et al.*, 2015), later confirmed by magnetostratigraphy (Fondevilla *et al.*, 2016).

Els Nerets

The locality of Els Nerets site is located to the north of the Vilamitjana village, near the Tremp municipality. It belongs to the 'grey' unit and consists of grey lutites of variable thickness sandwiched between two units of the Arén 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).

Les Torres

The site is placed in the eastern part of the Tremp Basin. It belongs to the 'lower red' unit and correlates with the chron C31r, having an early Maastrichtian age. This site has not been previously published in other scientific papers.

Serrat del Rostiar

The Serrat del Rostiar-1 site is located south to the Basturs village, in the eastern part of the Tremp basin. The site consists of grey mudstones with pedogenic nodules that represent palaeosoils developed in a floodplain environment, close to sandstone deposits interpreted as meandering rivers. It is laterally close to the Basturs Poble bonebed that corresponds to the lower part of the lower red unit (Riera *et al.*, 2009). Serrat del Rostiar-1 is correlated with an undetermined polarity interval according to the palaeomagnetic results of Vila *et al.* (2012). However, recent studies have posit an early Maastrichtian age for this site (Díez-Canseco *et al.*, 2014; Fondevilla *et al.*, 2016).

Serrat del Pelleu

The Serrat del Pelleu site is located near to the Serrat del Rostiar-1 site, south to the Basturs village. In a similar way, the Serrat del Pelleu site consists of a grey mudstone level linked to medium-to-fine ochre sandstones. Serrat del Pelleu site is also located in the undetermined polarity interval reported by Vila *et al*., (2012), but according to Fondevilla *et al*., (2016), this site correlates with the C29r (late Maastrichtian).

Pont d'Orrit

The Porrit-6 site is located near the village of Pont d'Orrit in the municipality of Tremp (Lleida), in the western part of the Tremp Basin (Sellés *et al*., 2014). The site belongs to the 'grey' unit, but is late Maastrichtian in age, correlating with the chron C30n.

Camí del Soldat

The Camí del Soldat site is located south to the Conques and Figuerola de Orcau villages. The site 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 alternations between sand and muddy sediments are a common feature of the meandering channels of the Tremp Formation (Díez-Canseco *et al*., 2014). Camí del Soldat is placed in the upper part of the lower red unit (Riera *et al*., 2009), and correlates with an inverse magnetochron regarded as C29r in the late Maastrichtian (Fondevilla *et al*., 2016), few metres below the Palaeocene laterally equivalent strata of the 'Vallcebre Limestone'.

Molí del Baró

The Molí del Baró-1 site is located north to the Sant Romà d'Abella village. It is composed by a thick sandstone body interbedded with reddish mudstones. This site is located in the upper part of the 'lower red' unit, approximately 100 m below the Tossal de la Doba and Sant Salvador de Toló limestones (laterally equivalent to the 'Vallcebre Limestone' (Riera *et al*., 2009), within the C29r magnetochron according to Fondevilla *et al*., (2016), thus, late Maastrichtian in age.

3.2.3 Localities of the Àger syncline

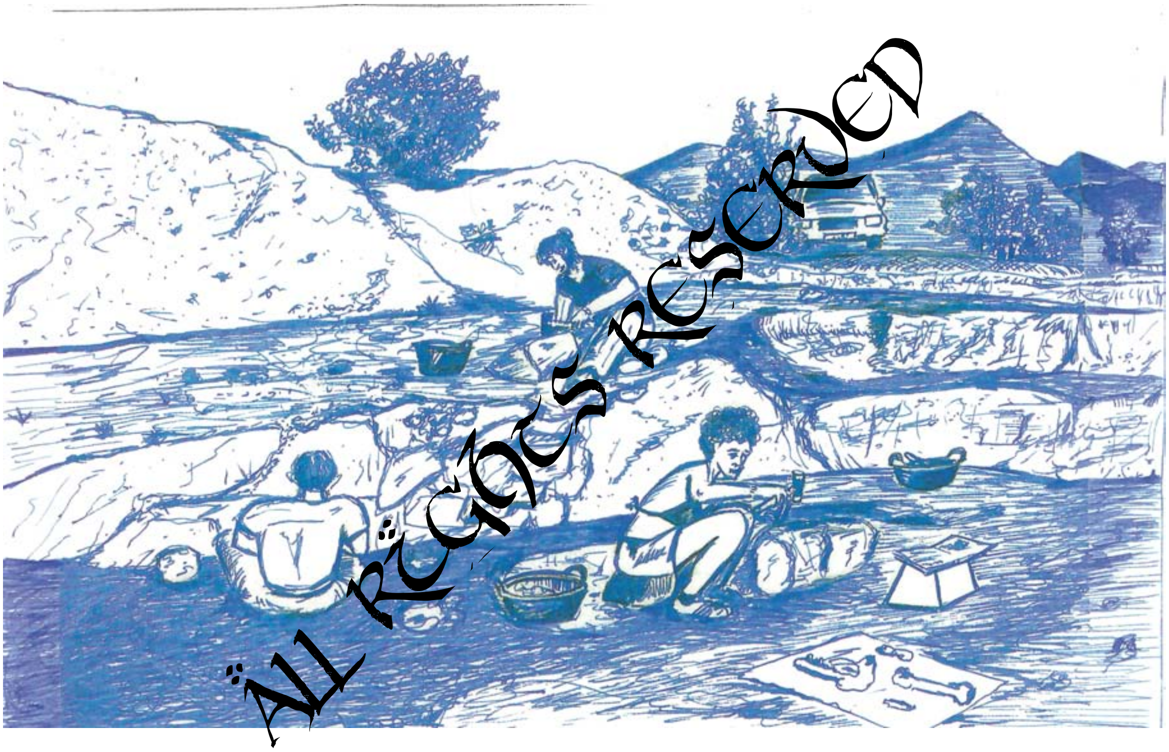
Fontllonga

In the Àger syncline, the Fontllonga-6 site is located towards the south-east of Àger village. It is a grey clay layer placed above a 70-m-thick limestone unit (Soler-Gijón & López-Martínez, 1998). This site also belongs to the 'lower red' unit and is correlated with C31r (Galbrun *et al*., 1993), giving an early Maastrichtian age. Fontllonga-6 has been interpreted as a large coastal plain with a significant marine influence, located a few kilometers south of the lagoon-barrier island and the inferred Late Cretaceous shoreline (Soler-Gijón & López-Martínez, 1998).

L'Espinau

The L'Espinau site is located near to Tartareu village. It is placed in a decimetric marly layer with grey colorations and organic remains, often in the form of coals. The palaeoenvironmental interpretation of this site is currently under study, but stratigraphically, the site is located in the mid-portion of a succession of lacustrine limestones to reddish ochre mudstones and coarse sandstones. Despite the fact that no direct age constraints are provided, this succession can be correlated with the well-documented Fontllonga section in the Àger syncline. Hence, the L'Espinau site can be placed in the lower part of the upper Maastrichtian, probably in the uppermost C31r (V. Fondevilla, personal communication).

Chapter 4. MATERIAL & METHODS



Art by José Píriz

4. MATERIAL & METHODS

4.1 Methodology

The material studied in this thesis (see Table 1) mostly consists of microvertebrate fossils. However, two new species of eusuchian crocodiles were described based on partial skeletons including associated teeth (see Chapter 7). These specimens allowed comparisons with isolated crocodilian teeth that are frequently found in the Tremp Formation beds. Concerning microfossils, fieldwork was carried out between 2010 and 2014, collecting rocks from different levels following two main requirements: low carbonated clays and low degree of oxidation, in order to help the breaking and dissolution of the sediments. About 3900 kg were collected from Els Nerets (375 kg), Serrat del Pelleu (525 kg), Fontllonga-6 (525 kg), Camí del Soldat (575 kg), Serrat del Rostiar-1 (625 kg) and L'Espinau (1250 kg).

Samples were then macerated employing successive water immersions and sun drying in order to shred the rock matrix. Screenwashing was carried out using running water and a sieve series of 1.4, 0.8 and 0.5 mm. The samples were then sorted under a Leica M60 binocular microscope. In some localities, such as Fumanya and Molí del Baró-1, vertebrate microfossils were recovered by picking them from rock matrices, instead of by screenwashing techniques; this took place during the digging works carried out in 2007, 2010 and 2011.

Photographs of selected specimens were taken under a Leica M60 stereomicroscope and a Zeiss Evo MA10 environmental scanning electron microscope (ESEM) at the Microscopy Services of the Universitat Autònoma de Barcelona and of the Universitat de Barcelona. For this reason, specimens to be scanned under ESEM were fixed over LEGO™ pieces through dimetil-hidantoine-formaldehide (DHFM). The DHFM is a synthetic resin that dries up and easily re-hydrates, commonly used in entomopraxis techniques. This allows fixing and release the fossil material without damage because of the reversibility of the process by adding water.

Isolated bones and teeth were grouped in morphotypes and described following relevant works with special emphasis on vertebrate microfossils (e.g., Estes, 1969; Li & Wilson, 1996; Li *et al.*, 1997; Grande & Bemis, 1998; Cavin, 1999; Cappetta & Corral, 1999; Poyato-Ariza *et al.*, 1999; Neuman & Brinkman, 2005; Taverne *et al.*, 2007; Brinkman, 2008; Grande, 2010; Berreteaga *et al.*, 2011; López-Arbarello, 2012; Taverne & Capasso, 2012; Brinkman *et al.*, 2014; Sweetman *et al.*, 2014; Cavin *et al.*, 2015; Pouech *et al.*, 2015; Corral *et al.*, 2016; Murray *et al.*, 2016; among others for fish microfossils; McGowan and Evans, 1995; Duffaud & Rage, 1999; Rage, 1999;

Folie & Codrea, 2005; Makádi, 2006, 2013a, 2013b; Blain *et al*., 2010; Szentesi & Venczel, 2010, 2012; Venczel & Szentesi, 2012; Company & Szentesi, 2012; Szentesi & Company, 2017; among others for herpetofaunal remains; Buscalioni *et al*., 1999, 2001; Delfino *et al*., 2008; Puértolas-Pascual *et al*., 2011, 2014, 2015 among others for crocodilian fossils; Buffetaut *et al*., 1996; Gheerbrant *et al*., 1997; Grigorescu *et al*., 1999; Laurent *et al*., 1999, 2002; Csiki-Sava *et al*., 2015, 2016 among others for microvertebrate assemblages). Then, each morphotype was compared with similar published material from geographically and/or chronologically close European localities to get more precise taxonomic determinations when possible. In addition, fossil specimens from Laño, Albaina and Quintanilla la Ojada localities (Basque-Cantabrian basin, Spain) as well as from the Iharkút site (Bakony Mountains, Hungary) — stored in the Arabako

Natur Zientzien Museoa (Vitoria, Álava, Spain), the Euskal Herriko Unibertsitatea (Bilbao, Spain) and the Magyar Természettudományi Múzeum (Budapest, Hungary), respectively — were compared by first hand. The microfossil specimens studied in this thesis are housed in the collection of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain), and at the Museu de la Conca Dellà (Isona, Lleida, Spain).

Vertebrate macrofossils coming from Fumanya, Casa Fabà, Fontllonga-6, Els Nerets, Cingles de Cal Ros, Cingles de la Creueta and Torrent del Jou were excavated or prospected during different fieldwork campaigns: Casa Fabà (2003), Fumanya (2004-2008), Cingles de Cal Ros, Cingles de la Creueta and Torrent del Jou (2012-2013), Fontllonga-6 (2014) and Els Nerets (2013-2015). The fossil material comprises isolated teeth and several dentaries belonging to crocodiles, but also two partial specimens including partial skulls, tooth bearing bones, several vertebrae, partial pelvic and scapular girdles and some appendicular bones. The specimens described in this thesis are housed at the collections of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain), Museu de la Conca Dellà (Isona, Lleida, Spain) and Museu de les Mines de Cercs (Sant Corneli, Barcelona, Spain).

Other specific analyses (i.e., phylogenetic, statistical tests) are explained in detail in the respective works. Statistical analyses (e.g., chi-square, linear regressions, ANOVAs) were performed following Quinn & Keough (2002) and Hammer & Harper (2006) and implemented in PAST statistical package (Hammer *et al*., 2001). Phylogenetic analyses of the two eusuchian specimens were carried out using the dataset of Brochu (2011) with a few minor modifications in some operational taxonomic units (OTUs) and characters according to previous works (Delfino *et al*., 2008; Puértolas-Pascual *et al*., 2011, 2014). The dataset was analysed with TNT v1.1 (Goloboff *et al*., 2008). Bremer supports and bootstrap frequencies were used to assess the robustness of the nodes.

4.2 Explanation of vernacular names & quotation marks use in this thesis

Regardless of which phylogenetic hypothesis or whether a different taxonomic rearrangement is followed, common names might often not correspond exactly with scientific nomenclature. As Nelson (2006:51) stated, "*this follows the principle of keeping common names as stable as possible; thus scientific names are intended to apply to monophyletic taxa while common names are intended only to refer to classical recognized groups, monophyletic or not*".

For instance, in this PhD dissertation I use the term "fishes" to name all craniates excluding tetrapods. The term "ray" is used here as a collective common name for all batoids; and the name "skates" is restricted to members of one particular family of rays (Rajidae). In the same way, the terms "shark" / "selachian" and "rays" / "batoids" still seem appropriate to denominate two different groups of chondrichthyans, even if the Hypnosqualean is accepted (i.e., neoselachian sharks are considered paraphyletic without rays) or both groups are considered sister-taxa. In addition, the terms "chondrosteans" and "holosteans" are used to denominate a grade of actinopterygian fishes that are not included within the neopterygians or the teleosteans, respectively, regardless if they are paraphyletic groups or whether the clade Holostei (*sensu* Grande, 2010) is accepted. Similarly, the term "amphibian" is applied to all non-amniote tetrapods, including lissamphibians; "lizard" refers to all non-ophidian lepidosaurians, regardless the phylogenetic position of Ophidia or "snakes"; and the term "crocodile" is used to refer to all crocodylomorph taxa whether or not they belong to Crocodylia.

On the other hand, scientific names that do not refer to monophyletic clades (i.e., paraphyletic) as well as those of informal clades are embedded within single quotation marks (e.g.,'Chondrostei', 'agnathans', the informal clade 'Allodaposuchia'). Likewise, the names of informal geological units are also embedded within single quotation marks (e.g., 'lower red' unit of the Tremp Formation).

4.3 Institutional abbreviations

IPS, Institut Català de Paleontologia Miquel Crusafont; MCD, Museu de la Conca Dellà; MMC Museu de les Mines de Cercs; MMB, Museu Municipal de Berga.

Table 1. Fossil material studied in this thesis, sorted by site and field code.

Field num.	Collection num.	High taxon	Low taxon	Element	Number	Publication
SERRAT DEL ROSTIAR-1						
SRm-8	IPS-86058	Squamata	Anguidae	Vertebra	1	Blanco *et al*., 2016; Chapter 6
SRm-9	IPS-84998	Squamata	?Gekkota	Frontal	1	Blanco *et al*., 2016; Chapter 6
SRm-11	IPS-84999	Squamata	Scincomorpha	Tooth	1	Blanco *et al*., 2016; Chapter 6
SRm-13	MCD-6754	Teleostei	cf. Cypriniformes	Pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
SRm-15	IPS-85000	Squamata	Scincomorpha	Tooth	1	Blanco *et al*., 2016; Chapter 6
SRm-16	IPS-85001	Squamata	Scincomorpha	Tooth	1	Blanco *et al*., 2016; Chapter 6
SRm-17	IPS-96630	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
SRm-22	MCD-6755	Holostei	*Lepisosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
SRm-23	IPS-85002	Squamata	Iguanidae	Tooth	1	Blanco *et al*., 2016; Chapter 6
SRm-30	IPS-85003	Anura	indet.	Urostil	1	Blanco *et al*., 2016; Chapter 6
SRm-33	IPS-96631	Sebecosuchia	cf. *Doratodon* sp.	Tooth	1	Unpublished; Chapter 7
SRm-35	IPS-96633	Hylaeochampsidae	?*Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
SRm-36	IPS-96634	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
SRm-38	IPS-96635	Crocodylomorpha	indet.	Tooth	1	Unpublished; Chapter 7
SRm-40	MCD-6756	Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
SRm-42	IPS-96636	Ziphosuchia	indet.	Tooth	1	Unpublished; Chapter 7
SRm-44	IPS-96637	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
SRm-45	IPS-96638	Sebecosuchia	cf. *Doratodon* sp.	Tooth	1	Unpublished; Chapter 7
SRm-46	MCD-6757	Teleostei	cf. Cypriniformes	Branchial arch (fragment)	1	Blanco *et al*., 2017; Chapter 5
SRm-48	IPS-96639	Crocodylomorpha	indet.	Tooth	1	Unpublished; Chapter 7
SRm-55	IPS-85004	Allocaudata	Albanerpetontidae	Frontal	1	Blanco *et al*., 2016; Chapter 6
SRm-60	IPS-86059	Anura	Paleobatrachidae	Ilium	1	Blanco *et al*., 2016; Chapter 6
SRm-62	MCD-6758	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
SRm-65	IPS-85005	Anura	Discoglossinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
SRm-67	IPS-87217	Anura	indet.	Tibiofibulae	---	Blanco *et al*., 2016; Chapter 6
SRm-68	IPS-86060	Anura	indet.	Vertebrae	2	Blanco *et al*., 2016; Chapter 6
SRm-70	IPS-86061	Anura	Discoglossinae	Humerus	1	Blanco *et al*., 2016; Chapter 6
SRm-71	IPS-85006	Anura	indet.	Radioulna	1	Blanco *et al*., 2016; Chapter 6
SRm-72a	IPS-85007	Anura	Paleobatrachidae	Vertebra	1	Blanco *et al*., 2016; Chapter 6
SRm-72b	IPS-86062	Anura	Discoglossinae	Sacral vertebra	1	Blanco *et al*., 2016; Chapter 6
SRm-72c	IPS-86063	Anura	Discoglossinae	Vertebra	1	Blanco *et al*., 2016; Chapter 6

Table 1. Continuation.

SRm-74	IPS-85009	Squamata	indet.	Dentary	1	Blanco *et al*., 2016; Chapter 6
SRm-75	IPS-85010	Allocaudata	Albanerpetontidae	humerus	1	Blanco *et al*., 2016; Chapter 6
SRm-76	IPS-85011	Anura	Discoglossinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
SRm-77	IPS-85012	Anura	Discoglossinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
SRm-78	IPS-85013	Anura	Alytinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
SRm-79	IPS-85014	Allocaudata	Albanerpetontidae	Humerus	1	Blanco *et al*., 2016; Chapter 6
SRm-80	IPS-85015	Anura	Discoglossinae	Scapula	1	Blanco *et al*., 2016; Chapter 6
SRm-81	IPS-85016	Squamata	indet.	Ischium	1	Blanco *et al*., 2016; Chapter 6
ESPINAU						
ES-12	IPS-96640	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
ES-13	IPS-96641	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
ES-14	MCD-6759	Teleostei	indet.	Fin ray	1	Blanco *et al*., 2017; Chapter 5
ES-15	IPS-96642	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
ES-16	IPS-96643	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-17	IPS-96644	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-18	MCD-6760	Selachii	Anacoracidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-19	IPS-96645	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
ES-20	IPS-96646	Ziphosuchia	indet.	Tooth	1	Unpublished; Chapter 7
ES-21	IPS-96647	Ziphosuchia	indet.	Tooth	1	Unpublished; Chapter 7
ES-22	MCD-6761	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-23	MCD-6762	?Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-24	MCD-6763	Pycnodontiformes	cf. *Coelodus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-25	MCD-6764	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-26	MCD-6765	Holostei	?Semionotiformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-27	MCD-6766	?Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-28	IPS-96648	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-29	IPS-96649	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-30	IPS-96650	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7
ES-33	IPS-85017	Anura	Paleobatrachidae	Humerus	1	Blanco *et al*., 2016; Chapter 6
ES-34	IPS-86064	Anura	indet.	Vertebrae	2	Blanco *et al*., 2016; Chapter 6
ES-36	MCD-6767	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-37	MCD-6768	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-40	MCD-6769	Amiiformes	cf. *Caturus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

ES-41	MCD-6770	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-42	MCD-6771	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-43	MCD-6772	?Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-44	IPS-96652	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-45	MCD-6773	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-46	MCD-6774	Phyllodontidae	cf. *Phyllodus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-47	MCD-6775	Teleostei	Perciformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-48	MCD-6776	Teleostei	Perciformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-49	IPS-96653	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-50	MCD-6777	Holostei	?Semionotiformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-51	MCD-6778	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-52	IPS-96654	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-53	IPS-96655	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-54	MCD-6779	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-55	IPS-96656	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-56	MCD-6780	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-57	MCD-6781	?Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-58	MCD-6782	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-59	IPS-96657	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-61	IPS-96659	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-62	IPS-96660	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-64	IPS-96661	Sebecosuchia	cf. *Doratodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-65	IPS-85795	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-71	MCD-6783	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-72	MCD-6784	Teleostei	Osteoglossidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-73	IPS-86065	Anura	indet.	Tibiofibulae	6	Blanco *et al*., 2016; Chapter 6
ES-76	IPS-96662	Gavialoidea	*cf. Thoracosaurus* sp.	Tooth	1	Unpublished; Chapter 7
ES-79	MCD-6785	Teleostei	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-80	IPS-85018	Squamata	Iguanidae	Tooth	1	Blanco *et al*., 2016; Chapter 6
ES-81	IPS-96663	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-82	IPS-85019	Anura	Alytinae	Sacral vertebra	1	Blanco *et al*., 2016; Chapter 6
ES-91	IPS-96664	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-92	MCD-6786	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-94	IPS-96665	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7

Table 1. Continuation.

ES-100	IPS-85020	Allocaudata	Albanerpetontidae	Premaxilla	1	Blanco *et al*., 2016; Chapter 6
ES-101	IPS-85021	Allocaudata	Albanerpetontidae	?Maxilla	1	Blanco *et al*., 2016; Chapter 6
ES-102	MCD-6788	Holostei	Lepisosteidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-103	MCD-6789	Phyllodontidae	cf. *Phyllodus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-104	MCD-6790	Teleostei	Osteoglossidae	Scale	2	Blanco *et al*., 2017; Chapter 5
ES-105	IPS-85022	Anura	Pelobatidae / Gobiatidae	Maxilla	1	Blanco *et al*., 2016; Chapter 6
ES-106	MCD-6791	Teleostei	cf. Cypriniformes	Branchial arch (fragment)	1	Blanco *et al*., 2017; Chapter 5
ES-107	IPS-96666	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-108	IPS-85023	Anura	indet.	Prearticular	1	Blanco *et al*., 2016; Chapter 6
ES-112	MCD-6792	Teleostei	Osteoglossidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-115	IPS-85024	Allocaudata	Albanerpetontidae	Dentary	1	Blanco *et al*., 2016; Chapter 6
ES-119	IPS-85025	Anura	Paleobatrachidae	Humerus	1	Blanco *et al*., 2016; Chapter 6
ES-120	IPS-85026	Anura	indet.	Humerus	1	Blanco *et al*., 2016; Chapter 6
ES-121	MCD-6793	Teleostei	cf. Cypriniformes	Branchial arch (fragment)	1	Blanco *et al*., 2017; Chapter 5
ES-123	IPS-85027	Allocaudata	Albanerpetontidae	Dentary	1	Blanco *et al*., 2016; Chapter 6
ES-124	IPS-86066	Anura	indet.	Vertebrae	2	Blanco *et al*., 2016; Chapter 6
ES-125	IPS-85028	Allocaudata	Albanerpetontidae	Humerus	1	Blanco *et al*., 2016; Chapter 6
ES-126	IPS-86067	Allocaudata	Albanerpetontidae	Dentary	1	Blanco *et al*., 2016; Chapter 6
ES-127	MCD-6794	Holostei	*Atractosteus* sp.	Hemitrichia	1	Blanco *et al*., 2017; Chapter 5
ES-129	MCD-6795	Teleostei	indet.	Vertebra	1	Blanco *et al*., 2017; Chapter 5
ES-130	MCD-6796	Teleostei	cf. Cypriniformes	Pharingeal tooth	3	Blanco *et al*., 2017; Chapter 5
ES-131	MCD-6797	Teleostei	indet.	Vertebra	1	Blanco *et al*., 2017; Chapter 5
ES-135	IPS-86069	Anura	indet.	Coracoid	1	Blanco *et al*., 2016; Chapter 6
ES-138	IPS-85029	Allocaudata	Albanerpetontidae	Dentary	1	Blanco *et al*., 2016; Chapter 6
ES-140	MCD-6798	Teleostei	Osteoglossidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-141	IPS-85030	Anura	Alytinae	Sacral vertebra	1	Blanco *et al*., 2016; Chapter 6
ES-142	IPS-85031	Anura	indet.	Radioulna	1	Blanco *et al*., 2016; Chapter 6
ES-143	IPS-85032	Anura	Alytinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
ES-144	IPS-85033	Anura	indet.	Urostil	1	Blanco *et al*., 2016; Chapter 6
ES-145	IPS-85034	Anura	Alytinae	Ilium	1	Blanco *et al*., 2016; Chapter 6
ES-146	IPS-85035	Anura	indet.	Vertebra	1	Blanco *et al*., 2016; Chapter 6
ES-147	IPS-85036	Anura	indet.	Vertebra	1	Blanco *et al*., 2016; Chapter 6
ES-150	MCD-6799	Amiiformes	Amiidae	Coronoid	1	Blanco *et al*., 2017; Chapter 5
ES-152	MCD-6801	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

ES-153	MCD-6802	Holostei	Lepisosteidae	Teeth	5	Blanco *et al*., 2017; Chapter 5
ES-155	MCD-6803	Chondrostei	indet.	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-156	MCD-6804	Holostei	Lepisosteidae	Scale	9	Blanco *et al*., 2017; Chapter 5
ES-157	MCD-6805	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-158	MCD-6806	Holostei	Lepisosteidae	Teeth	6	Blanco *et al*., 2017; Chapter 5
ES-159	MCD-6807	Teleostei	cf. Cypriniformes	Branchial arch (fragment)	1	Blanco *et al*., 2017; Chapter 5
ES-160	MCD-6808	Phyllodontidae	*Paralbula* sp.	Teeth	20	Blanco *et al*., 2017; Chapter 5
ES-162	MCD-6809	Phyllodontidae	cf. *Phyllodus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-163	MCD-6810	Teleostei	cf. Cypriniformes	Pharingeal tooth	2	Blanco *et al*., 2017; Chapter 5
ES-164	MCD-6811	Teleostei	Osteoglossidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-166	MCD-6812	Amiiformes	cf. *Caturus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-167	MCD-6813	Phyllodontidae	*Pseudoegertonia granulosus*	Teeth	4	Blanco *et al*., 2017; Chapter 5
ES-168	MCD-6814	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-169	MCD-6815	Phyllodontidae	Paralbulinae	Teeth	2	Blanco *et al*., 2017; Chapter 5
ES-170	MCD-6816	Phyllodontidae	Paralbulinae	Teeth	2	Blanco *et al*., 2017; Chapter 5
ES-171	MCD-6817	Phyllodontidae	Paralbulinae	Teeth	2	Blanco *et al*., 2017; Chapter 5
ES-172	MCD-6818	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-173	MCD-6819	Phyllodontidae	Paralbulinae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-174	MCD-6820	Phyllodontidae	*Pseudoegertonia granulosus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-175	MCD-6821	?Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-176	MCD-6822	Teleostei	Osteoglossidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-177	MCD-6823	Amiiformes	cf. *Caturus* sp.	Teeth	3	Blanco *et al*., 2017; Chapter 5
ES-178	MCD-6824	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-179	MCD-6825	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-180	MCD-6826	Amiiformes	cf. *Caturus* sp.	Teeth	4	Blanco *et al*., 2017; Chapter 5
ES-181	MCD-6827	Aspidorhynchidae	*Belonostomus* sp.	Teeth	4	Blanco *et al*., 2017; Chapter 5
ES-182	MCD-6828	Phyllodontidae	cf. *Phyllodus* sp.	Teeth	9	Blanco *et al*., 2017; Chapter 5
ES-183	MCD-6829	Phyllodontidae	Paralbulinae	Teeth	12	Blanco *et al*., 2017; Chapter 5
ES-184	MCD-6830	Holostei	?Semionotiformes	Teeth	10	Blanco *et al*., 2017; Chapter 5
ES-185	MCD-6831	?Pycnodontiformes	indet.	Teeth	2	Blanco *et al*., 2017; Chapter 5
ES-186	MCD-6832	Teleostei	indet.	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-187	MCD-6833	Teleostei	Osteoglossidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
ES-188	MCD-6834	Phyllodontidae	Paralbulinae	Teeth	6	Blanco *et al*., 2017; Chapter 5
ES-189	MCD-6835	Phyllodontidae	*Paralbula* sp.	Teeth	9	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

ES-190	MCD-6836	Phyllodontidae	*Pseudoegertonia granulosus*	Teeth	16	Blanco *et al*., 2017; Chapter 5
ES-191	MCD-6837	Holostei	*Atractosteus* sp.	Hemitrichia	2	Blanco *et al*., 2017; Chapter 5
ES-192	MCD-6838	Teleostei	Osteoglossidae	Scale	1	Blanco *et al*., 2017; Chapter 5
ES-193	MCD-6839	Holostei	*Atractosteus* sp.	Scale	3	Blanco *et al*., 2017; Chapter 5
ES-194	MCD-6840	Teleostei	Perciformes	Teeth	2	Blanco *et al*., 2017; Chapter 5
ES-195	IPS-96667	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-197	IPS-96668	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-198	IPS-96669	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-200	IPS-96671	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-203	IPS-96674	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-205	IPS-96676	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
ES-207	IPS-96678	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-208	IPS-96679	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-209	IPS-85796	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-210	IPS-85797	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-212	IPS-96680	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-214	IPS-96682	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
ES-215	IPS-96683	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
ES-217	IPS-96685	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ES-218	IPS-96686	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
ESP-333	MCD-6841	Teleostei	Acanthomorpha	Vertebrae	4	Blanco *et al*., 2017; Chapter 5
SERRAT DEL PELLEU						
SPE-9	IPS-96687	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
SPE-15	IPS-96688	Crocodylomorpha	indet.	Tooth	1	Unpublished; Chapter 7
SPE-29	IPS-96689	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
SPE-30	IPS-85799	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
SPE-32	IPS-85800	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
SPE-33	IPS-85801	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
SPE-34	IPS-96691	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
SPE-35	IPS-96692	Hylaeochampsidae	*?Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
SPE-36	IPS-96693	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
SPE-37	IPS-96694	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
SPE-38	IPS-96695	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7

Table 1. Continuation.

SPE-39	IPS-96696	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
SPE-40	IPS-96697	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
SPE-41	IPS-85802	Hylaeochampsidae	?*Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
SPE-43	IPS-96699	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
SPE-45	IPS-86070	Allocaudata	Albanerpetontidae	Humerus	1	Blanco *et al*., 2016; Chapter 6
SPE-46	IPS-86071	Anura	Discoglossinae	Tibiofibulae	6	Blanco *et al*., 2016; Chapter 6
SPE-49	IPS-86072	Anura	Discoglossinae	Humerus	3	Blanco *et al*., 2016; Chapter 6
SPE-50	IPS-86073	Anura	Discoglossinae	Prearticular	1	Blanco *et al*., 2016; Chapter 6
SPE-51	MCD-6843	Holostei	Lepisosteidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
CAMÍ DEL SOLDAT						
CSO-3	IPS-86074	Anura	indet.	Vertebrae	2	Blanco *et al*., 2016; Chapter 6
CSO-4	MCD-6844	Holostei	*Atractosteus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
CSO-5	IPS-96700	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
CSO-15	MCD-6845	Aspidorhynchidae	*Belonostomus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
CSO-16	MCD-6846	Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
CSO-17	IPS-96701	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
CSO-20	IPS-96702	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
CSO-21	IPS-86075	Anura	indet.	Urostil	1	Blanco *et al*., 2016; Chapter 6
CSO-23	MCD-6847	Phyllodontidae	*Paralbula* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
CSO-25	MCD-6848	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
CSO-26	MCD-6849	Teleostei	indet.	Cleithrum	1	Blanco *et al*., 2017; Chapter 5
MOLÍ DEL BARÓ-1						
MB02-12	MCD5555	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB02-17	MCD5544	Crocodylomorpha	indet.	Femur	1	Marmi *et al*., 2016; Chapter 8
MB07-57	MCD5571	Crocodylomorpha	indet.	Osteoderm	1	Marmi *et al*., 2016; Chapter 8
MB07-63	MCD5572	Crocodylomorpha	indet.	Osteoderm	1	Marmi *et al*., 2016; Chapter 8
MB07-69	MCD5559	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-41	MCD5567	Crocodylomorpha	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-97	MCD-5543	Anura	indet.	Tibiofibula	1	Marmi *et al*., 2016; Chapter 8
MB10-110	MCD5556	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-114	MCD5560	Ziphosuchia	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-133	MCD5548	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8

Table 1. Continuation.

MB10-145	MCD5561	Ziphosuchia	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-148		Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
MB10-159	MCD5565	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-160	MCD5568	Crocodylomorpha	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-165		Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
MB10-195	MCD5564	Ziphosuchia	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB10-207	MCD5562	Ziphosuchia	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-08b	MCD5547	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-16	MCD5563	Ziphosuchia	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-27	MCD-5541	Teleostei	Percomorpha	Scale	1	Marmi *et al*., 2016; Chapter 8
MB11-34	MCD5551	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-42	MCD-5540	Teleostei	Percomorpha	Scale	1	Marmi *et al*., 2016; Chapter 8
MB11-80		Ziphosuchia	indet.	Tooth	1	Unpublished; Chapter 7
MB11-82	MCD-6688	Teleostei	Osteoglossidae	Scale	1	Blanco *et al*., 2017; Chapter 5
MB11-87	MCD5573	Crocodylomorpha	indet.	Osteoderm	1	Marmi *et al*., 2016; Chapter 8
MB11-99	MCD5557	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-101	MCD5549	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-115	MCD5550	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-131	MCD5569	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MB11-133		Atoposauridae	*Theriosuchus* sp.	Tooth	1	Unpublished; Chapter 7
MB11-145	MCD-5542	Osteichthyes	indet.	Vertebra	1	Marmi *et al*., 2016; Chapter 8
MB11-149	MCD5570	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-4	MCD5558	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-6	MCD5552	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-7	MCD5553	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-20	MCD5566	Atoposauridae	*Theriosuchus* sp.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-23	MCD5554	Allodaposuchidae	indet.	Tooth	1	Marmi *et al*., 2016; Chapter 8
MdB-27	MCD-7006	Anura	indet.	Tibiofibulae	2	Marmi *et al*., 2016; Chapter 8
MdB-28	MCD-7007	Anura	indet.	Urostil	1	Marmi *et al*., 2016; Chapter 8
ELS NERETS						
EN-1	MCD-6850	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
EN-4	MCD-6853	Allodaposuchidae	indet.	Tooth	1	Unpublished; Chapter 7
EN-2	MCD-6851	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

EN-3	MCD-6852	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-5	MCD-6854	Teleostei	cf. Cypriniformes	Pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-6	MCD-6855	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-7	MCD-6856	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-8	MCD-6857	Amiiformes	Amiidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
EN-9	MCD-6858	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-11	MCD-6859	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-12	MCD-6860	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-13	MCD-6861	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
EN-21	MCD-6862	Pycnodontiformes	cf. *Coelodus* sp.	Tooth	1	Blanco *et al*., 2017; Chapter 5
EN-23	MCD-6863	Teleostei	cf. Cypriniformes	1°-2° pharingeal tooth	1	Blanco *et al*., 2017; Chapter 5
	IPS-13360	Hylaeochampsidae	?*Acynodon* sp.	Dentary	1	Unpublished; Chapter 7
NE-12z		Allodaposuchidae	indet.	Dentary	1	Unpublished; Chapter 7
BARRANC DE LA BOïGA						
BB-6	IPS-96703	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
BB-8	IPS-96704	Hylaeochampsidae	?*Acynodon* sp.	Tooth	1	Unpublished; Chapter 7
FONTLLONGA-6						
FON6-1	MCD-6864	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-2	MCD-6865	Holostei	Lepisosteidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-3	MCD-6866	Holostei	Lepisosteidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-5	MCD-6868	Allodaposuchidae	indet.	Dentary	1	Unpublished; Chapter 7
FON6-6	MCD-6869	Holostei	?Semionotiformes	Teeth	6	Blanco *et al*., 2017; Chapter 5
FON6-7	MCD-6870	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-8	MCD-6871	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-9	MCD-6872	Holostei	Lepisosteidae	Scale	6	Blanco *et al*., 2017; Chapter 5
FON6-10	MCD-6873	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-11	MCD-6874	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-12	MCD-6875	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-13	MCD-6876	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-14	MCD-6877	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-15	MCD-6878	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6-16	MCD-6879	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

FON6-17	MCD-6880	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-18	MCD-6881	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-19	MCD-6882	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-20	MCD-6883	Pycnodontiformes	indet.	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-26	MCD-6884	Holostei	?Semionotiformes	Teeth	2	Blanco *et al*., 2017; Chapter 5
FON6-27	MCD-6885	Holostei	Lepisosteidae	Scale	4	Blanco *et al*., 2017; Chapter 5
FON6-28	MCD-6886	Holostei	Lepisosteidae	Scale	8	Blanco *et al*., 2017; Chapter 5
FON6-29	MCD-6887	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-30	MCD-6888	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6-31	MCD-6889	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-1	MCD-6893	Holostei	?Semionotiformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-2	MCD-6894	?Pycnodontiformes	indet.	Teeth	2	Blanco *et al*., 2017; Chapter 5
FON6I-3	MCD-6895	Batoidea	*Rhombodus ibericus*	Teeth	3	Blanco *et al*., 2017; Chapter 5
FON6I-5	MCD-6897	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-6	MCD-6898	?Pycnodontiformes	indet.	Teeth	8	Blanco *et al*., 2017; Chapter 5
FON6I-9	MCD-6900	Holostei	Lepisosteidae	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-10	MCD-6901	Phyllodontidae	Paralbulinae	Teeth	3	Blanco *et al*., 2017; Chapter 5
FON6I-11	MCD-6902	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-12	MCD-6903	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-13	MCD-6904	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-14	MCD-6905	Batoidea	*Igdabatis indicus*	Teeth	7	Blanco *et al*., 2017; Chapter 5
FON6I-16	MCD-6907	Holostei	Lepisosteidae	Teeth	5	Blanco *et al*., 2017; Chapter 5
FON6I-17	MCD-6908	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-18	MCD-6909	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-19	MCD-6910	Holostei	Lepisosteidae	Scale	20	Blanco *et al*., 2017; Chapter 5
FON6I-20	MCD-6911	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-21	MCD-6912	Batoidea	*Rhombodus ibericus*	Teeth	2	Blanco *et al*., 2017; Chapter 5
FON6I-22	MCD-6913	Batoidea	*Rhombodus ibericus*	Teeth	3	Blanco *et al*., 2017; Chapter 5
FON6I-23	MCD-6914	Chondrostei	indet.	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-24	MCD-6915	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-25	MCD-6916	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-26	MCD-6917	Holostei	?Semionotiformes	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-27	MCD-6918	Holostei	Lepisosteidae	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-28	MCD-6919	Holostei	*Atractosteus* sp.	Scale	4	Blanco *et al*., 2017; Chapter 5

Table 1. Continuation.

FON6I-29	MCD-6920	Batoidea	*Rhombodus ibericus*	Teeth	3	Blanco *et al*., 2017; Chapter 5
FON6I-30	MCD-6921	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-31	MCD-6922	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FON6I-36	MCD-6924	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-38	MCD-6925	Holostei	*Atractosteus* sp.	Scale	1	Blanco *et al*., 2017; Chapter 5
FON6I-39	MCD-6926	Holostei	Lepisosteidae	Scale	3	Blanco *et al*., 2017; Chapter 5
CASA FABÀ						
see below	see below	*Allodaposuchus*	*Allodaposuchus hulki*	Partial skeleton (Holotype)	---	Blanco *et al*., 2015; Chapter 7
FUMANYA						
see below	see below	*Allodaposuchus*	*Allodaposuchus palustris*	Partial skeleton (Holotype)	---	Blanco *et al*., 2014; Chapter 7
	IPS-41760	Teleostei	Osteoglossidae	Partial skeleton	1	Blanco *et al*., 2017; Chapter 5
FUM-2	IPS-90127	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-3	IPS-90128	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-4	IPS-90129	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-7	IPS-90130	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-9	IPS-90131	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-10	IPS-90132	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-11	IPS-90133	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-12	IPS-90134	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-14	IPS-90135	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-15	IPS-90136	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-16	IPS-90137	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-18	IPS-90138	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-19	IPS-90139	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-25	IPS-90140	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-29	IPS-90143	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-31	IPS-90145	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-32	IPS-90146	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-34	IPS-90148	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-39	IPS-90152	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-41	IPS-90153	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-42	IPS-90154	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5

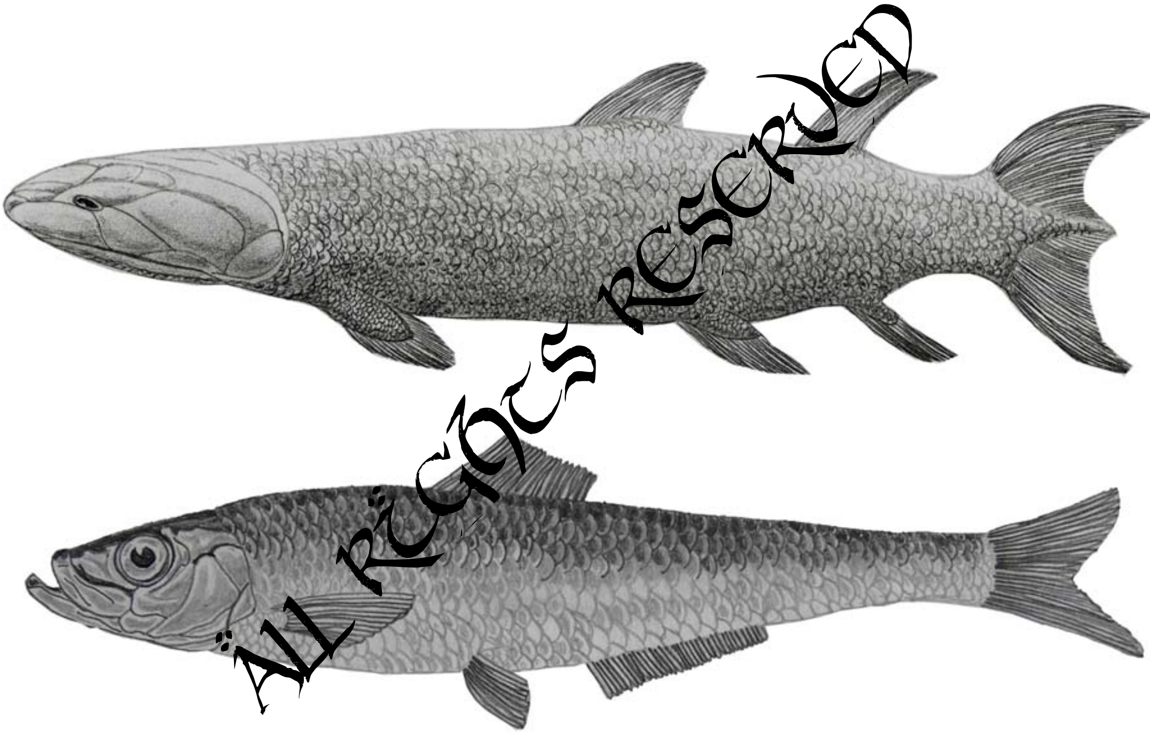
Table 1. Continuation.

FUM-44	IPS-90156	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-45	IPS-90157	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-46	IPS-90158	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-49	IPS-90159	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-50	IPS-90160	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-51	IPS-90161	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-52	IPS-90162	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7
FUM-53	IPS-90163	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-54	IPS-90164	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-55	IPS-90165	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-56	IPS-90166	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-57	IPS-90167	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-60	IPS-90168	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-61	IPS-90169	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-62	IPS-90170	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-64	IPS-90172	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-65	IPS-90173	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-66	IPS-90174	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-67	IPS-90175	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-69	IPS-90177	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-72	IPS-90179	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-74	IPS-90181	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-75	IPS-90182	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7
FUM-76	IPS-90183	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-77	IPS-90184	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-79	IPS-90185	Batoidea	*Rhombodus ibericus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-81	IPS-90186	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
FUM-82	IPS-90187	Batoidea	*Igdabatis indicus*	Tooth	1	Blanco *et al*., 2017; Chapter 5
LES TORRES-2						
LT2-6	IPS-96707	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
LT2-7	IPS-96708	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7
LT2-8	IPS-96709	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7
LT2-9	IPS-96710	*Allodaposuchus*	*Allodaposuchus palustris*	Tooth	1	Unpublished; Chapter 7

Table 1. Continuation.

PONT D'ORRIT-6						
PORRI6-7	IPS-96705	cf. *Allodaposuchus*	cf. *Allodaposuchus subjuniperus*	Tooth	1	Unpublished; Chapter 7
PORRI6-8	IPS-96706	Crocodylomorpha	indet.		1	Unpublished; Chapter 7
CINGLES DE LA CREUETA						
	IPS-81877	Allodaposuchidae	indet.	Tooth	1	Blanco *et al*., 2015; Chapter 8
CINGLES DE CAL ROS						
	IPS-81878	Theropoda	indet.	Diaphysis	1	Blanco *et al*., 2015; Chapter 8

Chapter 5. LATE CRETACEOUS (MAASTRICHTIAN) CHONDRICHTHYANS AND OSTEICHTHYANS FROM NORTHEASTERN IBERIA



Art by Josep Marmi

LATE CRETACEOUS (MAASTRICHTIAN) CHONDRICHTHYES AND OSTEICHTHYES FROM NORTHEASTERN IBERIA

Palaeogeography, Palaeoclimatology, Palaeoecology, 465, 278-294
(I.F.: 2,525; Q1 2015, Palaeontology)

Mi contribución en este trabajo consistió en la obtención, lavado y triado de muestras durante diversas campañas de campo (2013-2015) en colaboración con diverso voluntariado. Posteriormente realicé la ordenación y clasificación preliminar del material recogido en los yacimientos descritos, elaborando una base de datos completa (Tabla 1). Llevé a cabo la clasificación taxonómica y descripción del material perteneciente a condrictios y osteíctios incluyendo los análisis estadísticos especificados en el artículo, así como la redacción completa del manuscrito, material suplementario, y la elaboración de figuras y tablas.

Palaeogeography, Palaeoclimatology, Palaeoecology 465 (2017) 278–294

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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).

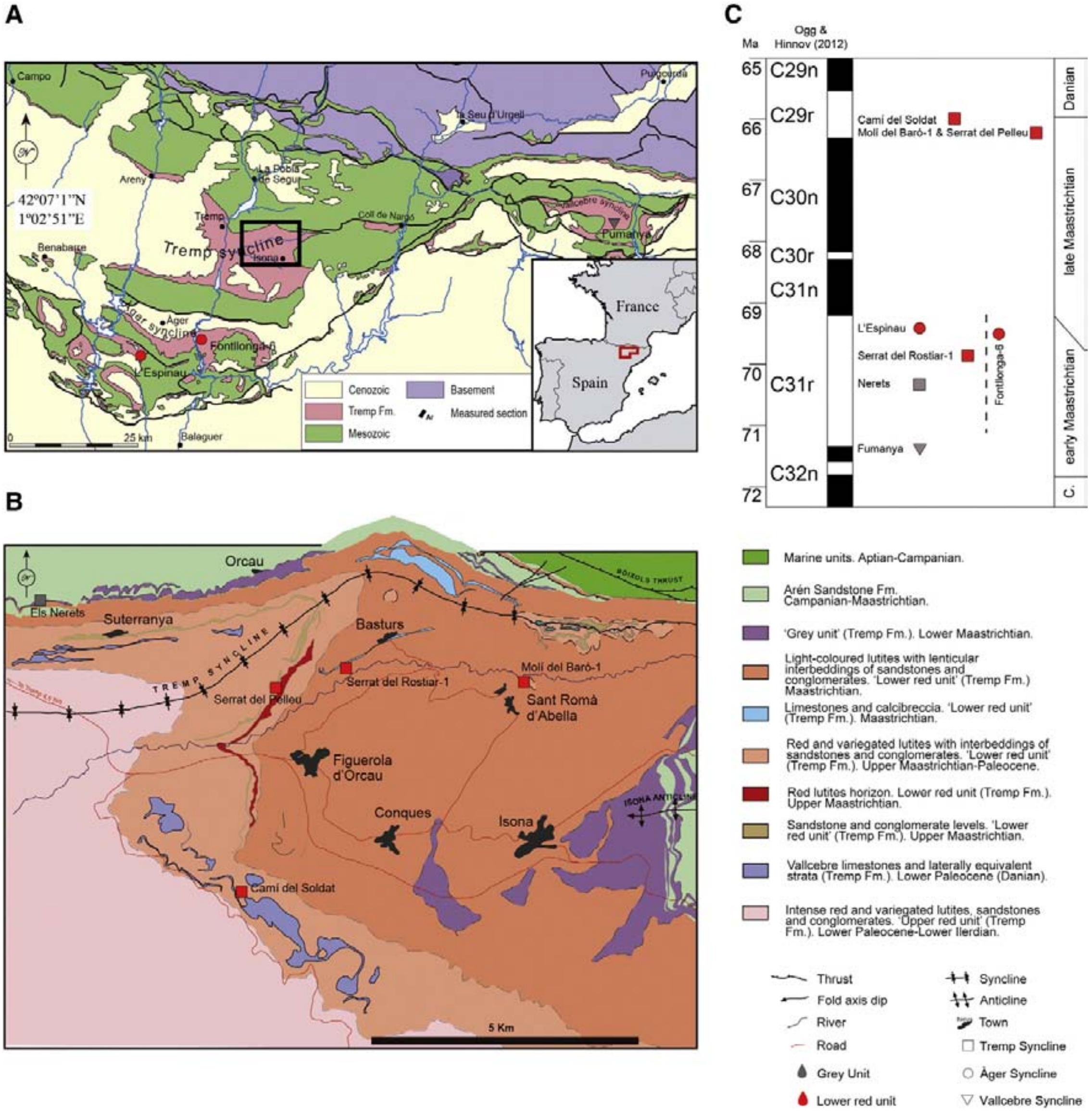


Fig. 1. Geographic and geological context of the studied sites. (A) Geological map of the south-central Pyrenean unit (enlarged from the western Europe map), showing the outcrops of the Cretaceous-Paleocene Tremp Fm. and the location of Fumanya, L'Espinau and Fontllonga sites (modified from Blanco et al., 2016). (B) Geological map of the Isona area (enlarged from A) with the position of the Camí del Soldat, Serrat del Pelleu, Serrat del Rostiar-1, Molí del Baró-1 and Els Nerets sites (modified from Blanco et al., 2016). (C) Temporal distribution of the aforementioned sites based on magnetostratigraphic data, after Ogg and Hinnov (2012), Oms et al. (2007, 2016) and Fondevilla et al. (2016).

In the Àger syncline, the bone layer of L'Espinau site, which has provided hundreds of dinosaur bones, is provisionally interpreted as a secondary deposit formed after successive water floods in a lacustrine environment (Battista et al., 2014). However, the microvertebrate remains from this site are regarded as belonging to inhabitants of the depositional setting (Blanco et al., 2016). On the basis of its stratigraphic correlation with the well-known Fontllonga section, this locality might be placed in the lower part of the upper Maastrichtian (Blanco et al., 2016) (Fig. 1C). The Fontllonga-6 site is a grey clay layer located above a 70-m-thick limestone unit (Soler-Gijón and López-Martínez, 1998). This site also belongs to the 'lower red' unit and is correlated with C31r (Galbrun et al., 1993; Gómez-Gras et al., 2016; Oms et al., 2016), giving an early Maastrichtian age (Fig. 1C). Fontllonga-6 has been interpreted as a large coastal plain with a significant marine influence, located a few kilometers south of the lagoon-barrier island and the inferred Late Cretaceous shoreline (Soler-Gijón and López-Martínez, 1998).

3. Materials and methods

The fieldwork was carried out between 2010 and 2011. Samples of about 375 kg of rock from Els Nerets, 525 kg from Serrat del Pelleu and Fontllonga-6, 575 kg from Camí del Soldat, 625 kg from Serrat del Rostiar-1 and 1250 kg from L'Espinau were collected for processing. Samples were then macerated employing successive water immersions and sun drying in order to shred the rock matrix. Screenwashing was carried out using running water and a sieve series of 1.4, 0.8 and 0.5 mm. The fossils from Fumanya and Molí del Baró-1 were recovered by picking them from rock matrices, instead of by screenwashing techniques; this took place during the digging work carried out in 2007, 2010 and 2011. The samples were then sorted under a Leica M60 binocular microscope. Through this process 34 specimens from Fumanya, 4 from Molí del Baró-1, 12 from Els Nerets, 5 from Serrat del Rostiar-1, 1 from Serrat del Pelleu, 6 from Camí del Soldat, 142 from Fontllonga-6 and 199 from L'Espinau were collected. Photographs were taken under a Zeiss Evo MA10 environmental scanning electron microscope (ESEM) at the Servei de Microscopia de la Universitat Autònoma de Barcelona and at the Universitat de Barcelona. The specimens described in this paper are housed in the collection of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain).

Isolated teeth were grouped and described in morphotypes (see Appendix 1). These morphotypes were compared with similar material from geographically and chronologically closer sites, available in the literature. In addition, fossil samples from Laño, Albaina and Quintanilla la Ojada localities (Basque-Cantabrian basin, Spain) were compared first hand. However, taxonomic classification should be taken with caution when working with isolated fish teeth. For instance, actinopterygian teeth often bear few diagnostic characters, and some taxa show great intraspecific variation, even within the mouth of the same individual (e.g., amiiforms or pycnodontiforms). For this reason, our conclusions are based on high taxonomic ranks and, specifically, on ecomorphotypes.

Several chi-square tests were carried out in order to assess significant differences of teleostean abundance 1) between early and late Maastrichtian samples; 2) between samples from different geological units; 3) between different palaeoenvironments; and 4) between different ecomorphotypes (see Appendix 3). Data were implemented in PAST (Hammer et al., 2001), following Quinn and Keough (2002) and Hammer and Harper (2006).

4. Results

More than 400 fish fossils were collected from the screenwashing and field campaigns, representing 23 different tooth-morphotypes, and including isolated scales, dermal elements, bones and a partial skeleton as well. At least 18 different taxa were identified in the whole sample from the southern Pyrenees (see Systematic Palaeontology in Appendix 1 and Table 1). Chondrichthyes are represented by isolated teeth from an indeterminate anacoracid shark and two different batoids (*Rhombodus ibericus* and *Igdabatis indicus*) (Fig. 2). Non-teleostean actinopterygians include one indeterminate chondrostean, two lepisosteids (*Atractosteus* and *Lepisosteus*), an indeterminate semionotiform, two amiiforms (one amiid and cf. *Caturus* sp.), pycnodontiforms (cf. *Coelodus* sp. and at least one other possible indeterminate pycnodontiform), as well as one aspidorhynchid (*Belonostomus* sp.) (Figs. 3 and 4). Teleostean remains were referred to two indeterminate osteoglossids, three different phyllodontids (*Paralbula* sp., *Pseudoegertonia granulosus* and cf. *Phyllodus* sp.), an indeterminate cypriniform and one sciaenid perciform, in addition to indeterminate teleostean fishes (Figs. 5 and 6).

The L'Espinau and Fontllonga-6 sites are the most diverse among the eight localities sampled, yielding chondrichthyans as well as several forms belonging to chondrosteans, basal neopterygians and teleostean bony fishes (Fig. 7; Table 1). In addition, Els Nerets, Serrat del Rostiar-1 and Camí del Soldat also show a relatively diverse bony fish record. Most of the fish groups described in this paper, with the exception of batoids, were found at L'Espinau, including an anacoracid shark. This is congruent with the highly diverse amphibian herpetofauna also found in this locality (Blanco et al., 2016). The Fontllonga-6 site yielded two different myliobatiforms, lepisosteids, semionotiforms, amiids, pycnodontiforms and phyllodontids. Amiids, pycnodontiforms and cypriniforms were recovered from the Els Nerets site, whereas lepisosteids, aspidorhynchids and phyllodontids were identified in the Camí del Soldat sample. Only lepisosteids, pycnodontiforms and cypriniforms were found at Serrat del Rostiar-1, contrasting with its diverse herpetofauna (Blanco et al., 2016). It is important to note the presence of two lepisosteid genera (*Lepisosteus* and *Atractosteus*) at this site (Fig. 4, Table 1). As regards the less diverse assemblages, a few tooth and scale remains provided evidence for lepisosteids at the Serrat del Pelleu site and osteoglossids at the Molí del Baró-1 site, in addition to the percomorph scales reported by Marmi et al. (2016). The Fumanya site yielded isolated teeth belonging to the same myliobatiform taxa occurring at Fontllonga-6, as well as the partial skeleton of an osteoglossid. The volume of sediment taken from Serrat del Pelleu, Camí del Soldat, Els Nerets and Serrat del Rostiar-1 was similar to that of the sample from Fontllonga-6 (525–625 kg) and half of the sample from L'Espinau, yet different amounts of specimens were recovered from each site: $n_{\mathrm{Nerets}} = 12$, $n_{\mathrm{Serrat\ del\ Rostiar}} = 5$, $n_{\mathrm{Serrat\ del\ Pelleu}} = 1$, $n_{\mathrm{Camí\ del\ Soldat}} = 6$, $n_{\mathrm{Fontllonga}} = 142$, $n_{\mathrm{Espinau}} = 199$ (Table 1). This suggests that the poor diversity in such microvertebrate assemblages could be related to environmental or preservational factors rather than poor or biased sampling. The fish fossils from Fumanya and Molí del Baró-1 were recovered by picking them from rock matrices during the digging works instead of screenwashing techniques, and these assemblages could be methodologically biased.

From a taphonomic point of view, the studied material is of a fragile nature and lacks any evidence of significant abrasion. Moreover, the well-preserved remains (i.e., complete scales, ganoid tubercles, ornamented unworned teeth) suggest that the microvertebrate remains studied herein were not transported far and correspond to animals that lived in or near the depositional settings.

5. Discussion

5.1. Faunal assemblage

During the Maastrichtian, a succession of environments evolved in the southern Pyrenean basin due to a marine regression, which favoured the development of rich ichthyofaunas in the aquatic habitats. The diversity of the chondrichthyans from the Maastrichtian southern Pyrenees is lower than in other, coeval Iberian localities. The batoids collected from the Fontllonga-6 and Fumanya sites correspond to the same genera reported by Kriwet et al. (2007) from the Fontllonga-6 and Figuerola-2 sites (this latter being located in the ‘grey’ unit of the Tremp Formation). However, these authors also reported selachians (an indeterminate lamniform and *Hemiscyllium*) and other batoids (*Coupatezia* and *Paratrygonorrhina*) from the Orcau-2 site (also located in the ‘grey’ unit). Moreover, an anacoracid lamniform was found in L'Espinau (‘lower red’ unit) in this study, but this taxon is clearly different from the lamniform reported by Kriwet et al. (2007). Selachians and batoids are absent in the other sites located in the ‘lower red’ unit (Serrat del Pelleu, Camí del Soldat, Molí del Baró-1 and Serrat del Rostiar-1). As a whole, our results and those of Kriwet et al. (2007) indicate that the chondrichthyan assemblage of the southern Pyrenees ($n = 369$) is less diverse than that from the Albaina site (upper Maastrichtian of the Basque Country), which yielded ten different selachian and nine batoid species ($n = 390$ specimens; Cappetta and Corral, 1999; Pereda-Suberbiola et al., 2015). Similar to the Albaina assemblage, another highly diverse chondrichthyan fauna was described from Quintanilla la Ojada (upper Maastrichtian of Burgos), yielding at least seven different sharks and six rays ($n = 161$ specimens; Corral et al., 2016). The differences in chondrichthyan diversity between the southern Pyrenees and the Basque-Cantabrian region might mostly be due to environmental factors. The Tremp Formation records a marine regression from transitional environments (‘grey’ unit) to fluvial

Table 1
Number of specimens in each locality (maximun number of individuals).

	Vallcebre Syncline	Tremp Syncline					Àger Syncline	
	Grey unit		Lower red unit					
	Fumanya	Els Nerets	Serrat del Rostiar-1	Serrat del Pelleu	Camí del Soldat	Molí del Baró-1	Fontllonga-6	L'Espinau
Chondrichthyes								
Elasmobranchii								
Lamniformes								
Anacoracidae indet.								1
Myliobatiformes								
Igdabatis indicus	14						15	
Rhombodus ibericus	19						33	
Osteichthyes								
Chondrostei								
Chondrostei indet.							1	1
Neoptertgii (non teleosteans)								
Lepisosteiformes								
Atractosteus sp.			1		2		7	35
Lepisosteus sp.			1					
Lepisosteidae indet.				1			62	
Semionotiformes								
?Macrosemiidae indet.							10	12
Amiiformes								
Amiidae indet.		1						1
cf. *Caturus* sp.								9
Pycnodontiformes								
cf. *Coelodus* sp.		1						1
Pycnodontiformes indet.			1		1		1	
?Pycnodontiformes indet.							10	7
Aspidorhynchiformes								
Belonostomus sp.					1			4
Teleostei								
Osteoglossiformes								
Osteoglossidae indet. 1								9
Osteoglossidae indet. 2	1					1		
Phyllodontidae								
Paralbula sp.					1			35
Pseudoegertonia granulosus								26
Paralbulinae indet.							3	25
cf. *Phyllodus* sp.								12
Cypriniformes								
cf. Cypriniformes indet.		10	2					8
Acanthomorpha								
Acanthomorpha indet.								4
Percomorpha indet.						2		
Sciaenidae indet.								4
Teleosteii indet.					1	1		5

settings with some marine influence ('lower red' unit), whereas both Albaina and Quintanilla la Ojada are interpreted as totally marine environments.

The osteichthyan assemblage from the studied sites is more diverse than those from other Campanian-Maastrichtian localities in Spain. One chondrostean, at least eight basal neopterygians and up to five teleosteans were collected from the southern Pyrenees localities ($n = 321$ specimens). In contrast, Laño only yielded lepisosteids, phyllodontids and probable palaeolabrids ($n = 20$ specimens and thousands of lepisosteid scales; Cavin, 1999; Pereda-Suberbiola et al., 2015), whereas pycnodontiforms, phyllodontids, enchodontids and indeterminate acanthomorphs were also reported from Albaina ($n = 796$ specimens; Poyato-Ariza et al., 1999; Pereda-Suberbiola et al., 2015). In addition, Quintanilla la Ojada yielded pycnodontiforms, amiids, phyllodontids and enchodontids ($n = 205$ specimens; Berreteaga et al., 2011). Enchodontids and palaeolabrids are the only taxa absent in the southern Pyrenean sites, whereas chondrosteans, osteoglossiforms, cypriniforms and perciforms are not present in other Maastrichtian sites in Spain.

More interesting are the differences in the 'holostean'-teleostean ratio observed between the early and late Maastrichtian samples. Non-teleostean neopterygians are more abundant in the early Maastrichtian localities, whereas teleosteans are dominant in the late Maastrichtian sites. Chi-square tests reveal significant differences between the early and late Maastrichtian samples ($p = 1.54 \times 10^{-17}$) regardless of the palaeoenvironment. These differences are significant irrespective of whether or not chondrichthyans are considered (see chi-square tests in Appendix 3). This is congruent with the low diversity and abundance of basal neopterygians compared to teleosteans in the Upper Cretaceous palaeoichthyological record of Spain. Basal neopterygians are typical members of Jurassic faunas, but were progressively replaced by teleosteans (e.g., Poyato-Ariza, 2005; Berreteaga et al., 2011; Poyato-Ariza and Martín-Abad, 2013). This is particularly evident for durophagous taxa: ginglymodians range from the Middle Triassic to the present and reached their maximum diversity during the Late Jurassic and Early Cretaceous (López-Arbarello, 2012), but they are only represented by macrosemiids and the non-durophagous Lepisosteidae during the Late Cretaceous (López-Arbarello, 2012). Similarly, pycnodontiforms range from the Late Triassic to the Eocene and dominated Early Cretaceous durophagous ichthyofaunas (Poyato-Ariza, 2005). Likewise, phyllodontids dominated the durophagous guild from the Late Cretaceous to the Eocene, before going extinct (Estes, 1969; Berreteaga et al., 2011). Ginglymodians and pycnodontiforms are abundantly recovered in Lower Cretaceous sites (Estes and Sanchíz, 1982; Buscalioni et al., 2008; Sweetman et al., 2014; Pouech et al., 2015), but phyllodontids largely exceed them in number in Upper Cretaceous localities (Berreteaga et al., 2011; Csiki-Sava et al., 2015; Pereda-Suberbiola et al., 2015; this study). Specifically in the

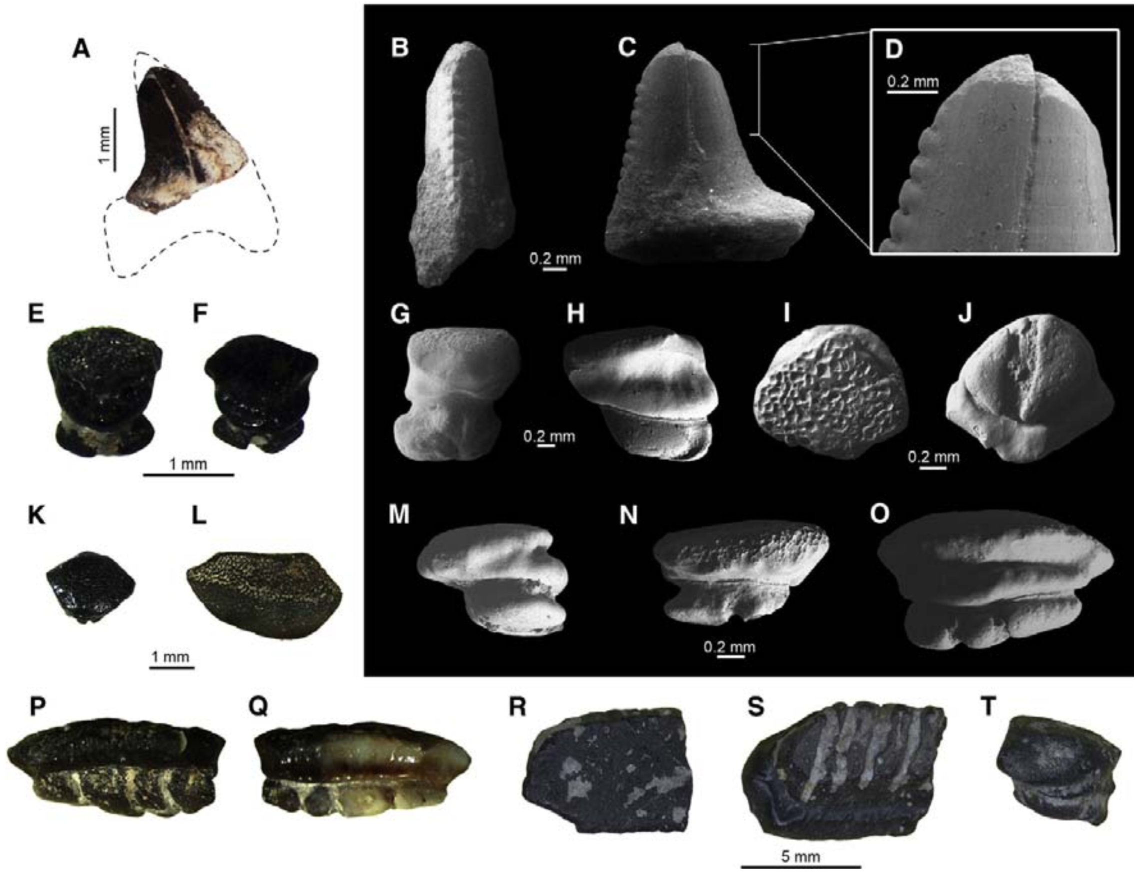


Fig. 2. Tooth remains referred to Chondrichthyes. (A–D) Anacoracidae indet. (A) showing the inferred outline of the complete tooth, in (B) mesial and (C) lateral views and (D) detail of the denticles. (E–J) *Rhombodus ibericus*: (E) anteromedial, (F) anterolateral and (G) posterior teeth, in (E–F) lingual, (G) labial, (H) lateral, (I) occlusal and (J) basal views. (K–T) *Igdabatis indicus*: (K–O) lateral teeth in (K–L) occlusal, (M) lateral, (N) labial and (O) lingual views; (P–T) medial teeth in (P) labial, (Q) lingual, (R) occlusal, (S) basal and (T) lateral views.

southern Pyrenees, semionotiforms, pycnodontiforms and phyllodontids are present in both early and late Maastrichtian sites (Fig. 7). Semionotiforms and pycnodontiforms are more abundant than phyllodontids in the early Maastrichtian (e.g., Fontllonga-6), but the latter subsequently became the most abundant durophagous species in the late Maastrichtian (e.g., L'Espinau). Teleosteans seem to be widely represented in the upper Maastrichtian of the southern Pyrenees, including osteoglossiforms, cypriniforms and perciforms, in addition to at least three phyllodontid taxa. Additional chi-square tests show no significant differences between the complete samples from the 'grey' and 'lower red' units ($p_{\text{chi-square}} = 0.047$; $p_{\text{Monte Carlo permutation}} = 0.053$) or between the samples from different palaeoenvironments ($p_{\text{chi-square}} = 0.055$; $p_{\text{Monte Carlo permutation}} = 0.075$). In other words, the increase in teleost abundance in the late Maastrichtian localities is not a result of a preservational factor related to the geological units or different depositional environments. It may represent a good example of ichthyofaunal turnover during the Late Cretaceous.

Some specimens from the southern Pyrenees localities are of particular interest. The partial osteoglossiform skeleton from Fumanya extends the chronological range of the group in Europe to the early Maastrichtian. Osteoglossiforms have been widely recovered from Cretaceous outcrops in Asia, South and North America (Yabumoto, 1994; Gayet et al., 2001; Murray et al., 2016), but until now the oldest known European fossil comes from the Paleogene (Taverne et al., 2007; Wilson and Murray, 2008). As regards Perciformes, some smooth hemispherical teeth with striated bases from the Campanian of southern France have been referred to Sparidae (Buffetaut et al., 1996), and similarly other findings from the late Maastrichtian of southern France have been referred with doubts to the same taxon (Laurent et al., 1999, 2002). However, their morphology is identical to our morphotypes 17 and 19 (see Appendix 1), so we regard these teeth as being better referred to Paralbulinae. The sciaenid (perciform) remains from L'Espinau, thus, represent the oldest evidence of this group in Europe. As no other acanthomorph taxon was recovered from the samples, we parsimoniously assume that the acanthomorph vertebrae from L'Espinau and the percomorph scales from Molí del Baró-1 (Marmi et al., 2016) might also belong to sciaenids. This group of perciforms has been abundantly recovered from the Maastrichtian of Montana (Brinkman et al., 2014), Wyoming (Marsh, 1889), New Jersey (Grandstaff et al., 1992) and Alberta (Langstrong, 1975), but it is absent in the Mesozoic record of Europe. In addition, the cypriniform remains from Els Nerets are the oldest evidence for this taxon worldwide, followed by those from Serrat del Rostiar-1 and L'Espinau. The Upper Cretaceous fossil record of more advanced ostariophyseans (e.g., Characiformes and Siluriformes) suggests a gap in the fossil record of the Cypriniformes, and Cretaceous representatives should be expected (Fink and Fink, 1996; Alves-Gomes, 2010). It is worth mentioning a controversial specimen referred to *Molinichthys inopinatus* Gayet, 1982. This taxon was erected on the

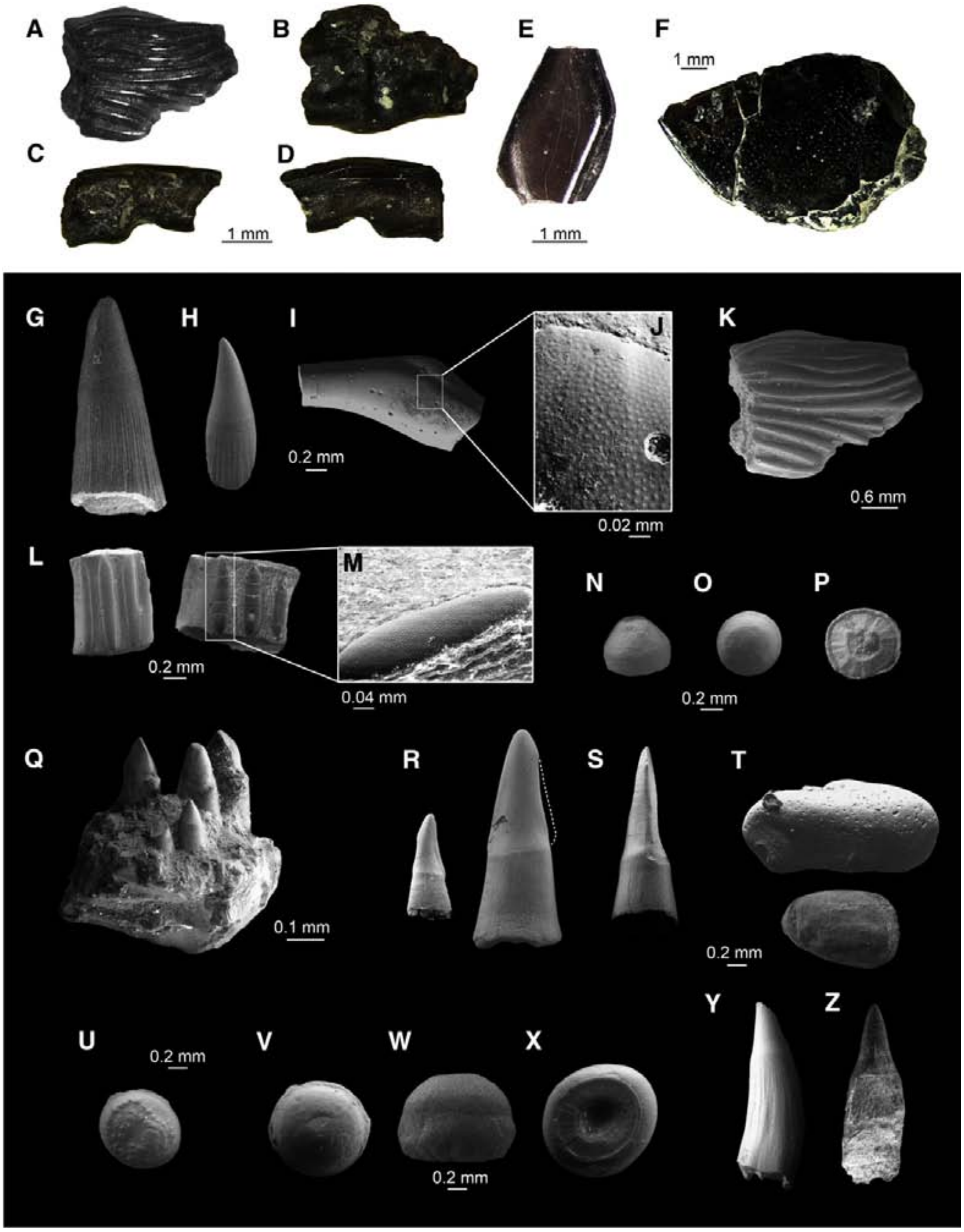
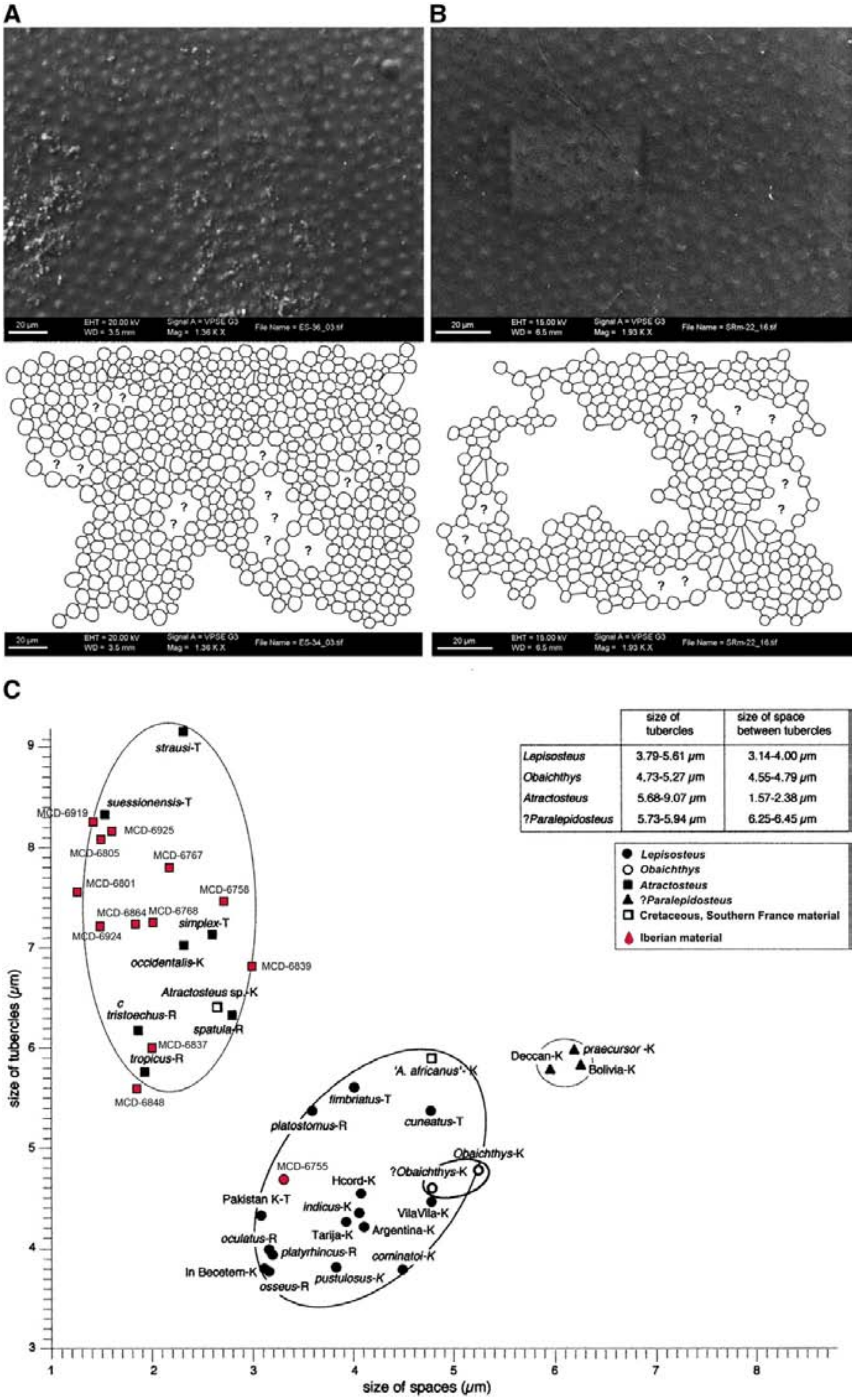


Fig. 3. Teeth and scales referred to non-teleostean Actinopterygii. (A–D) Dermal scute of Chondrostei indet. in (A) lateral, (B) medial and (C–D) marginal views. (E–J) *Atractosteus* sp.: (E–F) ganoid scales, (G–H) teeth in (G) mesial and (H) lateral views and (I–J) detail of the ornamentation of a ganoid scale. (K) Ornamentation of a chondrostean scute. (L–M) Hemitrichia of *Atractosteus* sp. and (M) detail of the ornamentation. (N–P) Teeth of Semionotiformes in (N) lateral, (O) occlusal and (P) basal views. (Q) Coronoid element of an indeterminate Amiidae. (R–S) cf. *Caturus* sp. teeth in (R) lingual and (S) lateral views. (T) Teeth of indeterminate Pycnodontiformes in occlusal view. (U) cf. *Coelodus* sp. teeth in occlusal view. (V–X) Teeth of ?Pycnodontiformes indet. in (V) occlusal, (W) lateral and (X) basal views. (Y) lateral dentary tooth of *Belonostomus* sp. in lateral view. (Z) Medial dentary tooth of *Belonostomus* sp. in caudal view.

basis of a supposed pharyngeal bone from the Maastrichtian of Bolivia, and was originally referred to Cyprinidae (Gayet, 1982). Nevertheless, its attribution to Cypriniformes is ambiguous because (1) the morphology of the branchial arch and teeth of *Molinichthys* differs from those of this group; (2) the material lacks apomorphic characters to assess its phylogenetic relationships; and (3) no other fossil or extant



	size of tubercles	size of space between tubercles
Lepisosteus	3.79-5.61 µm	3.14-4.00 µm
Obaichthys	4.73-5.27 µm	4.55-4.79 µm
Atractosteus	5.68-9.07 µm	1.57-2.38 µm
?Paralepidosteus	5.73-5.94 µm	6.25-6.45 µm

Fig. 4. Ganoid ornamentation of lepisosteid scales. (A) Detail of *Atractosteus* sp. and scheme of the measurements. (B) Detail of *Lepisosteus* sp. and scheme of the measurements. (C) Comparison of the sourthern Pyrenees sample with other lepisosteid scales (modified from Gayet et al., 2002).

cypriniform has been found in South America. Therefore, *Molinichthys* has subsequently been placed in an *incertae sedis* (Gayet, 1991) or even considered *nomen nudum* (Gayet and Meunier, 1998).

5.2. Trophic relationships

From an ecological viewpoint, the isolated teeth from the southern Pyrenees were assigned to a broad variety of ecomorphotypes. The most diverse assemblages are composed of ichthyophagous, soft- and hard-durophagous as well as microphagous or filter-feeder forms.

The ichthyophagous guild is composed of the ecomorphotypes referred to an anacoracid shark, *Atractosteus,* indeterminate lepisosteids, amiids, cf. *Caturus*, *Belonostomus* and osteoglossids (morphotypes 1, 7, 9, 10, 14, 15 and 16) (Fig. 2A-D, 3G-H, R-S, Y-Z, 5H). Although no tooth was confidently referred to *Lepisosteus*, its presence is supported by ganoid scales. The feeding habits of lepisosteids, amiids and osteoglossids can be inferred from their extant relatives (Etnier and Starnes, 1993; Grande and Bemis, 1998; Grande, 2010; Cavin et al., 2015) as well as some exceptionally preserved fossils (Grande, 1984; Taverne and Capasso, 2012). The typical spear-shaped tooth morphology of *Caturus* indicates predatory habits (Buscalioni et al., 2008; Cuny et al., 2010a; Sweetman et al., 2014; Pouech et al., 2015). The elongated rostrum of *Belonostomus* bearing needle-shaped teeth is also typical of a predatory fish. This probably exploited different trophic resources from *Caturus* (Bogan et al., 2011; Sweetman et al., 2014).

The soft-durophagous group comprises tritorial teeth referred to semionotiforms and perciforms (morphotypes 8 and 22) (Figs. 3N–P and 5Y–Z). These tritorial teeth are adapted to prey on soft-shelled or slippery items of prey (Weems, 1999; Buscalioni et al., 2008; Cicimurri and Knight, 2009). This ecomorphotype is not as massive as the molariform teeth referred to hard-durophagous fishes. Molariform ecomorphotypes were assigned to cf. *Coelodus*, indeterminate pycnodontiforms, *Paralbula*, *Pseudoegertonia* and *Phyllodus* (morphotypes 11, 12, 13, 17, 18, 19 and 20) (Figs. 3T–X and 5I–U). These massive teeth suggest feeding habits associated with hard-shelled prey items (Estes, 1969; Poyato-Ariza, 2005; Berreteaga et al., 2011; Poyato-Ariza and Martín-Abad, 2013; Sweetman et al., 2014). The presence of three phyllodontid taxa within the hard-durophagous guild is remarkable, but Estes (1969) suggested some dietary differences between phyllodontines and paralbulines. In addition to osteichthyans, batoid taxa should also be taken into account (morphotypes 2, 3, 4, 5 and 6) (Fig. 2E–T). Myliobatiforms (*Rhombodus* and *Igdabatis*) with grinding-type dentition are regarded as benthic carnivores that feed on hard-shelled molluscs on the sea bottom (Cappetta, 1987; Corral et al., 2016).

The teeth referred to cypriniforms (morphotype 21) consist of pharyngeal elements (Fig. 5W–X). Cypriniforms are toothless fishes whose branchial 'teeth' protect their branchial apparatus during the sucking effect required for feeding (Nelson, 2006). Therefore, cypriniforms belong to the microphagous or filtering guild. In addition, the presence of chondrosteans should also be included within the microphagous guild (Nelson, 2006; Brinkman, 2008).

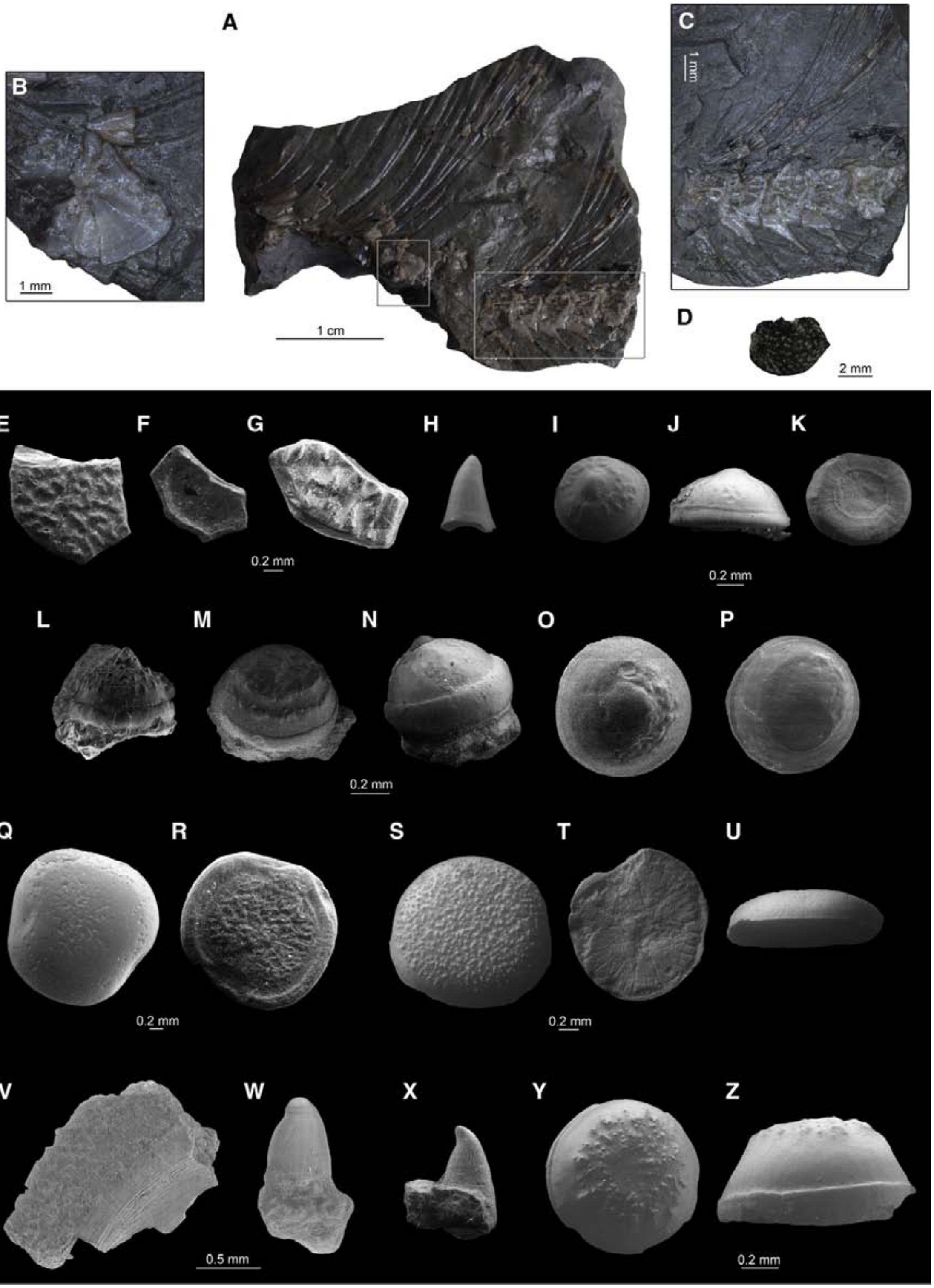
On the basis of these results, all the trophic guilds are well represented in both the 'grey' and 'lower red' units of the Tremp Formation (Fig. 8). As regards teleosteans, these are major components of the microphagous-filter guild in the early Maastrichtian samples, but are widespread in the other guilds in the late Maastrichtian. Another chi-square test shows significant differences in the abundance of teleosteans per guild between the early and late Maastrichtian, whether chondrichthyans are considered ($p = 1.01 \times 10^{-20}$) or not ($p = 1.35 \times 10^{-14}$). The scarcity of teleostean remains in other Cretaceous outcrops has been interpreted as a consequence of a mixture of ecological and taphonomic biases. Teleosteans were probably abundant, but as they occupied the lowest levels of the trophic web (i.e., microphagous and filter-feeders), many of them were edentulous or possessed small villiform teeth, which have not been preserved in the fossil record (Poyato-Ariza, 2005; Buscalioni et al., 2008; Berreteaga et al., 2011). However, teleosteans are well represented in the Maastrichtian of the southern Pyrenees, not only in the microphagous guild (cypriniforms), but also among the soft- and hard-durophagous feeders (sciaenids and phyllodontids, respectively) and within the ichthyophagous guild (osteoglossids).

5.3. Palaeoenvironmental implications

Chondrichthyans are mainly marine fishes with relatively few freshwater representatives (i.e., *Lissodus*, potamotrygonids and some species of *Dasyatis*) (Cappetta, 1987; Nelson, 2006). Some selachians living in coastal waters can also tolerate lower-salinity conditions and enter rivers upwards (Boeseman, 1964; Thorson et al., 1966; Cappetta, 1987; Underwood and Rees, 2002; Martin, 2005; Pillans et al., 2005; Sweetman and Underwood, 2006; Duffin and Sweetman, 2011). Freshwater chondrichthyans were diverse in the Late Cretaceous of North America (i.e., hybodontids, orectolobiformes, rhinobatoids and sclerorhynchids), although fully non-marine sharks and rays were not reported from Europe (Kirkland et al., 2013; Cook et al., 2014). Anacoracid sharks are considered open-sea nektonic faunas, whereas myliobatiforms are neritic inhabitants (Cappetta, 1987; Cappetta and Corral, 1999; Corral et al., 2016).

Osteichthyans are potentially misleading palaeoenvironmental indicators. The presence of any particular taxon cannot always be taken to reflect any particular environment. The study of the complete community is palaeoecologically reliable (Poyato-Ariza et al., 1998; Berreteaga et al., 2011), but it should be combined with other faunal and floral evidence, as well as with sedimentological or geochemical data, to be able to assess the original environment confidently. Chondrosteans include both freshwater and marine species; furthermore, other anadromous representatives generally spend part of their life alternating between marine and fluvial ecosystems (Nelson, 2006). Fossil and extant lepisosteids are represented mostly by freshwater species, able to tolerate brackish water (Wiley, 1976; Etnier and Starnes, 1993; Grande, 2010). In addition, semionotiforms and non-lepisosteid lepisosteiforms (i.e., *Lepidotes*, *Scheenstia*, *Isanichthys*, *Araripelepidotes*, *Pliodetes*) are present in deposits worldwide, regardless of the depositional environments (Forey et al., 2011; López-Arbarello and Alvarado-Ortega, 2011; López-Arbarello and Sferco, 2011; Sweetman et al., 2014; Bermúdez-Rochas and Poyato-Ariza, 2015; Pouech et al., 2015). The extant *Amia calva* is only known from freshwater environments (Grande and Bemis, 1998), but fossil amiids have also been found in marine or brackish settings (Martín-Abad and Poyato-Ariza, 2013). Moreover, pycnodontiforms have also been found in marine, brackish and freshwater environments (Poyato-Ariza et al., 1998; Poyato-Ariza, 2005; Pouech et al., 2015; Szabó et al., 2016b), and perciforms include both freshwater and marine genera (Weems, 1999; Nelson, 2006; Cicimurri and Knight, 2009). For this reason, the occurrence of all of the above taxa is not representative of any specific environment. However, several authors have noted that

Fig. 5. Fossil remains referred to Teleosteii. (A–C) Partial skeleton referred to Osteoglossidae indet. in lateral view, and detail of (B) one scale and (C) several vertebrae. (D–G) Squamulae of indeterminate osteoglossids in (D, E, G) lateral and (F) medial views. (H) Osteoglossid tooth in lateral view. (I–K) Teeth of *Paralbula* sp. in (I) occlusal, (J) lateral and (K) basal views. (L–O) Wear series of *Paralbula* teeth. (P) Tooth of an indeterminate paralbuline in occlusal view. (Q–R) Teeth of *Pseudoegertonia granulosus* in (Q) occlusal and (R) basal views. (S–U) Teeth of cf. *Phyllodus* sp. in (S) occlusal, (T) basal and (U) lateral views. (V) Branchial arch fragment of Cypriniformes indet. (W–X) Teeth of Cypriniformes indet. in lateral view. (Y–Z) Teeth of an indeterminate sciaenid (Perciformes) in (Y) occlusal, and (Z) lateral views.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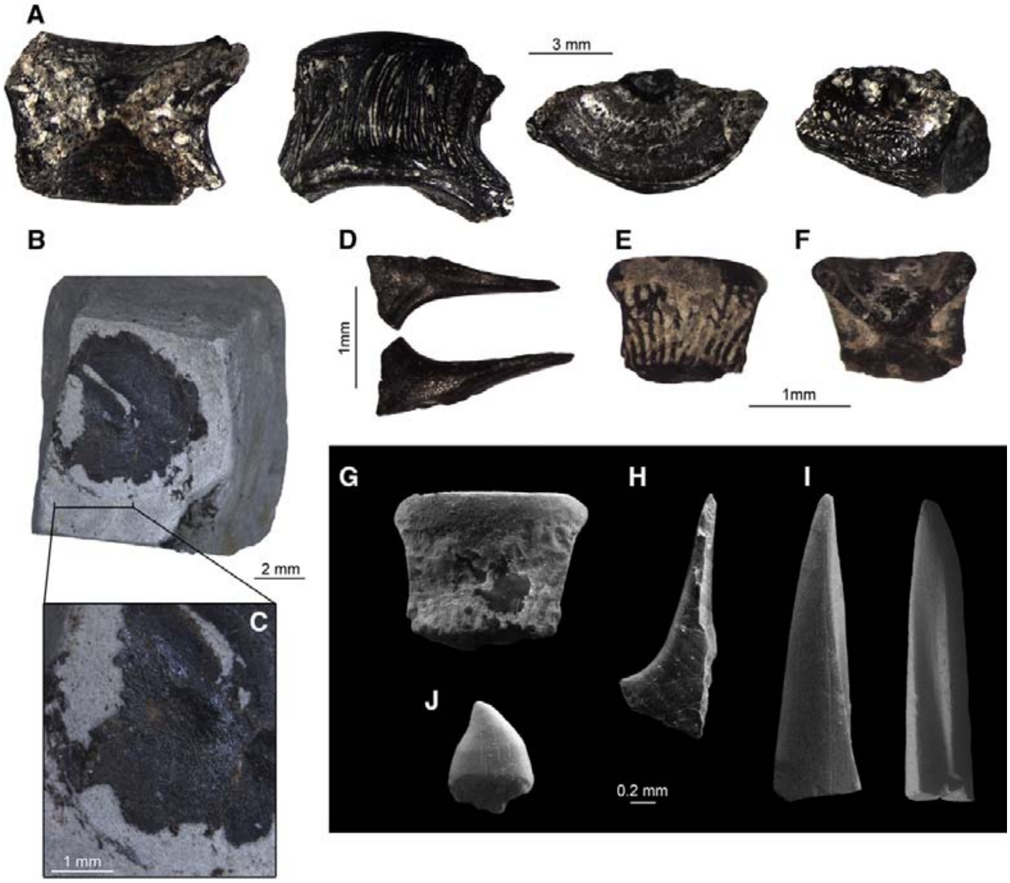


Fig. 6. Indeterminate teleostean remains. (A) Vertebral fragments. (B–C) Cycloid scale and (C) detail of the ornamentation. (D) Fragmentary cleithrum. (E–G) Vertebral fragments. (H) Detail of the cleithrum. (I) Spines. (J) Indeterminate tooth in lateral view.

pycnodontiforms are not well-adapted to upstream waters, unlike ginglymodians, suggesting a lacustrine lifestyle for freshwater pycnodontiforms (Poyato-Ariza, 2005; Pouech et al., 2015). In turn, *Caturus* and *Belonostomus* are considered marine predators, living in open seas or coastal habitats (Brinkman, 1990, 2008; Brito and Suárez, 2003; Cuny et al., 2010a; Sweetman et al., 2014; Martín-Abad and Poyato-Ariza, 2013). Phyllodontids mainly inhabited littoral and estuarine environments in epicontinental seas, although there are a few occurrences in freshwater settings, but always connected to coastal habitats (Estes, 1969). On the other hand, osteoglossiforms are tropical freshwater fishes currently distributed in South America, Africa and India, but their fossil remains are also reported from fresh, brackish and marine environments. However, according to Gayet (1987), all marine species are Palaeocene or younger (Nelson, 1969; Gayet et al., 2001). By contrast, Cypriniformes are freshwater inhabitants (Gayet, 1991; Nelson, 2006; Alves-Gomes, 2010) that have never developed tolerance for marine or brackish water.

The palaeoenvironment inferred for the ‘grey’ unit beds of the Tremp Formation is related to mudflats and coastal wetlands with a strong marine influence (e.g., Rosell et al., 2001; Oms et al., 2007, 2016) (Fig. 9A, B). The Fontllonga-6 site has also been interpreted as a large coastal plain near to a lagoon barrier island (Soler-Gijón and López-Martínez, 1998; Kriwet et al., 2007) (Fig. 9B). The ichthyofauna of the Fontllonga-6 site includes euryhaline (lepisosteids, semionotiforms, amiids, pycnodontiforms) and primarily marine fishes (batoids, phyllodontids). The low chondrichthyan diversity (i.e., the absence of sharks) may be related to the shallow water and brackish conditions unlike the in-shore and open-marine environments of the Quintanilla la Ojada and Albaina sites, respectively (Cappetta and Corral, 1999; Corral et al., 2016). The fish remains recovered from Fumanya suggest a similar ichthyofauna. Despite the lower diversity compared to Fontllonga-6, the differences in taxon occurrences may undoubtedly be due to methodological biases (see Material and methods). Previous studies inferred a brackish to freshwater lacustrine-palustrine environment as part of a more extensive lagoon for the ‘grey’ unit cropping out in the Fumanya locality (Rosell et al., 2001; Oms et al., 2007, 2016; Villalba-Breva et al., 2012) (Fig. 9A). The studied ichthyofauna is consistent with this type of environment, with taxa associated with marine-brackish waters (e.g., batoids) and the occurrence of osteoglossids, more related to freshwater, near to the lagoon. In turn, the ichthyofauna recovered from the Els Nerets site is mostly composed of cypriniform remains suggesting freshwater conditions, whereas euryhaline fishes (pycnodontiforms and amiids) are merely occasional, despite being located in the ‘grey’ unit (Fig. 9B). In this locality, the ‘grey’ unit ranges from 4 to 30 m in thickness, and the presence of dinoflagellate cysts in its upper part suggests a stronger marine influence (Torices et al., 2012). However, these authors also reported a diverse palynoflora including freshwater zygospores in the lower beds, where the studied

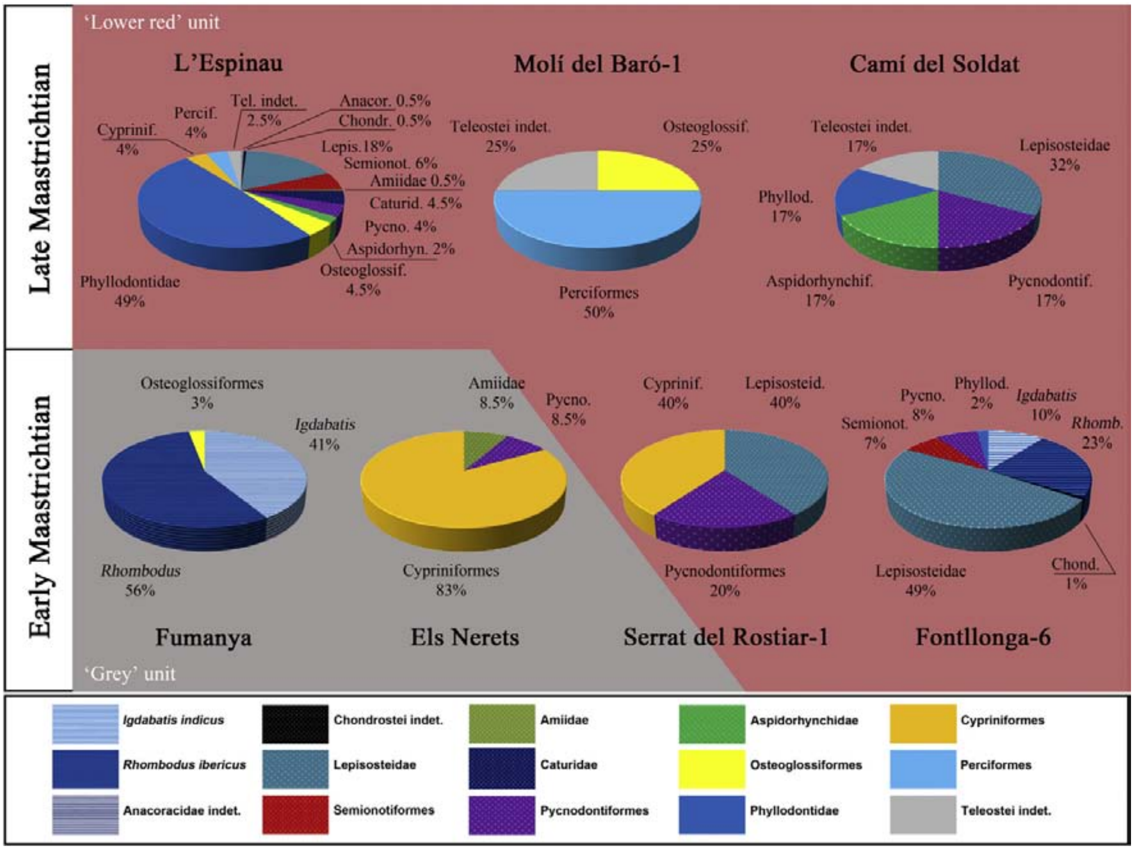


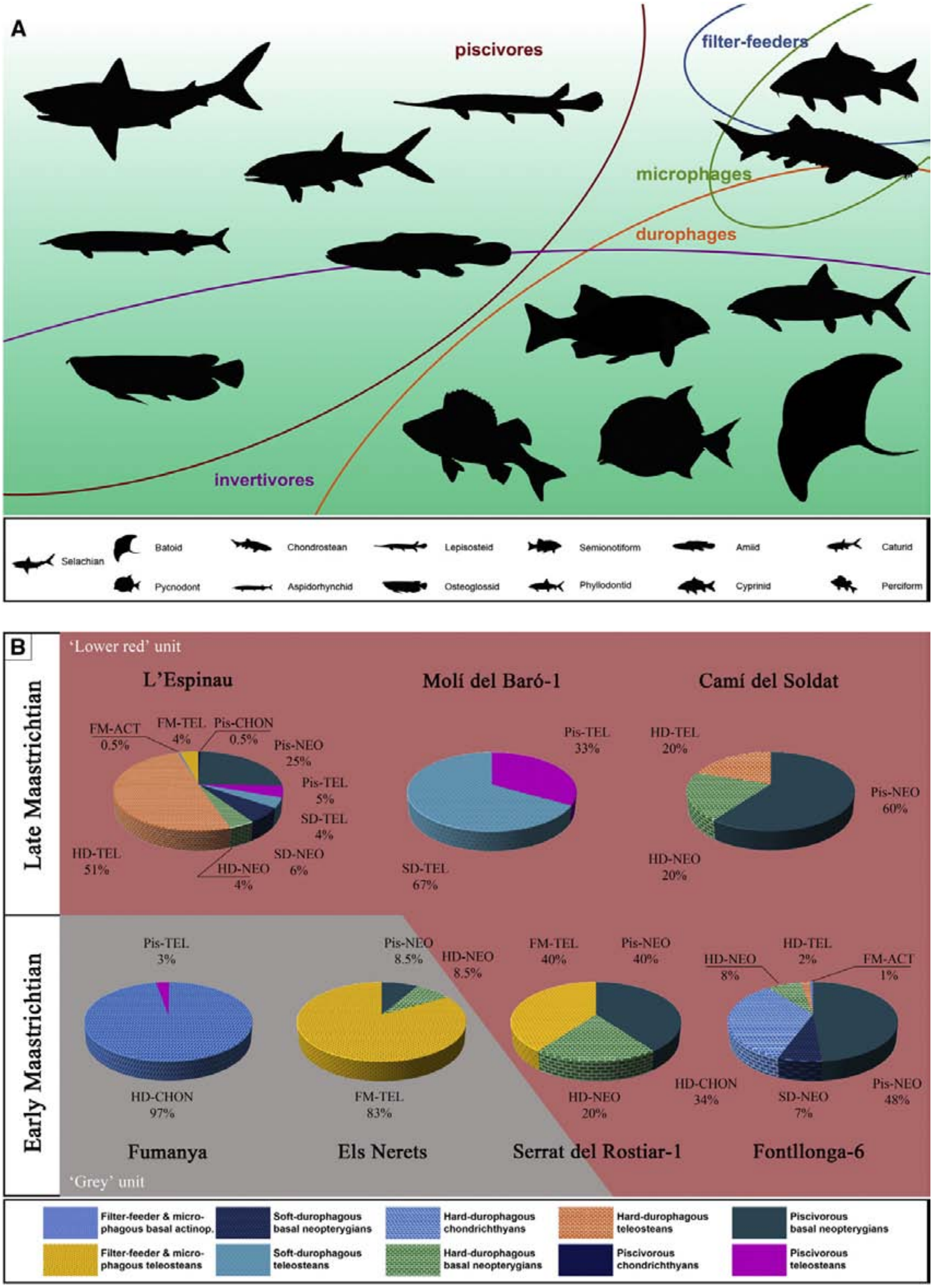
Fig. 7. Relative abundances of taxonomic fish groups in each locality: Fumanya (n = 34), Els Nerets (n = 12), Serrat del Rostiar-1 (n = 5), Camí del Soldat (n = 6), Molí del Baró-1 (n = 4), Fontllonga-6 (n = 142) and L'Espinau (n = 199). Serrat del Pelleu (n = 1) is not represented.

sample was collected, which is consistent with the presence of cypriniform fishes.

The palaeoenvironments of the red beds of the 'lower red' unit mostly include floodplains with ephemeral ponds and fluvial channels and mudflats, mainly freshwater environments with some marine influence (Díez-Canseco et al., 2014) (Fig. 9C). The ichthyofauna found at the sites of Serrat del Pelleu, Serrat del Rostiar-1 and Molí del Baró-1, together with the amphibian and squamate taxa reported by Blanco et al. (2016), is consistent with this palaeoenvironmental interpretation. Camí del Soldat, however, has yielded euryhaline (lepisosteids and pycnodontiforms) and primarily marine fishes (phyllodontids and *Belonostomus*), but no freshwater taxa. The faunal association also lacks squamates, and amphibians are rare (Blanco et al., 2016). Previous studies have demonstrated that the fluvial environments of the 'lower red' unit were closely connected to marine settings with seawater moving upstream because of flood-tide currents and accumulating in shallow pools at the margins of meandering rivers (Díez-Canseco et al., 2014; Marmi et al., 2016; Piga et al., 2016). Thus, the remains of lepisosteids, pycnodontiforms, phyllodontids and *Belonostomus* from the Camí del Soldat site might have been transported by tidal currents from marine settings. However, the fossil remains from Camí del Soldat do not show abrasion marks, but well-preserved ornamented surfaces (Figs. 3J and 5M), suggesting that the fish populations possibly inhabited more or less stably saline waters in the floodplain. The absence of herpetofauna and freshwater fishes might also suggest a close connection with the sea and relatively saline waters. Finally, the ichthyofauna from L'Espinau is composed of a mixture of euryhaline, freshwater (cypriniforms, osteoglossids), and marine species (anacoracids, *Caturus*, *Belonostomus*, phyllodontids). Remarkable is the absence of neritic batoids in conjunction with the occurrence of open-sea selachians. The anuran assemblage (i.e., palaeobatrachids and pelobatids or gobiatids) and the low squamate diversity of L'Espinau also suggest a relatively saline environment (Blain et al., 2010; Blanco et al., 2016; Szentesi and Company, 2016). The faunal association could reflect a confluence area of freshwater and coastal environments with an open connection to the sea (i.e., estuarine or coastal wetlands).

5.4. Palaeobiogeographical implications

As inhabitants of shallow marine ecosystems, batoids are considered good palaeobiogeographical indicators (Cappetta, 1987). The occurrence of the same species in two different landmasses points to a connection between continental platforms, whereas endemic species


A
piscivores
filter-feeders
microphages
durophages
invertivores
Selachian
Batoid
Pycnodont
Chondrostean
Aspidorhynchid
Lepisosteid
Osteoglossid
Semionotiform
Phyllodontid
Amiid
Cyprinid
Caturid
Perciform
B
'Lower red' unit
Late Maastrichtian
L'Espinau
FM-ACT 0.5%
FM-TEL 4%
Pis-CHON 0.5%
Pis-NEO 25%
Pis-TEL 5%
SD-TEL 4%
SD-NEO 6%
HD-NEO 4%
HD-TEL 51%
Molí del Baró-1
Pis-TEL 33%
SD-TEL 67%
Camí del Soldat
HD-TEL 20%
Pis-NEO 60%
HD-NEO 20%
Early Maastrichtian
Pis-TEL 3%
HD-CHON 97%
Fumanya
Pis-NEO 8.5%
HD-NEO 8.5%
FM-TEL 83%
Els Nerets
FM-TEL 40%
Pis-NEO 40%
HD-NEO 20%
Serrat del Rostiar-1
HD-NEO 8%
HD-TEL 2%
FM-ACT 1%
HD-CHON 34%
SD-NEO 7%
Pis-NEO 48%
Fontllonga-6
'Grey' unit
Filter-feeder & micro-phagous basal actinop.
Soft-durophagous basal neopterygians
Hard-durophagous chondrichthyans
Hard-durophagous teleosteans
Piscivorous basal neopterygians
Filter-feeder & micro-phagous teleosteans
Soft-durophagous teleosteans
Hard-durophagous basal neopterygians
Piscivorous chondrichthyans
Piscivorous teleosteans

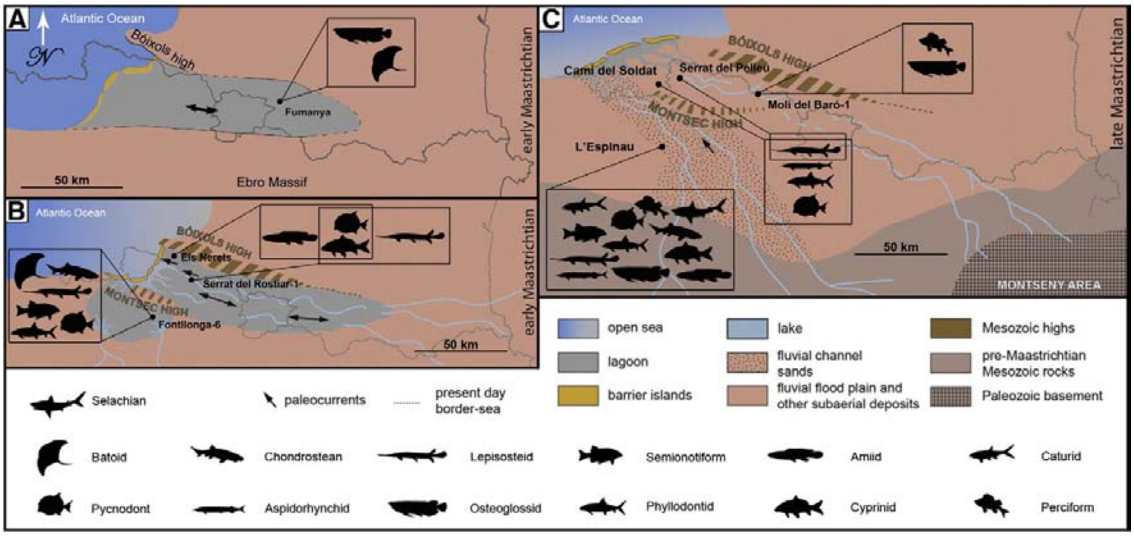


Fig. 9. Ichthyofauna related to different palaeoenvironments. Palaeogeography of the southern Pyrenees in (A) the early Maastrichtian (C32n), (B) in the late early Maastrichtian (C31r) and (C) in the late Maastrichtian (C31r-C29r). Modified from Oms et al. (2016) and Gómez-Gras et al. (2016) respectively.

suggest deep oceanic basins operating as geographical barriers. Thus, the occurrence of *Igdabatis indicus* in marine to transitional settings both in the southern Pyrenean basin and Indian localities suggests an interconnection between Ibero-Armorica and India during the Maastrichtian (Soler-Gijón and López-Martínez, 1998). Remains of *Igdabatis* from the Fontllonga-6 and Fumanya sites support the hypothesis that this genus probably originated in the shallow marine waters surrounding the Ibero-Armorican Domain during the early Maastrichtian, before dispersing to Africa and India through the Tethys Ocean, as was suggested by Corral et al. (2016). Even though *Rhombodus ibericus* is considered a Spanish endemic taxon, the presence of other *Rhombodus* spp. in India also supports a geographic interconnection (Prasad and Cappetta, 1993; Kriwet et al., 2007). Likewise, anacoracid sharks were active swimmers that could easily migrate through open seas. This would explain similarities between nektonic selachian faunas of the Maastrichtian of Spain and those of the rest of Europe and North America (Cappetta and Corral, 1999; Bourdon et al., 2011; Corral et al., 2016).

The non-teleostean neopterygian fauna reported from the Maastrichtian southern Pyrenean basin is congruent with other European Upper Cretaceous sites (Cavin, 1999; Berreteaga et al., 2011; Pereda-Suberbiola et al., 2015; Csiki-Sava et al., 2015, 2016; Szabó et al., 2016a, 2016b). Most of the basal neopterygian groups show a wide biogeographic range. Lepisosteiforms and semionotiforms reached an almost worldwide distribution, except Oceania and Antarctica (Wiley, 1976; Grande, 2010; López-Arbarello and Alvarado-Ortega, 2011; López-Arbarello, 2012). Amiiforms and pycnodontiforms were mainly distributed around the Western Tethys in the Northern Hemisphere during the Late Cretaceous, although they have also been reported from South America, Subsaharan Africa and East Asia (Grande and Bemis, 1998; Martín-Abad and Poyato-Ariza, 2013; Poyato-Ariza and Martín-Abad, 2013). On the other hand, *Belonostomus* remains have been abundantly recovered from Upper Cretaceous outcrops of Europe and North America (Woodward, 1888; Bardack, 1968; Langstrong, 1975; Brinkman, 1990, 2008; DeMar and Breithaupt, 2008; Brinkman et al., 2014; Sweetman et al., 2014), although some South American occurrences are also reported (Brito and Suárez, 2003).

Teleosteans show different biogeographical relationships. Osteoglossiforms reached a wide distribution during the Cretaceous, probably as a result of a widespread ancestral lineage (Wilson and Murray, 2008). The remains reported in the present paper represent the first evidence for this group in the Mesozoic record of Europe. Up to now, they were known in African, Asian and North and South American localities (Gayet, 1991; Li, 1996; Otero and Gayet, 2001; Nelson, 2006; Taverne et al., 2007; Wilson and Murray, 2008; Brinkman et al., 2014). On the other hand, phyllodontids and perciforms (specifically sciaenids) have only been recovered from the Upper Cretaceous of Europe and North America (Marsh, 1889; Estes, 1969; Langstrong, 1975; Breithaupt, 1982; Brinkman, 1990; Grandstaff et al., 1992; Poyato-Ariza et al., 1999; Berreteaga et al., 2011; Becker et al., 2010; Brinkman et al., 2014; Pereda-Suberbiola et al., 2015; Marmi et al., 2016). Both phyllodontid and perciform taxa collected in the southern Pyrenees suggest biogeographical affinities with North American species. Phyllodontids and perciforms were active swimmers that could have easily crossed the Atlantic Ocean.

6. Conclusions

Chondrichthyan and osteichthyan remains were recovered from eight new sites within the Tremp Formation. These outcrops represent transitional to continental environments, including coastal lagoons, estuaries, mudflats, fluvial channels and floodplains. These sites have yielded a diverse ichthyofauna including both marine and freshwater taxa, probably promoted by the diversity of habitats. The chondrichthyan assemblage is poor and the basal neopterygian composition is similar to other Maastrichtian sites of Europe, but

Fig. 8. (A) Ichthyofauna of the southern Pyrenees represented in different trophic guilds. Modified from Cavin et al. (2015). (B) Relative abundances of trophic guilds per locality: Fumanya (n = 34), Els Nerets (n = 12), Serrat del Rostiar-1 (n = 5), Camí del Soldat (n = 5), Molí del Baró-1 (n = 3), Fontllonga-6 (n = 142) and L'Espinau (n = 194). Serrat del Pelleu (n = 1) is not represented.

teleosteans are better represented in the Maastrichtian of the southern Pyrenees. Among them, at least three different phyllodontids, two possible osteoglossids, perciforms and cypriniforms were recovered. These represent the oldest evidence of osteoglossids and perciforms in Europe, as well as the oldest record of cypriniforms worldwide. Our data indicate that teleosteans became dominant ichthyofaunas during the late Maastrichtian, being present in all the trophic guilds. From a palaeobiogeographical point of view, the Maastrichtian ichthyofauna of the southern Pyrenees includes cosmopolitan and peri-Tethyan non-teleostean neopterygians, and other fauna with both Asian affinities (batoids) and North American affinities (anacoracids, aspidorhynchids and some teleostean groups).

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SUPPLEMENTARY MATERIAL

Appendix 1. Systematic palaeontology.

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Division NEOSELACHII Compagno, 1977
Subdivision SELACHII (*sensu* Nelson, 2006)
Superorder GALEOMORPHII Compagno, 1973
Order LAMNIFORMES Berg, 1958
Family ANACORACIDAE Casier, 1947
Anacoracidae indet.

Fig. 2A-D
Material: One tooth (tooth-morphotype 1: MCD-6760).
Localities: L'Espinau.

Description: Well-preserved partial single tooth. Its general shape resembles that of theropod dinosaurs: it is conical in outline but with a straight apicobasal axis and not posteriorly bended. The crown is mesiodistally narrow, but labiolingually thick and slightly compressed (but not as strongly as theropod teeth), showing an anterior serrated carina (Fig. 2A-B). The serrations of the cutting edge are strong, conspicuous and homogeneous in shape and size, but they are absent on the posterior carina (Fig. 2C-D). The apex is wide and blunt, and denticles disappear towards to the apex. The root is partially preserved, especially beneath the posterior margin of the crown, forming a nearly straight angle with the posterior carinae.

Discussion: The blunt and straight axis, the low lateral compression and the presence of the laterally expanded root prevent to refer this specimen to any archosaur taxon. Selachian teeth with similar morphology were frequently recovered from geographically and chronologically close sites. For instance, several *Squalicorax* morphotypes and species were reported from the Maastrichtian localities Quintanilla de la Ojada, Albaina and Southern France (Cappetta & Corral, 1999; Vullo, 2005; Corral et al., 2016). Nevertheless, the preserved part of MCD-6760 is very similar in outline, the narrow subtriangular crown and shape of denticles to the teeth of *Scindocorax* (Figs. 7-9 in Bourdon et al., 2011). Although the assignation to the genus *Scindocorax* could not be totally asserted due to morphological variation and the partial preservation of MCD-6760, its morphology is congruent with a representative of the family Anacoracidae. Ecomorphologically, serrated teeth belong to active predators of medium or large-bodied preys, although scavenger behaviour might occasionally occur.

Subdivision BATOMORPHII Cappetta, 1980 (Batoidea *sensu* Nelson, 2006)
Order MYLIOBATIFORMES Compagno, 1973

Family MYLIOBATIDAE Bonaparte, 1838
Genus *Igdabatis* Cappetta, 1972
Igdabatis indicus Prasad & Cappetta, 1993

Fig. 2K-T

Material: 29 isolated teeth (MCD-6880, MCD-6881, MCD-6902, MCD-6903, MCD-6905, MCD-6908, MCD-6922, IPS-90130, IPS-90137, IPS-90139, IPS-90140, IPS-90146, IPS-90148, IPS-90153, IPS-90154, IPS-90156, IPS-90158, IPS-90159, IPS-90166, IPS-90186, IPS-90187). Tooth-morphotypes 2-5.

Localities: Fontllonga-6, Fumanya Sud.

Description: Elongated teeth with convex lingual and concave labial margins, showing arcuate shape with acute lateral edges in occlusal view. The crown surface is rugose and ornamented by small polygonal pits (Fig. 2L). The middle part of the crown is slightly higher than the lateral ends in mesial or distal view. The labial margin of the crown is slightly sloping and shows faint vertical ridges, whereas the lingual margin bears a rounded bulge (Fig. 2M-Q). The root is polyaulacorhize, being divided in several lobes and grooves of variable width. The two lateral lobes are triangular in shape, whereas the others are rectangular (Fig. 2S). Medial and lateral teeth show significantly different shape. Medial teeth (tooth-morphotype 2) are from 2 to 3 times wider than long, and the different height between the middle and lateral margins is more conspicuous. On some of them, the crown slopes in the lateral ends showing a labio-marginal facet (Fig. 2P-T). Lateral teeth close to the medial series (tooth-morphotype 3) are also wider than long, showing hexagonal or subtrapezoidal shape. The number of lobes and grooves of the root, despite variable, are lower than in the medial teeth (Fig. N-O). The most lateral teeth (tooth-morphotype 4) have elliptical or rounded crown, and the root is divided in only two dissimilar lobes. In these teeth the height of the crown is reduced and does not show a decrease in height at lateral ends (Fig. 2K, M-N). In addition, similar teeth with cuspidate crowns (tooth-morphotype 5) belonging to juvenile specimens were also found in the sample.

Discussion: Elongated and arcuate, but not sigmoidal, medial teeth; higher middle part of the crown; hexagonal and sub-trapezoidal lateral teeth; medial and closer lateral teeth wider than long; crown higher than root; pit-ornamented occlusal surface; well-marked lingual bulge; and polyaulacorhize root with rectangular lobes, are diagnostic characters of *Igdabatis indicus* (Prasad & Cappetta, 1993). This species was originally described as an endemic taxon from the Maastrichtian of India, but later was also reported from several sites in the Tremp Formation (Soler-Gijón & López-Martínez, 1998; Kriwet et al., 2007). Soler-Gijón & López-Martínez (1998) recovered 132 teeth from Fontllonga-6 locality (1 complete, 2 fragmentary medial and 129 lateral teeth). We have recovered 1 complete, 7 fragmentary medial and 19 lateral teeth. Both studies also described teeth from juvenile specimens. In Prasad & Cappetta (1993), the relationship of shape and tooth-position is discussed. Ecomorphologically, *Igdabatis* shows grinding dentition (narrowly imbricated teeth with high crowns and polygonal outline forming a dental plate with a nearly flat surface), characteristic of benthic forms feeding on hard preys with resistant shells (Cappetta, 1987).

Family RHOMBODONTIDAE Cappetta, 1987
Rhombodus ibericus Kriwet, Soler-Gijón & López-Martínez, 2007

Fig. 2E-J
Material: 52 isolated teeth (tooth-morphotype 6: MCD-6882, MCD-6887–6889, MCD-6895, MCD-6897, MCD-6909, MCD-6911– 6913, MCD-6920, MCD-6921, IPS-90127–90129, IPS-90131–90136, IPS-90138, IPS-90143, IPS-90145, IPS-90152, IPS-90157, IPS-90160, IPS-90161, IPS-90163–90165, IPS-90167–90170, IPS-90172–90175, IPS-90177, IPS-90179, IPS-90181, IPS-90183–90185).
Localities: Fontllonga-6, Fumanya Sud.

Description: Small teeth with high crowns, rhombic in outline. The occlusal surface is flat and ornamented with polygonal pits (Fig. 2E-I). The ornamentation extends to the marginolabial face in most specimens and some vertical ridges could be present. The crown bears a prominent U-shaped lingual bulge. The marginolingual face is smooth, but shows a shallow transversal depression above the bulge (Fig. 2H). The root is narrower than the crown, and bilobated (holoaulacorhize). A deep median groove separates the two lobes and shows a central nutritive foramen (Fig. 2J). The studied teeth show a certain range of morphological variation, but this heterodonty does not reach the degree showed by other taxa (i.e., *Igdabatis*).

Discussion: Small but proportionally massive, rhombic crowns; flat occlusal surface ornamented with pits; crowns much higher than roots; U-shaped lingual bulge; smooth marginolabial face; and holoaulacorhize root with central nutritive foramen are diagnostic characters of *Rhombodus ibericus* (Kriwet et al., 2007). This species was erected precisely based on material recovered from Fontllonga-6 locality. For the moment, it is considered an Iberian endemism, but it could be also present in Indian deposits (Prasad & Cappetta, 1993; Soler-Gijón & López-Martínez, 1998; Kriwet et al., 2007). Therefore, its presence would be linked to that of *Igdabatis indicus*. Lateral, very lateral, medial, anterior and posterior teeth were recovered from Fontllonga and Fumanya sites. For details regarding to shape and tooth-position, readers can look up the work authored by Kriwet et al. (2007). Ecomorphologically, *Rhombodus* shows grinding dentition, characteristic of benthic predators feeding on hard preys with resistant shells (Cappetta, 1987).

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Series CHONDROSTEI Müller, 1844 (*sensu* Patterson, 1982)
Chondrostei indet.

Fig. 3A-D, 3K
Material: One nearly complete (MCD-6803) and one fragmentary (MCD-6914) dermal scutes.
Localities: L'Espinau, Fontllonga-6.

Description: Scutes are mediolateral thick bony “scales”. The most complete scute is leaf-shaped in outline. The external (lateral) surface is flattened and ornamented by longitudinal cranio-caudal continuous and anastomosated ridges. The relief formed by the ridges is shiny and covered by ganoine. This ganoine layer does not show tubercles as that of lepisosteid scales. The internal (marginals and medial) surface is formed by a smooth bony plate. In medial side there are two anterior (one dorsal and one ventral) and one median posterior keels for body attachment.

Discussion: Chondrosteans are bony fishes with cartilaginous skeleton, and partially covered by bony scales, also called scutes (Kardong, 2007). Isolated scutes recovered form Late Cretaceous outcrops are often referred to chondrosteans (i.e., Bryant, 1989; Brinkman et al., 2014). The ornamentation of MCD-6803 and MCD-6914 is similar to scutes of *Gyrolepis* (Cuny et al., 1994; Lakin et al., 2016) and differs from those of Acipenseriformes (Hilton & Grande, 2006; Nelson, 2006; Kardong, 2007; Elvira et al., 2015). However, *Gyrolepis* is a Triassic chondrostean, and we do not dare to report youngest chronological range based on fragmentary scales. Nevertheless, MCD-6803 and MCD-6914 are congruent with family Palaeoniscidae, which ranges from the Silurian to the Cretaceous (Mäars, 2001; Sepkoski, 2002).

Series NEOPTERYGII Reagan, 1923
Superdivision HOLOSTEI Müller, 1844 (*sensu* Grande, 2010)
Division GINGLYMODII Cope, 1872 (*sensu* López-Arbarello, 2012)
Order LEPISOSTEIFORMES Hay, 1929 (*sensu* López-Arbarello, 2012)
Family LEPISOSTEIDAE Cuvier, 1825
Genus *Atractosteus* Rafinesque, 1820
Atractosteus sp.

Fig. 3E-J, 3L-M, 4A

Material: 29 Fragmentary scales (MCD-6758, MCD-6767, MCD-6768, MCD-6783, MCD-6786, MCD-6801, MCD-6804, MCD-6805, MCD-6824, MCD-6825, MCD-6839, MCD-6848, MCD-6864, MCD-6919, MCD-6924, MCD-6925), 3 hemitrichia (MCD-6794, MCD-6837), 13 isolated teeth (tooth-morphotype 7: MCD-6788, MCD-6802, MCD-6806, MCD-6844).

Localities: Serrat del Rostiar, L’Espinau, Camí del Soldat, Fontllonga-6.

Description: Material referred to *Atractosteus* includes teeth and scales. Teeth are high and conical in shape, very slightly bended lingually, with a translucent cap of acrodine on the tip. Unlike the acrodine tip, the tooth enamel is dark and opaque, ornamented by longitudinal ridges. Teeth are circular in cross-section. The base is not constricted, being the thickest part of the tooth, which is getting narrower to the apex (Fig. 3G-H). The plicidentine can be seen in the external surface as the ridges of the enamel, from the base towards the apex. These ridges disappear at half height where the acrodine cap begins. Based on the size and apical curvature, these teeth could be part of the outer tooth-row consisting in small conical teeth.

Several ganoid scales were also present in the studied material. They are flattened, mostly rhomboid or drop-shaped in outline and blackish in colour (Fig. E-F). The scales are composed by a thick bony base covered with an external shiny layer of ganoine. On some of them a haft-like, anterodorsal process is preserved, which attaches the main portion of the scale to the body of the gar. There is a thin margin around the ganoine-covering, where the bony base of the scale does not bear ganoine. Although the scales are fragmentary, they vary in shape because they covered different parts of the body. For instance, there are scales coming from the middle-midline (MCD-6801, MCD-6824, MCD-6864), posterior-midline (MCD-6758, MCD-6825) and posterior-?ventral (MCD-6767, MCD-6848) parts of the body, as well as others too fragmentary to determinate their in-life position.
Hemitrichia are modified scales forming lepidotrichia (the dermal supporting elements (rays) in the fins). Each lepidotrichium is formed by two juxtaposed hemitrichia. The recovered hemitrichia are stout rectangular elements ornamented by three transversal ganoid ridges (Fig. L-M).

Discussion: Similar teeth and ganoid scales were published by Sauvage (1897-98), Cavin (1999), Grigorescu et al. (1999) and Szabó et al. (2016a). Lepisosteids are characterized by a set of synapomorphies (Wiley, 1976), among which the presence of opisthocoelous vertebrae, plicidentine teeth, and ganoid diamond-like scales are the most striking. Ganoid scales are typical of Ginglymodii (*sensu* López-Arbarello, 2012), not especially of lepisosteids. However, Gayet & Meunier (1986, 2001) and Gayet et al. (2002) pointed out that the layout and size of the ganoine tubercles are diagnostic of lepisosteid genera. All the scales were pictured under scanning electron microscope, and their tubercles were measured in size and distance to each other (Fig. 4A; Table S1). Comparison with other lepisosteid scales indicates that the microornamentation in the former scales and hemitrichiae is close to *Atractosteus* (Fig. 4C). Concerning teeth, plicidentine structure is diagnostic of Lepisosteidae, without closer taxonomic information (see discussion about indeterminate lepisosteids below). However, in the case of teeth from Espinau and Camí del Soldat localities, as no other lepisosteid taxa are present, we tentatively refer them to small teeth of the secondary row of *Atractosteus*, following the most parsimonious reasoning.

Genus *Lepisosteus* Lacépède, 1803
Lepisosteus sp.

Fig. 4B
Material: One fragmentary scale (MCD-6755).
Localities: Serrat del Rostiar.

Description: Material confidently referred to *Lepisosteus* includes only one fragmentary scale. Like those referred to *Atractosteus*, the scales seems to be rhomboid or diamond-shaped without morphological differences to the former scales of *Atractosteus*. These scales are also composed of a thick basal bony plate and covered by an external ganoine layer. However, the tubercles of ganoine on the scales of *Lepisosteus* are smaller and more distant from each other (Fig. 4B; Table S1).

Discussion: As other authors suggested (Gayet & Meunier, 1986, 2001; Gayet et al., 2002), generic and specific determination of lepisosteid scales could be stated by scanning electron observations. The scale was pictured under scanning electron microscope, and their tubercles were measured in size and distance to each other (Fig. 4B; Table S1). The results of comparison with other lepisosteid scales suggested that the microornamentation of MCD-6755 is close to *Lepisosteus* (Fig. 4C).

Lepisosteidae indet.

Fig. 3G-H

Material: Nine teeth (tooth-morphotype 7: MCD-6843, MCD-6865, MCD-6866, MCD-6900, MCD-6907) and 54 fragmentary scales (MCD-6870–6879, MCD-6885, MCD-6886, MCD-6904, MCD-6910, MCD-6915, MCD-6916, MCD-6918, MCD-6926).

Localities: Serrat del Pelleu, Fontllonga-6.

Description: Teeth and scales identical to those previously described for *Atractosteus*. Teeth with simple, pointed, conical tip. The teeth reach their maximal thickness at their base, and they are getting narrow apicobasally. A visible, longitudinal striation runs towards on the teeth (this striation is the external expression of the plicidentine tooth structure). These striae disappear around the half-high of the tooth. The tooth enamel is mostly dark (brownish or black), but the acrodine tip is bright and translucent.

Discussion: Teeth with plicidentine structure are diagnostic of Lepisosteidae, but no closer determination is possible based on isolated teeth. Teeth of gars arrange in two rows, a primary tooth-row of larger fangs and a secondary row formed by small conical teeth similar in size, laterally (externally) placed to the former. Their presence could be referred to the tribe Lepisosteini (Grande, 2010). Gars have a conservative structure and morphology in dentition, showing heterodonty between the different rows, but not in position within the row. Fangs are also taxonomically informative. The fangs of genus *Atractosteus* display a characteristic lanceolated arrow-shaped tip, whereas fangs of *Lepisosteus* are large, sharp and proportionally higher and narrower than those of the external row. All the recovered teeth (including those referred to *Atractosteus*) undoubtedly belong to the secondary tooth-row. The absence of the larger tooth could be explained by taphonomical bias: while a gar has several hundreds of teeth in the outer row, the inner row is made up only by a few dozens of fangs.

Scales also resemble in shape to those described above for *Atractosteus* and *Lepisosteus*, however, they are too fragmentary, worn and/or digested to observe their tubercles. Without tubercles, no other diagnostic character of the scales could distinguish the lepisosteid genera. Despite seven scales from Fontllonga-6 site show *Atractosteus* morphology, the worn ones summarize 54 remains. Therefore we considered risky to refer all the Fontllonga material (including eight teeth: MCD-6865, MCD-6866, MCD-6900, MCD-6907) to *Atractosteus*, because both genera could be present in the same site, as found in Serrat del Rostiar. Additionally, as no more diagnostic remains were found in Serrat del Pelleu locality, we are only able to refer MCD-6843 to an indeterminate lepisosteid or lepisosteine. Ecomorphologically, lepisosteid teeth are typical of piscivorous fishes, but they also prey birds, turtles and small mammals as corroborated by the habits of extant taxa, like *Lepisosteus osseus* Linnaeus 1758 and *Atractosteus spatula* Lacépède 1803 (Grande, 2010).

Order SEMIONOTIFORMES Woodward, 1890 (*sensu* López-Arbarello, 2012)
?Family MACROSEMIIDAE Thiollière, 1858 (*sensu* López-Arbarello, 2012)
?Macrosemiidae indet.

Fig. 3N-P

Material: 22 teeth (tooth-morphotype 8: MCD-6765, MCD-6777, MCD-6830, MCD-6869, MCD-6884, MCD-6893, MCD-6917).

Localities: L'Espinau, Fontllonga-6.

Description: Low and bulky teeth with a slight constriction at the base and circular cross-section. The occlusal surface is rounded and smooth, lacking ornamentation and carinae, but bears a central papilla in some unworn specimens (Fig. 3N-O). Their enamel is opaque and shiny. In basal view, there is a well-marked small or medium-sized foramen. Dentine surface is relatively wide and nearly smooth or bearing very fine transversal ridges whereas there is only a thin layer of enamel (Fig. 3P).

Discussion: These "button-like" teeth were traditionally referred to oral teeth of *Lepidotes* (i.e., Estes & Sanchíz, 1982; Buscalioni et al., 2008; Cavin et al., 2010, 2015; Cuny et al., 2010a, b; Forey et al., 2011). However, this taxon was recently splitted into several genera within the orders Lepisosteiformes (*Scheenstia,* and *Lepidotes* sensu stricto) and Semionotiformes (*Callipurbeckia*). All these genera, as well as *Macrosemimimus* and other semionotiforms, show strong or moderate tritorial dentition as adaptation to a durophagous diet (Jain 1983; López-Arbarello, 2012; Schröder et al., 2012). Therefore, these features are not taxonomically significant. However the genus *Lepidotes* was restricted to the Early Jurassic and the genus *Scheenstia* (or "*Lepidotes*" before its review) is only know from the Late Jurassic to the Early Cretaceous (Jain & Robinson, 1963; Estes & Sanchíz, 1982; Buscalioni et al., 2008; López-Arbarello & Sferco, 2011; López-Arbarello, 2012; Sweetman et al., 2014; Pouech et al., 2015). Thus, we could tentatively refer this morphotype to a semionotiform taxa. Among Semionotiformes, the family Macrosemiidae is the only confidently reported in the Upper Cretaceous (López-Arbarello, 2012). Ecomorphologically, teeth with similar width and height are named tritorial, and are typical of fishes with light durophagous diets (e.g., crustaceans) (Buscalioni et al., 2008).

Division HALECOMORPHI Cope, 1872 (*sensu* Grande & Bemis, 1998)
Order AMIIFORMES Hay, 1929 (*sensu* Grande & Bemis, 1998)
Family AMIIDAE Bonaparte, 1838
Amiidae indet.

Fig. 3Q

Material: A coronoid element with teeth in situ (tooth-morphotype 9: MCD-6799) and one isolated teeth (MCD-6857).

Localities: L'Espinau, Els Nerets.

Description: MCD-6799 is a coronoid fragment bearing two rows of small pointed styliform teeth (Fig. 3Q). 'Styliform' is the term used to describe higher than wider teeth, opposite to 'tritorial'. The teeth are mostly straight with shiny and translucent crown and circular in cross-section. The teeth lack any kind of ornamentation, striations or carinae, on the base and the tip. MCD-6857 is an isolated tooth with similar shape, but has lost its apical acrodine cap.

Discussion: Similar styliform teeth were referred to Amiidae when compared with material from other geographically close Cretaceous sites (Grande & Bemis, 1998; Berreteaga et al., 2011; Sweetman et al., 2014). Isolated tooth remains of amiids are hard to identify at low taxonomic rank, because tooth morphology of amiid fishes could vary in the in-life position (see Grande & Bemis, 1998). Amiiform teeth resemble those of lepisosteids in its conical shape and bearing a translucent tip. However, amiiform teeth do not show plicidentine structure, and the acrodine cap is proportionally larger than in lepisosteids. The tooth bearing bone shows some diagnostic characters of the coronoid elements. It is flattened dorsoventrally, whereas the tooth bearing part of the dentary is weakly flattened mediolaterally, and that of the maxilla is circular in cross section. In addition, the teeth on the dentary and the maxilla are arranged in one row, but the coronoid elements bear several rows of teeth (Grande & Bemis, 1998). Ecomorphologically, amiid teeth are typical of fishes with ichthyophagous diet and predatory habits (Grande & Bemis, 1998; Poyato-Ariza & Martín-Abad, 2013). The extant *Amia calva* Linnaeus 1766 is a voracious predator, which feeds on other fishes, amphibians, crustaceans and insects (Etnier & Starnes, 1993; Cavin et al., 2015).

Family CATURIDAE Owen, 1860
Genus *Caturus* Agassiz, 1843
cf. *Caturus* sp.

Fig. 3R-S

Material: 9 isolated teeth (tooth-morphotype 10: MCD-6769, MCD-6812, MCD-6823, MCD-6826).

Localities: L'Espinau.

Description: Narrow styliform teeth with lanceolate, high and pointed crown. The base is columnar with dark enamel and slight ornamentation consisting of thin parallel striae. The tooth base is circular in cross-section. The crown bears an acrodine cap of smooth and translucent enamel, with two sharp mesial and posterior carinae (Fig. 3R). These carinae are worn or broken in most specimens, lacking their typical spear-shape. The crown is straight to very slightly lingually bent, triangular in cross-section (Fig. 3S).

Discussion: Amiiform fishes have been reported from several Mesozoic localities of Europe, not only as isolated teeth, but also as well preserved, full body fossils (Poyato-Ariza & Martín-Abad, 2013). This tooth morphology refers to the common marine amiiform genus *Caturus*, which was reported from Mesozoic sediments of England (Sweetman et al., 2014), France (Kriwet et al., 1997; Knoll and López-Antoñanzas, 2014; Pouech et al., 2015), Portugal (Poyato-Ariza & Martín-Abad, 2013) and Spain (Buscalioni et al., 2008; Klug & Kriwet, 2012; Kriwet, 2005; Poyato-Ariza & Martín-Abad, 2013). Conical "bicoloured" teeth with striations in the base remind those of Lepisosteidae but, unlike lepisosteids, *Caturus* teeth lacks plicidentine and show an elongated acrodine cap with large carinae. On the contrary, lepisosteid teeth do not bear any carinae running from the acrodine cap toward the crown-base boundary. Ecomorphologically, these teeth refer to ichthyophagous predatory fishes (i.e., Buscalioni et al., 2008; Poyato-Ariza & Martín-Abad, 2013).

Order PYCNODONTIFORMES Berg, 1933
Family PYCNODONTIDAE Agassiz, 1833 (*sensu* Nursall, 1996)
Genus *Coelodus* Heckel, 1854
cf. *Coelodus* sp.

Fig. 3U
Material: Two isolated teeth (tooth-morphotype 11: MCD-6763, MCD-6862).
Localities: L'Espinau, Els Nerets.

Description: Molariform teeth with low oval crown showing a deep central depression. The central depression is smooth. MCD-6763 shows two concentric rows of tubercles with others randomly placed (Fig. 3U). MCD-6862, however, is less rounded than the former; its central depression is bigger and does not show any crenulations around.

Discussion: Coelodus teeth are characterized by the presence of a groove or depression on the crowns, without a central papilla (Poyato-Ariza & Wenz, 2002). These teeth are similar to some published specimens and referred to *Coelodus* (i.e., Buscalioni et al., 2008; Knoll & López-Atoñanzas, 2014; Szabó et al., 2016b), but also show differences to other *Coelodus* teeth (i.e., Poyato-Ariza, 2005). Classification of isolated pycnodontid teeth is often hard to carry out due to the great heterodonty of this group and the absence of diagnostic characters of a complete tooth-plate. Therefore we tentatively referred these specimens to cf. *Coelodus* sp. Our conclusions, however, will be based on all the pycnodontiform morphotypes as a whole. Ecomorphologically, these morphotypes belong to a durophagous fish feeding on hard preys (i.e., bivalves and gastropods) (Poyato-Ariza, 2005; Buscalioni et al., 2008; Poyato-Ariza & Martín-Abad, 2013).

Pycnodontiformes indet.

Fig. 3T
Material: Three flat molariform teeth (tooth-morphotype 12: MCD-6756, MCD-6846, MCD-6883).
Localities: Serrat del Rostiar, Camí del Soldat, Fontllonga-6.

Description: This morphotype comprises molariform teeth with very low, thin and flat crowns. The occlusal surface is smooth. Two of them (MCD-6756, MCD-6846) are rounded to oval in outline, but MCD-6883 is mediolaterally elongated (Fig. 3T).

Discussion: The term 'molariform' is used to refer to this particular morphotype, in which crowns use to be wider than high, without implying any kind of homology with mammalian molars. The use of this term replaces the use of 'durophagous', which refers to function and feeding habits rather than form (Poyato-Ariza, 2005). Molariform teeth are characteristic of Pycnodontiformes (Poyato-Ariza & Wenz, 2002; Poyato-Ariza, 2005), but no closer classification could be possible. Molariform teeth are present on the vomer and prearticular bones of this group, and several molariform morphotypes could be found in the same specimen, so they do not necessarily indicate the presence of two different taxa. Indeed, the overall morphology matches very well with those molariforms present in the prearticular of *Coelodus* (e.g., Szabó et al., 2016b), thus they might belong to the same specimen that those of the former morphotype. Ecomorphologically, this morphotype belongs to hard-durophagous feeders (Poyato-Ariza, 2005; Buscalioni et al., 2008; Poyato-Ariza & Martín-Abad, 2013).

?Pycnodontiformes indet.

Fig. 3V-X
Material: 17 bulky molariform teeth (tooth-morphotype 13: MCD-6762, MCD-6766, MCD-6772, MCD-6781, MCD-6821, MCD-6831, MCD-6894, MCD-6898).
Localities: L'Espinau, Fontllonga-6.

Description: This morphotype is composed by bulky, rounded molariform teeth with low and massive crown (Fig. 3V-X). The crown is smooth and shiny. They are nearly circular in cross-section. In basal view, there is a well-marked basilar foramen rounded by striated dentine. The layers of the dentine and the enamel are thick and well-developed (Fig. 3X).

Discussion: Globular teeth with a well marked basilar foramen surrounded by ridges are referable to paralbuline phyllodontids. However, some specimens bear jaw fragments added rather than being stacked in sets, which prevents to refer them to phyllodontids. This morphotype also differs to the later in the great development of the basilar foramen. In basal view, indeed, these teeth are similar to the semionotiform morphotype. Nearly identical teeth were referred to an indeterminate pycnodontiform by Berreteaga et al. (2011) from the Maastrichtian outcrops of Quintanilla de la Ojada (Burgos, Spain). Following these authors, we tentatively refer this morphotype to a possible pycnodontiform, although we cannot totally reject its belonging to a semionotiform taxon. Ecomorphologically, these morphotype belongs to hard-durophagous feeders (Poyato-Ariza, 2005; Buscalioni et al., 2008; Poyato-Ariza & Martín-Abad, 2013).

Order ASPIDORHYNCHIFORMES Bleeker, 1859 (*sensu* Arratia, 1999)
Family ASPIDORHYNCHIDAE Nicholson & Lydekker, 1889
Genus *Belonostomus* Agassiz, 1843
Belonostomus sp.

Fig. 3Y-Z
Material: Five isolated teeth (MCD-6827, MCD-6845). Tooth-morphotypes 14-15.
Localities: L'Espinau, Camí del Soldat.

Description: Two recovered morphotypes of isolated teeth were referred to *Belonostomus* sp. One of them (tooth-morphotype 14) is composed by a single specimen (MCD-6845; Fig. 3Z). The tooth is styliform, straight, pointed and circular in cross-section. It lacks any type of ornamentation in both base and tip. A conspicuous neck is present on the boundary between the apex and the elongated base. The tip suddenly becomes narrower apically, which makes unique tooth morphology.

The second morphotype (tooth-morphotype 15) comprised several teeth (MCD-6827) with very different morphology respect to the former (Fig. 3Y). It also corresponds to conical styliform teeth, circular in cross-section, but robust and slightly lingually curved. The base shows dark enamel ornamented with thin vertical and parallel ridges which ascend to the neck of the apex. The apex bears a translucent acrodin cap and lacks any carinae. The neck with the acrodin cap shows a labial bump (or lingual bulge) between the shaft of the crown and the acrodine cap in mesial/posterior view.

Discussion: The teeth of *Belonostomus* show two notable similarities to those of gars: ridged bases and acrodin caps. However, gar teeth show plicidentine and lack the labial bump and the lingual bulge in the neck of acrodin cap. In other words, the conical outline of gar teeth is continuous in mesial or posterior view. Nearly identical *Belonostomus* teeth have been reported from the Bathonian and Berriaisan of France (Knoll & López-Antoñanzas, 2014; Pouech et al., 2015; respectively) and from the Barremian of England (Sweetman et al., 2014). The genus *Belonostomus* comprises long-snouted fishes with very different heterodont dentition (Woodward, 1888). Teeth assigned to this genus can be of very different size and shape. Their lower jaw is composed by splenials, dentaries and an unpaired presymphiseal bone (= predentary). Dentary bears a linear series of thin small teeth and splenial bears a cluster of mammiliform teeth, whereas the presymphiseal bone shows a central series of stout conical larger teeth flanked by two rows of small slender teeth in the lateral margins of the bones (Woodward, 1888; Bardack, 1968; Bogan et al., 2011). The medial presymphiseal teeth decrease in size anteriorly and show striated enamel in the shaft with acrodine translucent cap, as well as those from the upper jaw (premaxilla and palatine). The lateral ones are about a quarter size of the medial teeth, and could be straight or posteriorly curved (Bardack, 1968). Therefore, our first morphotype clearly correspond to the small lateral teeth form the presymphiseal bone, whereas the second morphotype might correspond to the larger medial teeth of the presymphiseal or from the upper jaw. Ecomorphologically, both morphotypes correspond to an ichthyophagous fish, well adapted to predatory habits (Bogan et al., 2011).

Subdivision TELEOSTEI Müller, 1846 (*sensu* Arratia, 1999)
Superorder OSTEOGLOSSOMORPHA Greenwood et al., 1966
Order OSTEOGLOSSIFORMES Regan, 1909
Family OSTEOGLOSSIDAE Bonaparte, 1832
Osteoglossidae indet.

Fig. 5A-H

Material: 7 isolated squamulae (MCD-6784, MCD-6790, MCD-6811, MCD-6822, MCD-6838, MCD-6688), 3 teeth (tooth-morphotype 16: MCD-6792, MCD-6798, MCD-6833) and an articulated partial skeleton (IPS-41760).

Localities: L'Espinau, Molí del Baró, Fumanya.

Description: Several small polygonal squamulae were found. Three of them are mediolaterally flattened (MCD-6784, MCD-6811, MCD-6822). The internal (medial) face is smooth delimited by margins forming a high ridge, whereas the lateral side is ornamented by granular tubercles (Fig. 5E-F). Other three squamulae (MCD-6790, MCD-6838) are elongated and thicker, ornamented by transversal ridges in the external side, and smooth in the medial one (Fig. 5G). In turn, MCD-6688 is not ornamented by ridges, but small pits (Fig. 5D). Teeth are large, nearly straight and slight lateromedially compressed. The crowns are blunt and lack ornamentation (Fig. 5H).

IPS-41760 consists of an abdominal body section preserved in articulation. It shows 6 vertebrae in lateral view (Fig. 5A). Their lateral surface is ornamented with three grooves divided by two ridges. The four best preserved vertebrae also show their respective haemal arches (Fig. 5C). One cycloid scale is preserved close to the vertebrae (Fig. 5B). The scale is rounded and bears concentric *circuli* on the periphery ornamented by small crenulations. *Circuli* disappear to the focus, *radii* are absent. Some neural arches, haemal spines and ribs are also preserved, as well as impressions of missing elements.

Discussion: Osteoglossiforms are an order of primitive teleosteans, comprising heavily ossified fishes. Their scales became small bony plates (squamulae) separated from each other by narrow grooves. Close identical squamulae have been referred to several taxa within Osteoglossidae: MCD-6784, MCD-6790, MCD-6811, MCD-6822 and MCD-6838 resemble squamulae referred to *Scleropages* (Taverne et al., 2007) whereas MCD-6688 is similar to those of *Phareodus* (Grande, 1984). Similar teeth are usually referred to osteoglossomorphs (i.e., Li, 1996; Li et al., 1997; Gayet, 1991; Taverne et al., 2007; Brinkman, 2014). Although we consider that the isolated material is not enough diagnostic to make specific assignments, the different scale-morphotypes may suggest two different osteoglossid species in the sampled localities.

The overall morphology of IPS-41760, the shape of the scale, the vertebrae and the strong and robust haemal arches resemble those of osteoglossids (i.e., Li & Wilson, 1996; Li et al., 1997; Taverne & Capasso, 2012; Murray et al., 2016). The sculptured vertebrae are similar to those of *Phareodus* (Li et al., 1997). However, the lack of the final part of the tail prevents to refer this specimen confidently to any specific taxon.

Superorder ELOPOMORPHA Greenwood, Rosen, Weitzman & Myers, 1966
Order ELOPIFORMES Greenwood, Rosen, Weitzman & Myers, 1966
Superfamily ALBULOIDEA Greenwood, Rosen, Weitzman & Myers, 1966
Family PHYLLODONTIDAE Sauvage, 1875 (*sensu* Estes, 1969)
Subfamily PARALBULINAE Estes, 1969
Genus *Paralbula* Blake, 1940
Paralbula sp.

Fig. 5I-P

Material: 36 isolated teeth (tooth-morphotype 17: MCD-6764, MCD-6773, MCD-6778, MCD-6779, MCD-6808, MCD-6814, MCD-6818, MCD-6835, MCD-6847).

Localities: L'Espinau, Camí del Soldat.

Description: Hemispherical and undistorted small teeth. They are globular in lateral view, delimited by a thin margin protruding around the base of the crown, whereas they are totally circular in occlusal view (Fig. 5I-K). The enamel is smooth in most of the teeth, or shows a central papilla and/or a circular row of faint tubercles in the unworn specimens. Different wearing stages were found, from totally unworn to smooth worn specimens (Fig. 5L-P). In basal view, there is a well-developed basilar foramen bounded by strong striated borders and a thick enamel layer (Fig. 5K).

Discussion: Family Phyllodontidae is characterized by tooth plates with multiple superposed sets of replacement teeth, called phyllodont dentition. Phyllodontidae includes the subfamilies Phyllodontinae and Paralbulinae (Estes, 1969). Hemispherical, globular or bulbous teeth, and a well-developed basilar foramen are characteristic of paralbulines, whereas phyllodontine teeth are flattened, with smooth basilar surface and directly successional, placed in compact stacks (Estes, 1969). According to Estes (1969), Paralbulinae includes the genera *Paralbula* and *Pseudoegertonia*. Teeth of *Paralbula* present similar size, characterized by hemispherical shape, thick enamel and being undistorted by growth pressures. Teeth from L'Espinau and Camí del Soldat show diagnostic characters of *Paralbula.* Furthermore, they seem more similar to *Paralbula marylandica* Blake 1940 than *P. casei* Estes 1969*,* in having smooth or sparsely punctuated tooth surface unlike the coarsely ornamented teeth of *P. casei* (Estes, 1969). However, since no complete or partial plate has been recovered, we prefer to refer the isolated teeth to *Paralbula* sp.

Genus *Pseudoegertonia* Dartevelle & Casier, 1949
Pseudoegertonia granulosus (Arambourg, 1952)

Fig. 5Q-R

Material: 26 isolated teeth (tooth-morphotype 18: MCD-6761, MCD-6770, MCD-6771, MCD-6780, MCD-6782, MCD-6813, MCD-6820, MCD-6836).

Localities: L'Espinau.

Description: Large and bulbous teeth, but flatter than hemispheric. They also show a fine margin protruding around the base of the crown. The enamel is ornamented by faint granular pattern (Fig. 5Q). In basal view, there is a large and poorly-marked basilar foramen as well as a thick layer of enamel (Fig. 5R).

Discussion: Bulbous teeth with a well-developed basilar foramen are characteristic of paralbulines. *Pseudoegertonia* is characterized by large-sized bulbous teeth with thick enamel and distorted by growth pressures. The basilar foramen is not as well-marked as in *Paralbula*. Teeth from L'Espinau show diagnostic characters of *Pseudoegertonia*. Two species of *Pseudoegertonia* show ornamented occlusal surface: the Cretaceous *P. granulosus* (Arambourg, 1952) and the Palaeocene *Pseudoegertonia straeleni* Dartevelle & Casier, 1949; although the later could be a junior synonym (Estes, 1969; Becker et al., 2010). Specimens from L'Espinau show similar morphology to *Pseudoegertonia* specimens from the Maastrichtian-Palaeocene outcrops of Arkansas (Becker et al., 2010).

Paralbulinae indet.

Fig. 5P

Material: 28 isolated teeth (tooth-morphotype 19: MCD-6815–6817, MCD-6819, MCD-6829, MCD-6834, MCD-6901).

Localities: L'Espinau, Fontllonga-6.

Description: Hemispherical undistorted teeth. The enamel is completely smooth and some specimens show wear facets (Fig. 5P). They also show a fine margin protruding around the base of the crown. In basal view, there is a large and well-marked basilar foramen as well as a thick enamel layer, similar to teeth of the morphotype 17 (Fig. 5K).

Discussion: Hemispherical, globular or bulbous teeth with a well-developed basilar foramen are characteristic of paralbulines. Undistorted teeth suggest *Paralbula* affinities. In basal view there are no differences from the morphotype 17 referred to *Paralbula*, and these teeth match well as the most worn stage of the *Paralbula* teeth in occlusal view (Fig. 5L-P). However, no wear facets have been reported in *Paralbula*, because teeth were probably replaced before a complete wear (Estes, 1969). Ecomorphologically, all the morphotypes referred to phyllodontids correspond to durophagous feeders, preying on hard-shelled invertebrates (Estes, 1969).

Subfamily PHYLLODONTINAE Sauvage, 1875 *sensu* Estes, 1969
Genus *Phyllodus* Agassiz, 1843
cf. *Phyllodus* sp.

Fig. 5S-U

Material: 12 isolated teeth (tooth-morphotype 20: MCD-6774, MCD-6789, MCD-6809, MCD-6828).

Localities: L'Espinau.

Description: Large teeth with massive and flat low crown. They are subcircular in occlusal view, but flat and elongated in lateral view. Their diameter in occlusal view is three or four times their occluso-basal length (Fig. 5U). The enamel is ornamented with fine pointed tubercles in some unworn teeth or shallow small ridges in other more worn ones (Fig. 5S). There is no protruding margin around the base. In basal view, no basilar foramen is present. The pulp surface is completely smooth (Fig. 5T).

Discussion: In phyllodontines, the replacement teeth grow in compacted stacks causing flattened teeth, loss of the striated basilar foramen and the surrounding bony matrix. Teeth of *Egertonia* are regularly convex and less flattened than *Phyllodus* (Estes, 1969). Large flat teeth recovered from L'Espinau locality are very similar to those placed in a complete tooth plate from the upper Maastrichtian beds of Albaina (Spain) and referred to *Phyllodus* (Poyato-Ariza et al., 1999), as well as that from Laño (Spain) referred with caution this genus (Pereda-Suberbiola et al., 2015). Ecomorphologically, the morphotype referred to *Phyllodus* corresponds to durophagous fish, feeding on hard-shelled invertebrates (Estes, 1969).

Superorder OSTARIOPHYSI Jordan & Evermann 1896
Order CYPRINIFORMES Bleeker 1859
cf. Cypriniformes indet.

Fig. 5V-X

Material: Four fragmentary branchial arches (MCD-6757, MCD-6791, MCD-6793, MCD-6807) and 16 isolated teeth (tooth-morphotype 21: MCD-6754, MCD-6796, MCD-6810, MCD-6851, MCD-6852, MCD-6854–6856, MCD-6858–6861, MCD-6863).

Localities: Serrat del Rostiar, L'Espinau, Els Nerets.

Description: The fragmentary branchial arches are elongated bones D-shaped in cross section. The medial side is flat bearing small circular pits surrounded by outstanding margins (Fig. 5V). The lateral side is more or less convex, depending of the in-life position. The isolated pharyngeal teeth are nearly conical, slightly compressed laterally. The crown is mainly straight and bears an apical papilla posteriorly directed (Fig. 5W, X).

Discussion: Fishes possessing this kind of bony element belong to the superorder Ostariophysi and this branchial system is called the Weberian apparatus. The morphology of the recovered teeth is closely similar to the order Cypriniformes (Doadrio, 1990; Fink & Fink, 1996; Miranda & Escala, 2003). According to Fink & Fink (1996), based on records from Europe, Asia, Africa, and South America, the stratigraphically oldest known ostariophyseans correspond to the Gonorynchiformes (Early Cretaceous), followed by the Characiformes and Siluriformes (Late Cretaceous) and ending with Cypriniformes (Early Cenozoic) and Gymnotiformes (Late Cenozoic). Phylogenetically, gonorynchiforms are the most basal members of the ostariophyseans, but characiforms and siluriforms are more advanced than cypriniforms, even though their fossil records are stratigraphically older. This hypothesis was accepted and corroborated by Nelson (2006) and Alves-Gomes (2010). This disagreement between the fossil record and the phylogenetic relationships demonstrates that the fossil record of cypriniforms is incomplete and the information of the oldest fossil forms is missing. Therefore, according to the phylogenetic hypothesis, we should expect that Cypriniformes would have arisen in the Cretaceous and they constitute a ghost lineage during this period. According to Doadrio (1990) or Miranda & Escala (2003), the taxonomical identification of Cypriniformes based on the pharyngeal system is possible if the complete branchial or pharyngeal arch is analyzed. Identifications at family or genus level are not possible using isolated teeth. Even so, the morphology of the fossil specimens from Serrat del Rostiar, L'Espinau, and Els Nerets localities resemble those of Cyprinidae. Although the records of cyprinids across the Cenozoic are commonly known, the age of the earliest cyprinids is difficult to document precisely, because of their occurrence in freshwater environments. The Cyprinidae family first appeared in the Eocene epoch and the oldest record is *Parabarbus* sp. from the lower Eocene of Kazakhstan (Sytchevskaya, 1986). According to Böhme & Ilg (2003), the first fossil cyprinids of Europe and North Africa were discovered in Early Oligocene sediments. Doadrio (1990) and De la Peña (1995) mentioned the cyprinids from the Tertiary of the Iberian Peninsula as well. However, as pointed above, we do not dare to report first occurrence of cyprinids based on isolated teeth, so the attribution to Cypriniformes is the most accurate identification which can be given for the moment. Ecomorphologically, it is possible to include these fossil specimens in a filter-feeder or microphagous fluvio-lacustrine ecomorphotype.

Unranked EUTELEOSTEI Rosen 1973
Unranked ACANTHOMORPHA Rosen 1973
Superorder PERCOMORPHA Johnson & Patterson, 1993
Order PERCIFORMES Günther, 1880
Family SCIAENIDAE Cuvier, 1928
Sciaenidae indet.

Fig. 5Y-Z
Material: 4 isolated teeth (tooth-morphotype 22: MCD-6775, MCD-6776, MCD-6840).
Localities: L'Espinau.

Description: Molariform teeth with small subconical crown. In lateral view, the crown is low and wide at the base, with pending margins and flat occlusal surface (Fig. 5Z). The enamel is smooth in the margins, but ornamented in unworn specimens. The occlusal surface bears a central apical concavity surrounded by several papillae forming a ring (Fig. 5Y).

Discussion: These teeth show the same morphology than *Fisherichthys folmeri* Weems, 1999. Cicimurri & Knight (2009) reported isolated diagnostic teeth of *Fisherichthys* from the

Lower Eocene of South Carolina (USA), near of the Paleocene-Eocene boundary. However, the large chronological gap prevents us to refer these specimens to the same taxon, giving the oldest record of *Fisherichthys* based on isolated teeth. According to Cicimurri & Knight (2009), the morphology of these teeth is unique, but we prefer to refer the Cretaceous specimens to an indeterminate sciaenid fish pending more fossil evidences. Sciaenids have been reported from Upper Cretaceous outcrops of North America (i.e., *Platacodon nanus* Marsh, 1889) (Marsh, 1889; Langstron, 1975; Armstrong-Ziegler, 1978; Breithaupt, 1982; Grandstaff et al., 1992; Brinkman et al., 2014), nevertheless, their tooth morphology is completely different to *Fisherichthys* and teeth from L'Espinau. Cicimurri & Knight (2009) also remark that no comparable material has been reported from Europe or Africa, despite vertebrate assemblages are generally similar through the North Atlantic, pointing three hypotheses: (1) it is an endemic taxon, (2) its absence is due to a methodological or taphonomical bias because of its small size, (3) or it has not been recognized as a distinct taxon because worn teeth could resemble those of phyllodontids. Our data might suggest the third hypothesis. Additionally, Marmi et al. (2016) report two ctenoid scales referred to Percomorpha from the Maastrichtian beds of the Molí del Baró-1 site (MCD-5540 and MCD-5541). As neither more diagnostic remains of sciaenids nor other percomorph taxon was recovered from Molí del Baró-1 or any other site in the Tremp Formation, we parsimoniously assume that scales and teeth could belong to the same taxon.

Fisherichthys comes from brackish-water environments with emergent swamps, adapted to predate on externally slippery hard preys, like squids or holothurians (Weems, 1999; Cicimurri & Knight, 2009 and references therein). Therefore, ecomorphologically this morphotype corresponds to soft durophagous feeders.

Acanthomorpha indet.

Fig. 6A
Material: Four isolated vertebrae (MCD-6841).
Localities: L'Espinau.

Description: Centra of acanthomorph fishes are trapezoid to wedge-like in dorsoventral view. The zygapophyseal articulations are well-developed, the rib articulation surfaces are positioned laterally on the neural arch (rather than low on the centrum). Only two vertebrae are partially preserved, however, with a diagnostic dorsoventral contour. These centrum is posteriorly wider than anteriorly, which feature gives a trapezoid (or hourglass-like) dorsoventral contour (Fig. 6A). The large zygapophyses are clearly visible. The presence, size and shape of the zygapophyses refer the specimen as a possible precaudal centrum. The dorsal surface and the preserved portions of the lateral surfaces are made up by a network of bone-fibers. A mid-dorsal pit is present. The other remains are less preserved in portion and quality, and they do not give any additional features.

Discussion: Comparable acanthomorph vertebrae have been published by Brinkman & Neuman (2002), Neuman & Brinkman (2005), Larson et al. (2010), Brinkman et al. (2014).

Acanthomorph fishes represent more than 60% of all extant taxa, their oldest record goes back to the Cenomanian (Chen et al., 2003). Due to their fragmentary nature, these vertebrae do not allow a closer taxonomic determination. Nevertheless, as no other acanthomorph taxon was recovered from L'Espinau site, we parsimoniously assume that these four vertebrae might belong to the sciaenid taxon described above.

Teleosteii indet.

Fig. 6B-J
Material: Two isolated vertebrae (MCD-6795, MCD-6797), one isolated tooth (tooth-morphotype 23: MCD-6785), one fragmentary fin ray (MCD-6759), one cleithrum (MCD-6849) and one cycloid scale (MCD-6832).
Localities: L'Espinau, Camí del Soldat.

Description: The vertebrae are very fragmentary. They show amphicoelous morphology, which is visible on the cross-section (Fig. 6F). Their outer surface is made up by a network of bone-fibers (Fig. 6E). The overall morphology of MCD-6849 resembles a probable cleithrum. The bone is elongated and flat, expanded in both edges (Fig. 6D). But most of the borders are broken around (Fig. 6H). MCD-6785 is a conical tooth, labiolongually flattened with the apex oriented posteriorly (Fig. 6J). MCD-6832 is a fish scale of the cycloid type (Fig. 6B-C).

Discussion: All the indeterminate teleostean remains are undiagnostic or too fragmentary to determinate. The outer vertebral surface is similar those of the acanthomorphs. However, this network is less thick on these indeterminate teleostean vertebrae. Elopomorph centra with similar structure have been reported by Brinkman, 2014) and Brinkman et al. (2013). This group is widely known from Late Cretaceous sediments. The cleithrum could be diagnostic if it was complete, but its broken outline prevents a reliable classification. Moreover, cycloid scales are broadly displayed by most teleost taxa (Nelson, 2006; Kardong, 2007).

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SUPPLEMENTARY MATERIAL

Appendix 2. Measurements of the lepisosteid scales.

	Average tubercle diameter	Average inter-tubercular distance
MCD-6755	4.79 µm (n=173)	3.3 µm (n=386)
MCD-6758	7.47 µm (n=131)	2.7 µm (n=284)
MCD-6768	7.27 µm (n=41)	2 µm (n=84)
MCD-6767	7.8 µm (n=291)	2.17 µm (n=753)
MCD-6801	7.56 µm (n=97)	1.25 µm (n=222)
MCD-6805	8.08 µm (n=65)	1.48 µm (n=121)
MCD-6837	6.53 µm (n=36)	2 µm (n=63)
MCD-6839	6.82 µm (n=45)	2.99 µm (n=83)
MCD-6848	5.6 µm (n=46)	1.83 µm (n=100)
MCD-6864	7.23 µm (n=74)	1.83 µm (n=183)
MCD-6925	8.13 µm (n=47)	1.52 µm (n=112)
MCD-6919	8.22 µm (n=67)	1.46 µm (n=169)
MCD-6924	7.24 µm (n=46)	1.48 µm (n=109)

Table S1: Measurements of size and distance between the ganoid tubercles on the lepisosteid scales. Specimens are plotted in Fig. 4.

SUPPLEMENTARY MATERIAL

Appendix 3. Chi-square analyses.

Chi-square 1: Teleostean-basal neopterygian dominance in the early and late Maastrichtian, regardless of the palaeoenvironment and the geological unit of respective localities belong.

Test 1a: *Without chondrichthyes and chondrosteans*. The aim of this test was to elucidate if teleosteans are significantly dominant in the late Maastrichtian localities from northeastern Iberia. For this reason, we summarized teleosteans and basal neopterygians from the early Maastrichtian (Fumanya, Els Nerets, Serrat del Rostiar-1 and Fontllonga-6) as well as in the late Maastrichtian localities (L'Espinau, Serrat del Pelleu, Molí del Baró-1 and Camí del Soldat). Numbers are counts of fossils (i.e., maximum number of individuals).

	'Holosteans'	Teleosteans
early Maast	95	16
late Maast	74	134

Chi-square statistics	$\chi^2=72.659$
Degrees of freedom	$\nu=1$
Probability of no association	$p=1.54x10^{-17}$
Monte Carlo permutation	p=0.0001

Test 1b: *With all the fish taxa*. The test was carried out taking into account chondrichthyes and chondrosteans. In this case, we repeated the analysis in order to test the same hypothesis as in the later analysis. Numbers are counts of fossils (i.e., maximum number of individuals).

	Non-teleosts	Teleosteans
early Maast	177	16
late Maast	76	134

Chi-square statistics	$\chi^2=132.67$
Degrees of freedom	$\nu=1$
Probability of no association	$p=1.07x10^{-30}$
Monte Carlo permutation	p=0.0001

Chi-square 2: Teleostean-basal neopterygian dominance in the 'grey' and 'lower red' units of the Tremp Formation, regardless the palaeoenvironment and the age of their respective localities.

Test 2a: *Without chondrichthyes and chondrosteans*. In this case, we evaluated if the samples from the 'lower red' and the 'grey' units are significantly different. We summarized teleosteans and basal neopterygians in the samples from the 'grey' unit (Fumanya and Els Nerets) and from the 'lower red' unit (Fontllonga-6, Serrat del

Rostiar-1, L'Espinau, Serrat del Pelleu, Molí del Baró-1 and Camí del Soldat). Numbers are counts of fossils (i.e., maximum number of individuals).

	'Holosteans'	Teleosteans
'grey'	2	11
'lower red'	167	139

Chi-square statistics	$\chi^2=7.6885$
Degrees of freedom	$\nu=1$
Probability of no association	p=0.0055575
Monte Carlo permutation	p=0.0093

Test 2b: *With all the fish taxa.* In this case we repeated the analysis including chondrichthyes and chondrosteans in order to test the same hypothesis as in the later analysis. Numbers are counts of fossils (i.e., maximum number of individuals).

	Non-teleosts	Teleosteans
'grey'	35	11
'lower red'	218	139

Chi-square statistics	$\chi^2=3.9356$
Degrees of freedom	$\nu=1$
Probability of no association	p=0.047276
Monte Carlo permutation	p=0.0532

Chi-square 3: Teleostean-basal neopterygian dominance in the continental freshwater and the coastal and brackish lagoonal environments, regardless the geological unit and the age of their respective localities.

Test 3a: *Without chondrichthyes and chondrosteans.* The aim of this test was to elucidate if samples coming from brackish and freshwater environments differ significantly in their teleostean composition. For this reason, we summarized teleosteans and basal neopterygians from the continental freshwater (Els Nerets, Serrat del Rostiar-1, Serrat del Pelleu, Molí del Baró-1 and Camí del Soldat) and the coastal settings (Fumanya, Fontllonga-6 and L'Espinau). Numbers are counts of fossils (i.e., maximum number of individuals).

	'Holosteans'	Teleosteans
Freshwater	10	18
Coastal/ lagoon	159	132

Chi-square statistics	$\chi^2=3.6722$
Degrees of freedom	$\nu=1$
Probability of no association	p=0.055326
Monte Carlo permutation	p=0.0754

Test 3b: *With all the fish taxa.* In this case we repeated the analysis including chondrichthyes and chondrosteans in order to test the same hypothesis as in the later analysis. However, we considered of a more reliable nature the result of the chi-square test without chondrichthyes and chondrosteans (test 3a), since the chondrichthyes

included in this test could suppose an environmental bias because they are restricted to saltwater. Numbers are counts of fossils (i.e., maximum number of individuals).

	Non-teleosts	Teleosteans
Freshwater	10	18
Coastal/ lagoon	243	132

Chi-square statistics	$\chi^2=9.4328$
Degrees of freedom	$\nu=1$
Probability of no association	$p=0.0021314$
Monte Carlo permutation	$p=0.0033$

Chi-square 4: Teleostean dominance in the trophic guilds during the early and late Maastrichtian, regardless the palaeoenvironment and the geological unit of their respective localities.

Test 4a: *Without chondrichthyes and chondrosteans.* In this case we examined if teleosteans were significantly widespread in the trophic guilds of the late Maastrichtian. For this reason, we calculated the abundance (percentages) of teleosteans per guild in the early Maastrichtian (Fumanya, Els Nerets, Serrat del Rostiar-1 and Fontllonga-6) and the late Maastrichtian localities (L'Espinau, Serrat del Pelleu, Molí del Baró-1 and Camí del Soldat). Numbers are percentages (%) of teleosteans within each trophic guild.

	early Maast	late Maast
Piscivores	1.36986301	15.8730159
Soft-duroph.	0	45.4545455
Hard-duroph.	18.75	91.6666667
Filter-feeders	100	100

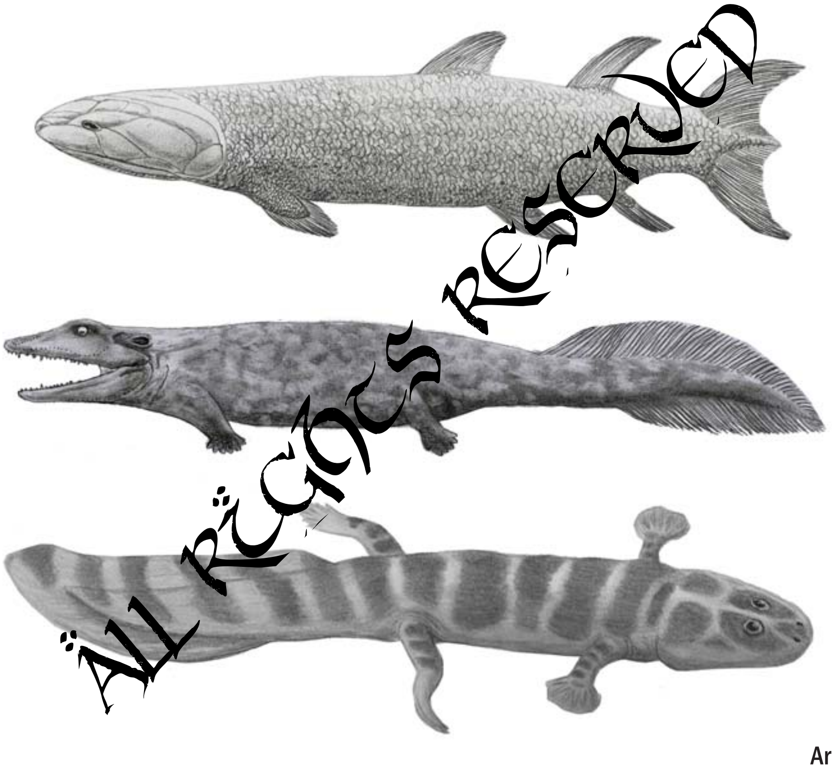
Chi-square statistics	$\chi^2=67.659$
Degrees of freedom	$\nu=3$
Probability of no association	$p=1.35x10^{-14}$
Monte Carlo permutation	$p=0.0001$

Test 4b: *With all the fish taxa.* In this case we repeated the analysis including chondrichthyes and chondrosteans in order to test the same hypothesis as in the later analysis. Numbers are percentages (%) of teleosteans within each trophic guild.

	early Maast	late Maast
Piscivores	1.36986301	15.625
Soft-duroph.	0	45.4545455
Hard-duroph.	3.09278351	91.6666667
Filter-feeders	92.3076923	88.8888889

Chi-square statistics	$\chi^2=96.211$
Degrees of freedom	$\nu=3$
Probability of no association	$p=1.01x10^{-20}$
Monte Carlo permutation	$p=0.0001$

Chapter 6. LATE CRETACEOUS (MAASTRICHTIAN) AMPHIBIANS AND SQUAMATES FROM NORTHEASTERN IBERIA



Art by Josep Marmi

LATE CRETACEOUS (MAASTRICHTIAN) AMPHIBIANS AND SQUAMATES FROM NORTHEASTERN IBERIA

Cretaceous Research, 57, 624-638 (I.F.: 2,196; Q1 2015, Palaeontology).

Mi contribución en este trabajo consistió en la obtención, lavado y triado de muestras durante diversas campañas de campo (2013-2015) en colaboración con diverso voluntariado. Posteriormente realicé la ordenación y clasificación preliminar del material recogido en los yacimientos descritos, elaborando una base de datos completa (Tabla 1). Llevé a cabo la clasificación taxonómica y descripción del material perteneciente a anfibios y escamosos en colaboración con especialistas en dichos taxones (Dr. Hugues Alexandre Blain, IPHES y Dr. Arnau Bolet, ICP, respectivamente), así como la redacción completa del manuscrito y la elaboración de figuras y tablas.

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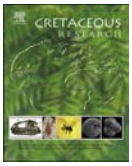

Late Cretaceous (Maastrichtian) amphibians and squamates from northeastern Iberia

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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 fluvio-deltaic, 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

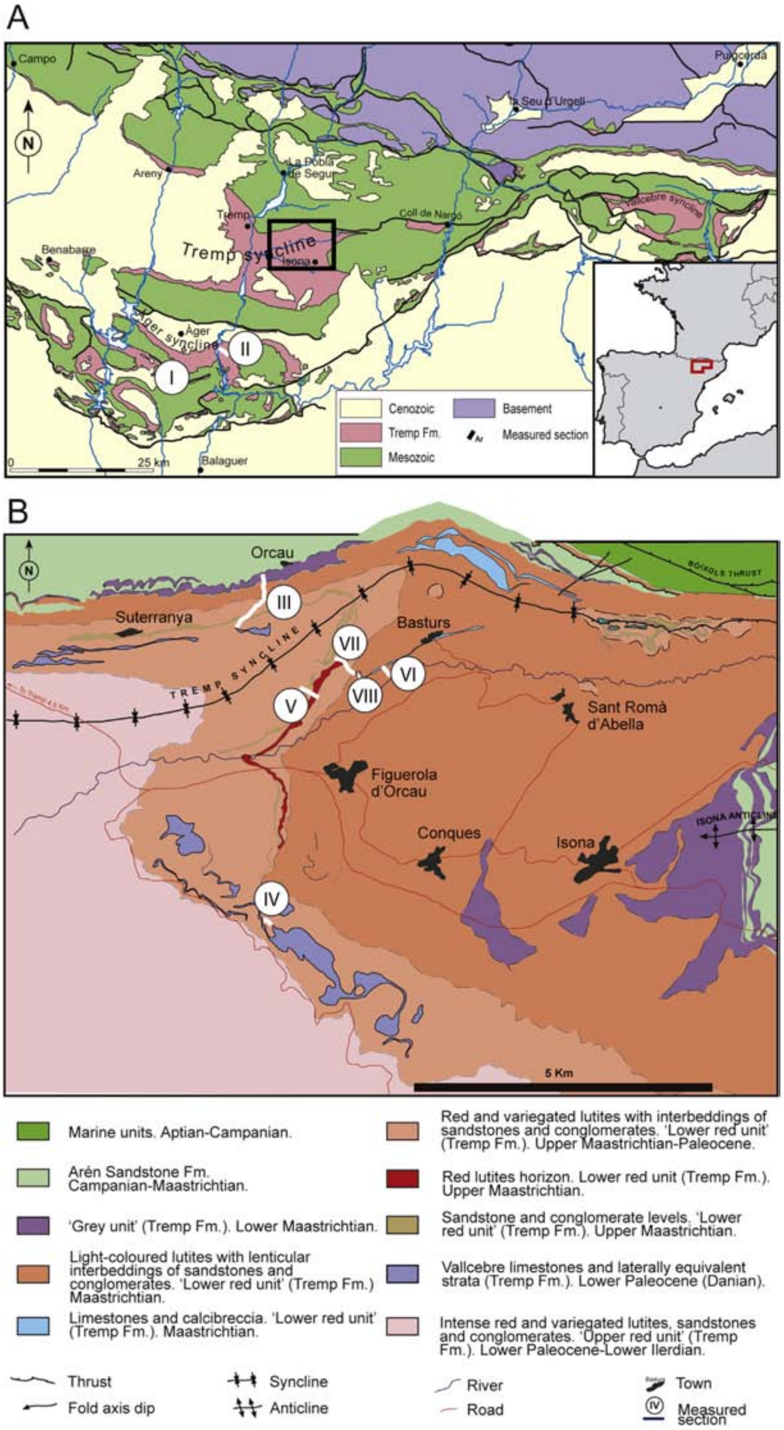

Fig. 1. Geographic and geological context of the studied sites. **A,** Geological map of the south-central Pyrenean unit (enlarged from the western Europe map), showing the outcrops of the Cretaceous-Paleocene Tremp Fm. and the location of the L'Espinau (I) and Fontllonga (II) sections. Modified from López-Martínez and Vicens (2012). **B,** Geological map of the Isona area (enlarged from A) with the position of the Camí del Soldat (IV), Serrat del Pelleu (V) and Serrat del Rostiar-1 (VI) sites; auxiliary sections from Orcau (III) and Basturs areas (VII and VIII) are represented. Modified from Riera et al. (2009).

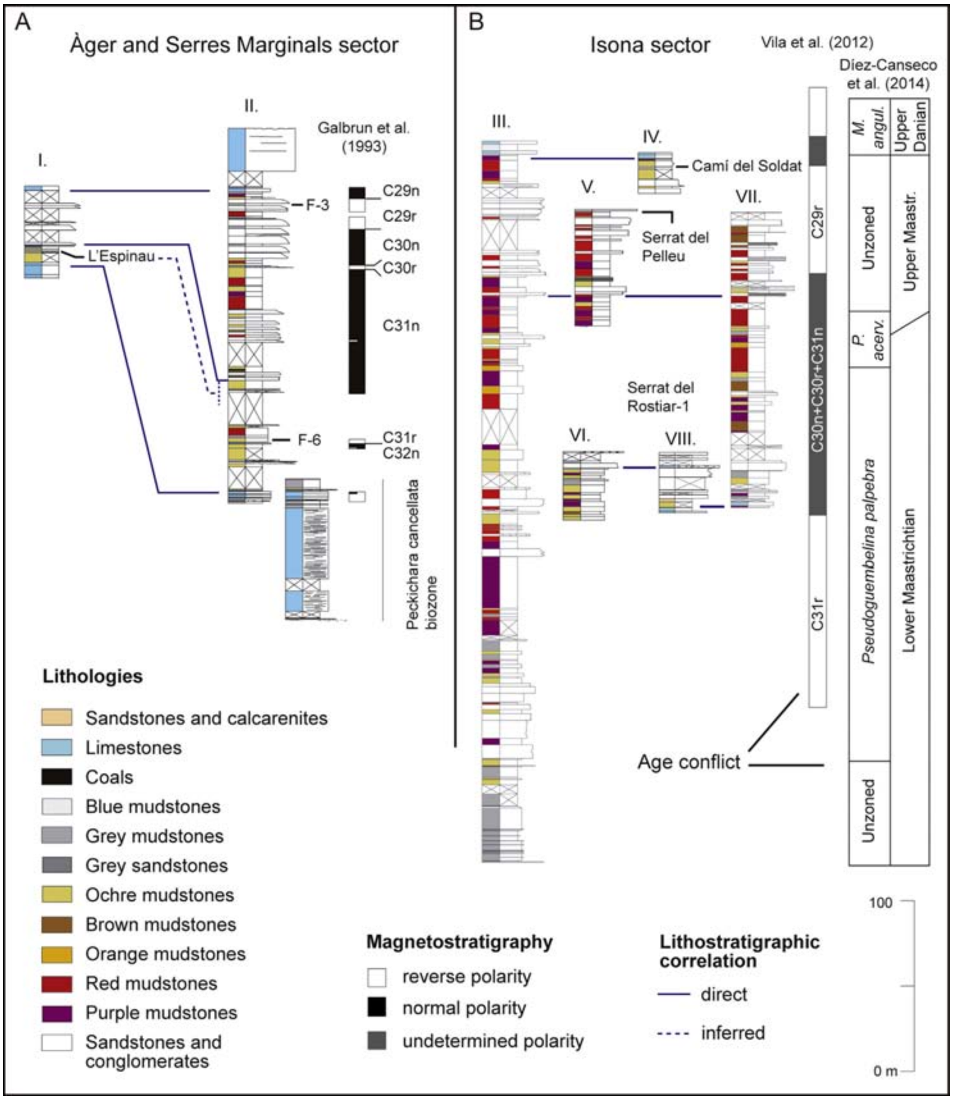

Fig. 2. Stratigraphic framework of the studied sites. **A,** Correlation panel of the Serres Marginals and Àger syncline. Magnetostratigraphy and charophyte biozonation are taken after Galbrun et al. (1993) and Villalba-Breva and Martín-Closas (2013), respectively. **B,** Correlation panel of the Isona area. Magnetostratigraphy and planktonic biozonation are taken after Vila et al. (2012) and Díez-Canseco et al. (2014), respectively. These two proposals do not match each other. Section III is modified from Oms et al. (2014). The Camí del Soldat site is projected in section IV, which corresponds to section VII in Riera et al. (2009). Section VII corresponds to section XIV in Riera et al. (2009). Sections VI and VIII correspond to sections I15B and I16B in Riera (2010), respectively.

alternations between sand and muddy sediments are a common feature of the meandering channels of the Tremp Formation (Díez-Canseco et al., 2014). In a similar way, the Serrat del Pelleu site consists of a grey mudstone level linked to medium-to-fine ochre sandstones. It yielded abundant bone remains, mainly corresponding to turtles and hadrosaurs, and a large number of teeth belonging to several crocodylomorph taxa (Blanco and Bolet, 2014). On the one hand, the Camí del Soldat site, placed in the upper part of the lower red unit (Riera et al., 2009), correlates with an inverse magnetochron regarded as C29r, a few metres below the Palaeocene 'Vallcebre limestones and laterally equivalent strata'. On the other, the Serrat del Pelleu site is located in an undetermined polarity interval interpreted as the upper part of the C30n magnetochron (Fig. 2B; Vila et al., 2012, 2013). In both cases, data provided by Díez-Canseco et al. (2014) are in agreement with a late Maastrichtian age.

The L'Espinau site is placed in a decimetric marly layer with grey colorations and organic remains, often in the form of coals. A complete study of this site is currently in progress, but Battista et al. (2014) provisionally regarded the bone layer, which has provided hundreds of hadrosaur bones, as a secondary deposit generated by successive water floods that reworked and oriented macroremains.

This site appears isolated from any sandstone unit but close to lacustrine limestones. Stratigraphically, L'Espinau is located in the mid-portion of a succession of lacustrine limestones to reddish-ochre mudstones and coarse sandstones. At the top of the section, the lateral equivalents of the Vallcebre limestone are deposited. Despite the fact that no direct age constraints are provided, this succession can be correlated with the well-documented Fontllonga section in the Àger syncline. Hence, the L'Espinau site can be placed in the lower part of the upper Maastrichtian (Fig. 2A).

3. Materials and methods

Fieldwork was carried out between 2010 and 2011. Samples of about 525 kg of rock from Serrat del Pelleu, 575 kg from Camí del Soldat, 625 kg from Serrat del Rostiar-1, and 1250 kg from L'Espinau were collected for processing. Samples were then macerated employing successive water immersions and sun dries in order to break up the rock matrix. Screen-washing was carried out using running water and a sieve mesh series of 1.4, 0.8 and 0.5 mm. The sample was then sorted under a Leica M60 binocular microscope. Photographs were taken under a Zeiss Evo MA10 scanning environmental microscope (ESEM) at the Servei de Microscopia de la Universitat Autònoma de Barcelona and at the Universitat de Barcelona. The specimens described in this paper are housed in the collection of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain).

We followed the previous works of Sanchíz (1998), Duffaud and Rage (1999) and Blain (2010, 2013) for the classification and nomenclature of lissamphibians. The classification of squamates is according to Estes et al. (1988).

4. Systematic palaeontology

4.1. Serrat del Rostiar-1

Class: Amphibia Linnaeus, 1758
Subclass: Lissamphibia Haeckel, 1866
Order: Allocaudata Fox and Naylor, 1982.
Family: Albanerpetontidae Fox and Naylor, 1982.
Albanerpetontidae indet.
Fig. 3A–C.

Material: A partial frontal (IPS-85004), two proximal and one distal fragment of humeri (IPS-85010a, IPS-85010b, IPS-85014).

Description: A posterior portion of a frontal (1.0 mm long) shows the dorsal surface ornamented with polygonal pits (Fig. 3A). The ventrolateral crest occupies the entire preserved length of the ventral side. The shafts of the humeri become slender and wider toward the epiphyses (Fig. 3B, C). The proximal epiphyses (IPS-85014, IPS-85010b) show a large groove in the medial surfaces for the articulation with the scapular girdle (Fig. 3B). The shaft becomes narrower distally. In the distal epiphysis (IPS-85010a), the ulnar epicondyle (medial epicondyle) is markedly less pronounced than the radial (lateral epicondyle), and the humeral ball is well-developed (Fig. 3C). The *fossa cubitus ventralis* is nearly symmetrical and clearly visible proximally to the humeral ball.

Discussion: Albanerpetontids are known from several Upper Cretaceous (Campanian-Maastrichtian) localities in Spain: Laño (Basque-Cantabrian region, Duffaud and Rage, 1999; Pereda-Suberbiola et al., 2015), Blasi-2 (southern Pyrenees, Blain et al., 2010), and Chera (Valencia province, Company and Szentesi, 2012). The ornamentation of the frontal (Fig. 3A) is characteristic of albanerpetontid amphibians, a group identified at Serrat del Rostiar-1 also based on humeral morphology. The frontal is diagnostic at the generic level within this family (McGowan and Evans, 1995; Duffaud and Rage, 1999; Grigorescu et al., 1999). However, the fragmentary nature of IPS-85004 prevents any comparison. Additionally, the overall morphology of the humeri is also characteristic of the Albanerpetontidae (Estes and Hoffstetter, 1976; Fox and Naylor, 1982; Duffaud and Rage, 1999). However, the humerus shape is very homogeneous in albanerpetontids, preventing identification at lower taxonomic levels. Nevertheless, slight differences can be assessed. For instance, IPS-85010a closely resembles the material figured from Blasi-2 and attributed to *Albanerpeton* aff. *nexuosum* (Fig. 2L in Blain et al., 2010). At the same time, both humeri differ from the indeterminate form recovered from Laño due to the absence of a foramen on the margin of the *fossa cubitus ventralis* and the lack of a second foramen nearly connected to the first with a groove, proximally to the *fossa cubitus ventralis* (Fig. 1 in Duffaud and Rage, 1999).

Order: Anura Fischer von Waldheim, 1813
Family: Alytidae Fitzinger, 1843
Subfamily: Discoglossinae Günther, 1858
Discoglossinae indet.
Fig. 4A–F.

Material: One fragment of right (IPS-85011) and two left (IPS-85005, IPS-85012) ilia, a partial left scapula (IPS-85015), a distal fragment of humerus (IPS-86061), a sacral vertebra (IPS-86062) and a partial vertebra (IPS-86063).

Description: Three fragmentary ilia, one right (IPS-85011; Fig. 4A) and two left (IPS-85012, IPS-85005; Fig. 4B, C, respectively) were assigned to discoglossines. Specimens collectively show a nearly rounded acetabulum, the posterior part of the iliac shaft bearing a dorsal crest (vexillum), and the *pars descendens*. The *pars descendens* is almost reduced, and a supraacetabular fossa is present between the acetabulum and the dorsal crest (Fig. 4A–C). IPS-85011 and IPS-85012 are 1.21 mm and 1.54 mm long, respectively. IPS-85005 is similar in size to IPS-85011 (1.22 mm long), and both are smaller than IPS-85012, suggesting the presence of different ontogenetic stages at this locality.

IPS-85015 is a left scapula (Fig. 4D). The *processus glenoidalis* (except for the articulation with the humerus) and *processus acromialis* are broken off. The scapula is somewhat gracile, with a well-pronounced constriction in its medium part and might have been rather short dorsoventrally.

IPS-86061 is a distal fragment of a right humerus (1.79 mm long). The condylar ball is well-developed, almost spherical, and clearly shifted laterally. The ulnar condyle is broken, but it seems to be larger than the lateral one. The *fossa cubitus ventralis* is filled with sediment, but looks asymmetrical. It is deeper and clearly outlined in the medial view, but the lateral edge is shallower.

A partial centrum of a sacral vertebra (IPS-86062) preserves a single anterior condyle and probably had two posterior condyles (one of them is broken) (Fig. 4E). The anterior condyle (0.6 mm lateromedially wide) is divided dorsoventrally by a shallow groove. The preserved posterior condyle is similar in size (0.5 mm lateromedially wide). IPS-86063 (Fig. 4F) is a slightly smaller vertebra with an anterior rounded condyle and a posterior cotyle dorsoventrally compressed.

Discussion: Similar material was recovered from the localities of Blasi-2 and Laño (Duffaud and Rage, 1999; Blain et al., 2010). IPS-86061 resembles MPZ 2009/243 from Blasi-2 (Fig. 3J in Blain et al., 2010), MCNA 6431 from Laño (Fig. 8 in Duffaud and Rage, 1999) and IPS-86072 from Serrat del Pelleu (Fig. 4L) in the morphology and position of the condylar ball and in having an asymmetrical *fossa cubitus ventralis*, deeper in the medial side and shallower in the lateral one. The anterior laminar part (*crista anterior*) of the scapula (IPS-85015) is well-developed but has a smaller extension typical of Alytidae (*Latonia*, *Discoglossus*, *Alytes* and probably *Enneabatrachus*) and its anterior margin is relatively shorter than in palaeobatrachids. The similar size of the anterior

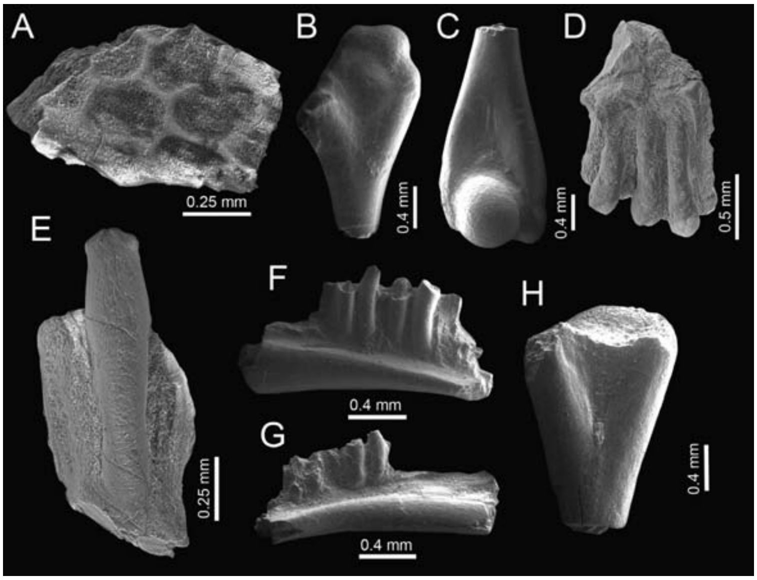

Fig. 3. Albanerpetontid amphibians from Serrat del Rostiar-1 (A–C) and L'Espinau localities (D–H). **A,** Frontal (IPS-85004) in dorsal view. **B,** Proximal (IPS-85010b) and **C,** distal (IPS-85010a) epiphyses of humeri in ventral view. **D,** Left premaxilla (IPS-85020) in lingual view. **E,** ?Maxilla (IPS-85021) in lingual view. **F,** Left dentary (IPS-85024) and **G,** right dentary (IPS-85027) in lingual view. **H,** Proximal fragment of humerus (IPS-85028) in ventral view.

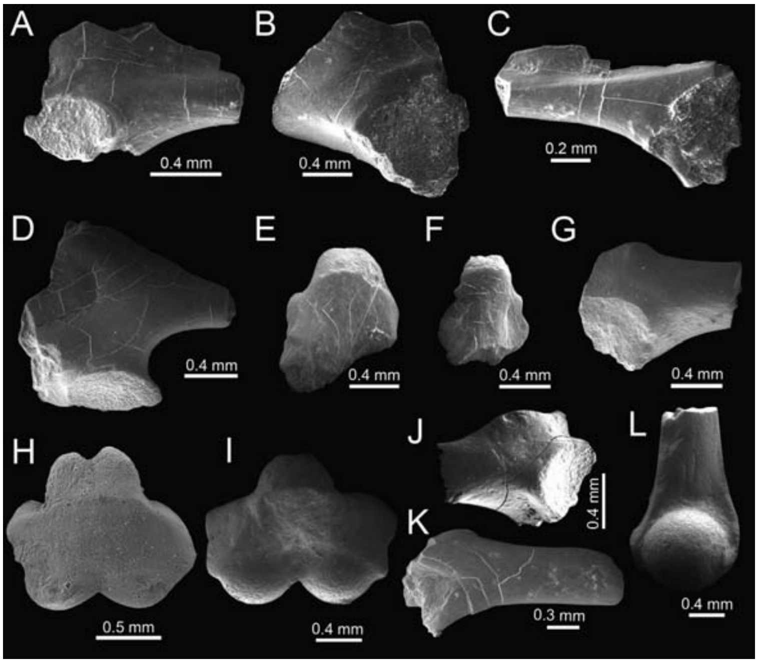

Fig. 4. Alytid anurans from Serrat del Rostiar-1 (A–G), L'Espinau (H–K) and Serrat del Pelleu localities (L). **A,** Right ilium (IPS-85011) in lateral view. **B,** Left ilium (IPS-85012) in lateral view. **C,** Left ilium (IPS-85005) in lateral view. **D,** Left scapula (IPS-85015) in lateral view. **E,** Sacral (IPS-86062) and **F,** trunk vertebrae (IPS-86063) in ventral view. **G,** Alytinae: right ilium (IPS-85013) in lateral view. **H,** Sacral vertebra (IPS-85019). **I,** Sacral vertebra (IPS-85030). **J,** Left (IPS-85032) and **K,** right ilium (IPS-85034) in lateral view. **L,** Distal epiphysis of humerus (IPS-86072) in ventral view.

and posterior condyles of the sacral vertebra, the nearly circular acetabular fossa, the presence of a supraacetabular fossa, a reduced *pars descendens*, and the shallow dorsal crest of the ilium are characteristic of the subfamily Discoglossinae (sensu Rage and Hossini, 2000; see also Sanchíz, 1998), which includes the genera *Paradiscoglossus*, *Eodiscoglossus*, *Paralatonia*, *Latonia* and *Discoglossus* (Blain et al., 2010, 2013). The ilia from Serrat del Rostiar are similar in shape to those recovered from the Blasi-2 site, which were referred to aff. *Paradiscoglossus*. The close geographical location and age might support the same taxonomic assignment as the specimens from Blasi-2. However, because the material from Serrat del Rostiar-1 is more fragmentary that the specimens from Blasi-2, it is assigned to Discoglossinae indet. as the remaining bones.

Subfamily: Alytinae Fitzinger, 1843

Alytinae indet.

Fig. 4G.

Material: One fragment of right ilium (IPS-85013).

Description: The single specimen (Fig. 4G) is a right ilium (1.26 mm long) that preserves part of the acetabulum and shows a *tuber superius* over it, lacking the dorsal crest (vexillum). The *tuber superius* is low and rounded in outline. Although partially preserved, the preacetabular region seems to be reduced.

Discussion: The different morphology of IPS-85013 suggests the presence of two different alytids in the Serrat del Rostiar-1 site. The absence of the dorsal crest and the presence of a low and rounded *tuber superius* are features typical of the Alytinae. The morphology of the *tuber superius* and *pars descendens* resembles that of the extant genus *Alytes* (e.g., Holman, 1998; Bailon, 1999). However, this genus has not been reported from the Cretaceous record worldwide. In general morphology, IPS-85013 also resembles the ilia of *Kizylkuma antiqua* Nessov, 1981 (Fig. 37 in Sanchiz, 1998) from the Turonian-Santonian of Uzbekistan. This species was erected based on an isolated maxilla (Nessov, 1981), but associated humeri and *Alytes*-like ilia allowed its inclusion within Alytinae (Roček and Nessov, 1993). This species represents the oldest record of alytine anurans. In addition, remains from the Maastrichtian of India were also assigned to *Kizylkuma* (Prasad and Rage, 1991, 1995), with doubts (Sanchiz, 1998), even if the morphology of the Indian ilia is somewhat different from our material and those described from Uzbekistan.

Family: Palaeobatrachidae Cope, 1865

Palaeobatrachidae indet.

Fig. 5A, B.

Material: One fragment of ilium (IPS-86059), and a partial vertebra (IPS-85007).

Description: IPS-86059 (Fig. 5A) is a fragment of the left ilium (3.96 mm long) preserving the acetabulum and part of the iliac shaft. The acetabulum is wide (2.28 mm) and rounded with a well-developed acetabular rim extending anteroventrally beyond the margin of the main body of the bone. The preacetabular region and the *pars descendens* are nearly absent, hidden by the acetabulum. The junction between the acetabular region and the iliac shaft is not waisted. The shaft lacks a dorsal crest, and the *tuber superius* is almost flattened and seems lenticular in shape, but is partially covered by sediment. The supraacetabular fossa is absent, and the dorsal margin of the ilium is relatively straight and close to the dorsal margin of the acetabulum. The *pars ascendens* is missing. IPS-85007 (Fig. 5B) is a partial vertebra, showing a slightly depressed, crescent-like anterior condyle and developed transverse processes, forming a well-marked curvature at the contact with the condyle in ventral view.

Discussion: The absence of dorsal crest and supraacetabular fossa, a wide acetabulum, and prominent acetabular rim are typical features of the Palaeobatrachidae (e.g., Rage and Hossini, 2000). Several ilia of palaeobatrachid anurans have been recovered from Blasi-2 and Laño. Specimens from Serrat del Rostiar-1 are similar in shape and size to those described by Duffaud and Rage (1999) and Blain et al. (2010). However, they are, so far, too fragmentary to perform a detailed comparison.

Anura indet.

Fig. 6A, B.

Material: A proximal fragment of an urostyle (IPS-85003), a proximal epiphysis of a radioulna (IPS-85006), two partial vertebrae (IPS-86060a, IPS-86060b), tibiofibular and radioulnar fragments (IPS-87217).

Description: Fragments of tibiofibulae and radioulnae (IPS-87217) were abundant in the Serrat del Rostiar-1 sample. These fragments generally correspond to broken shafts. IPS-85006 is a proximal epiphysis of a radioulna with a well-developed olecranon cavity. In the lateral view, a proximodistally-oriented sulcus can be observed along the shaft (Fig. 6A). Additionally, other axial elements were recovered. IPS-86060a and IPS-86060b are two partial vertebral centra with subspherical condyles. IPS-85003 (Fig. 6B) is the proximal edge of an urostyle (1.51 mm long). It has two anterior cotyles for articulation with the sacral vertebra. The condyles are slightly dorsoventrally compressed and well separated from each other. The upper part of the dorsal crest is not preserved, revealing the floor of the neural canal, and the ventral surface of the bone is nearly flat.

Discussion: Similar bones were recovered from the localities of Blasi-2 (Fig. 3K–U in Blain et al., 2010), Chera (Fig. 3F–H in Company and Szentesi, 2012), and L'Espinau (see below). These bones are characteristic of anurans and are different from other amphibian groups. However, the absence of more complete and diagnostic material prevents a more detailed assignment within the lower taxonomic groups recognised here.

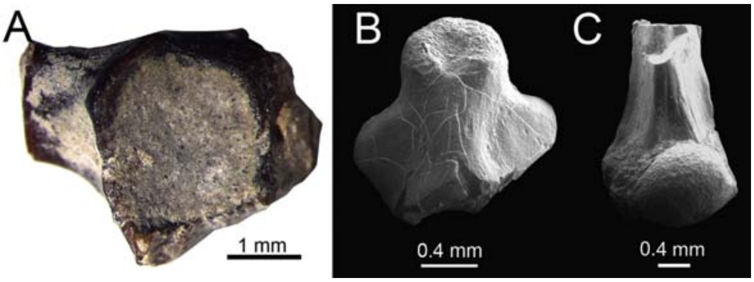

Fig. 5. Palaeobatrachid anurans from Serrat del Rostiar-1 (A–B) and L'Espinau localities (C). **A,** Left ilium (IPS-86059) in lateral view. **B,** Trunk vertebra (IPS-85007) in ventral view. **C,** Distal humeral epiphysis (IPS-85017) in ventral view.

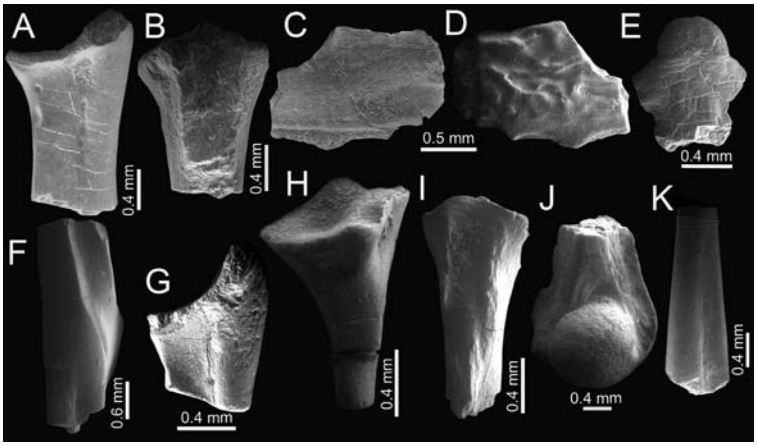

Fig. 6. Indeterminate (A–B, E–K) and pelobatid or gobiatid anurans (C, D) from Serrat del Rostiar-1 (A–B) and L'Espinau localities (C–K). **A,** Radioulna (IPS-85006) in lateral view. **B,** Urostyle (IPS-85003) in dorsal view. **C-D,** Maxilla of Pelobatidae or Gobiatidae indet. (IPS-85022) in lingual (C) and lateral (D) view. **E,** Trunk vertebrae (IPS-85036) in ventral view. **F,** Prearticular (IPS-85023) in dorsal view. **G,** Radioulna (IPS-85031) in lateral view. **H,** Coracoid (IPS-86069) in lateral view. **I,** Urostyle (IPS-85033) in dorsal view. **J,** Humeral epiphysis (IPS-85026) in ventral view. **K,** Shaft fragment of tibiofibula (IPS-86065).

Class: Diapsida Osborn, 1903
Superorder: Lepidosauria Haeckel, 1866
Order: Squamata Oppel, 1811
Infraorder: Gekkota Camp, 1923
?Gekkota indet.
Fig. 7A.

Material: One frontal (IPS-84998).

Description: IPS-84998 is a very small and well-preserved frontal, 0.86 mm long and 1.12 mm wide at its maximum width (Fig. 7A). Its posterior portion produces two posterolateral rami, whose lateral extremities are broken. The bone is narrow in the interorbital region and lacks its anterior end. In ventral view of the preserved portion, the *cristae cranii* are poorly developed, resulting in a poorly differentiated subolfactory tract. Medially, a rather straight suture is present only on the ventral side of the bone, suggesting that fusion of the left and right elements was advanced. The dorsal surface of the bone is smooth, lacking any trace of ornamentation except for a very subtle pitting.

Discussion: IPS-84998 differs from frontals of most gekkotans in the absence of well-developed *cristae cranii* fusing together ventrally. However, this fusion is sometimes restricted to a more anteriorly situated region of the frontal, which is not preserved in IPS-84998. Moreover, in some gekkotans, the *cristae cranii* does not meet medioventrally, so affinities to the group cannot be ruled out. The specimen resembles in overall morphology a frontal (PSMUBB V 389) from the Maastrichtian of Romania referred to 'Lacertilia' (Folie and Codrea, 2005). Both forms share the almost smooth dorsal surface of the frontal, but differ in the angle at which the posterior rami diverge. The affinities between the Iberian and Romanian forms are unclear, but they might represent closely related forms of a previously unrecorded group in the Cretaceous of Europe.

Infraorder: 'Scincomorpha' Camp, 1923
'Scincomorpha' indet.
Fig. 7B–D.

Material: Three tooth-bearing bones (IPS-84999, IPS-85000, IPS-85001).

Description: Three fragments of tooth-bearing bone (or bones), which are 0.78–1.17 mm long and 0.84–0.86 mm high. Teeth show a pleurodont implantation and are well spaced. They are conical in shape and bicuspid with a well-developed anterior cusp (Fig. 7B, C).

Discussion: Fragments of tooth bearing bones with a similar dentition, referred to Scincomorpha indet. or Scleroglossa indet., were described from the upper Campanian-lower Maastrichtian of Laño (Spain), the Maastrichtian of the Haţeg Basin (Romania) and the 'Senonian' of La Neuve (France) (Rage, 1999; Grigorescu et al., 1999; Garcia et al., 2000; respectively). However, the former 'scincomorphs' bear diminutive secondary cups unlike specimens IPS-84999, IPS-85000 and IPS-85001, which show a well-developed secondary cusp, approaching in size that of the main cusp. As in previous studies (Rage, 1999; Grigorescu et al., 1999; Garcia et al., 2000), the available material is too fragmentary to allow a specific or generic assignment, but tooth morphology contrasts with the chisel-like morphology of bicuspid anguimorphans. Thus, this form from Serrat del Rostiar-1 seems to be related to 'scincomorphans' rather than gekkotans, iguanians and anguimorphans.

Infraorder: Anguimorpha Fürbringer, 1900
Family: Anguidae Oppel, 1811
?Anguidae indet.
Fig. 7E–G.

Material: One vertebra (IPS-86058).

Description: The specimen is a partially preserved vertebra. It consists of an isolated centrum proportionally more elongated (2.61 mm) than wide (1.06 mm). The neural arch is lacking, and the centrum shows two longitudinal grooves in the dorsal (internal) side (Fig. 7E). The lateral margins are slightly concave, resulting in a slightly constricted centrum (Fig. 7F). The condyle is strongly dorso-ventrally compressed (Fig. 7G).

Discussion: The morphology of this vertebra fits well with those of the upper Maastrichtian locality of Blasi-2 referred by Blain et al. (2010) to an indeterminate anguid. The strong dorso-ventral constriction of the condyle, the size and proportions of the centrum and a very subtle lateral constriction (less evident in the specimens from Blasi-2) suggest a close affinity between both forms. Although fragmentary vertebrae of anguines and amphisbaenians are difficult to differentiate, amphisbaenian affinities are discarded based on the close match with the anguid vertebrae from

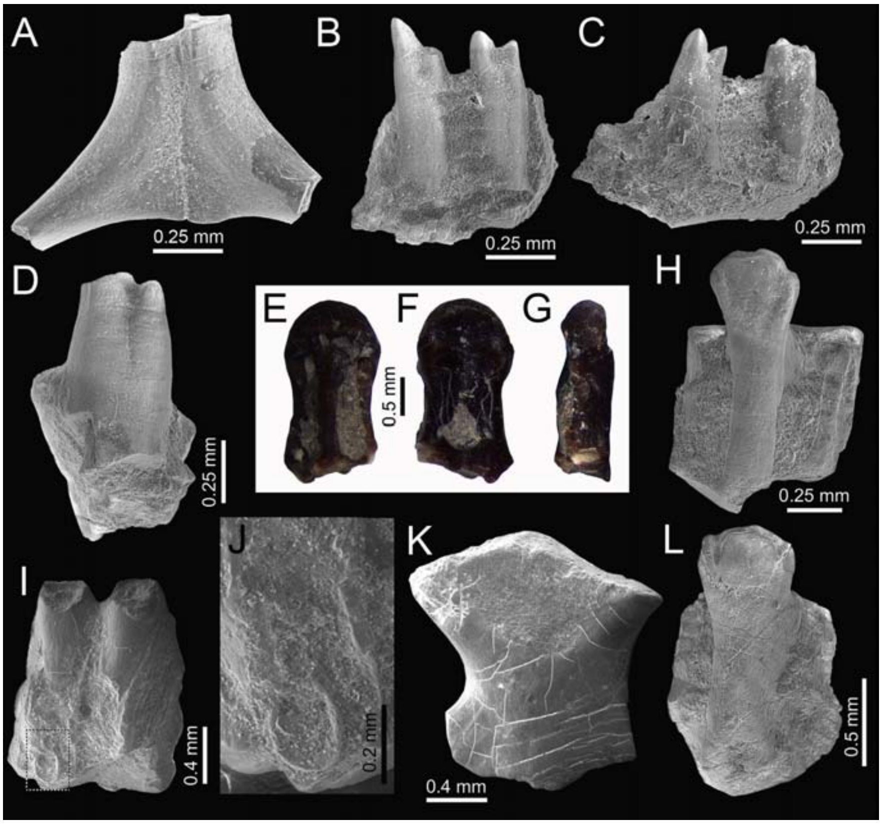

Fig. 7. Squamates from Serrat del Rostiar-1 (A–K) and L'Espinau localities (L). **A,** Frontal (IPS-84998) of an indeterminate ?Gekkota in ventral view. **B**–**D,** Tooth-bearing bones (IPS-84999, IPS-85000, IPS-85001, respectively) of an indeterminate 'scincomorph' lizard in lingual view. **E**–**G,** Vertebra of Anguidae indet. (IPS-86058) in dorsal (E), ventral (F) and lateral (G) view. **H,** Iguanid tooth (IPS-85002) in lingual view. **I,** Tooth-bearing bone (IPS-85009) of Squamata indet. in lingual view. **J,** Detail of IPS-85009, showing a replacement tooth. **K,** Ischium (IPS-85016) of Squamata indet. in lateral view. **L,** Iguanid tooth (IPS-85018) in lingual view.

Blasi-2 and the lack of a Cretaceous record for the group after the reinterpretation of the specimens from Laño as anguids (Blain et al., 2010).

Suborder: Iguania Cuvier, 1817
Family: Iguanidae Gray, 1827
Iguanidae indet.
Fig. 7H.

Material: One tooth-bearing bone (IPS-85002).

Description: An indeterminate tooth-bearing fragment of bone, showing a single spatulate tooth. The tooth is pleurodont, with a cylindrical shaft (1.12 mm long) and a spatulate tricuspid crown (0.43 mm antero-posteriorly long). The crown is labio-lingually compressed and bears a wide central cusp and two smaller anterior and posterior secondary cusplets, separated from the main cusp by faint grooves in lingual view (Fig. 7H).

Discussion: Similar teeth were described from Laño, and were referred to Iguanidae (Figs. 1–2 in Rage, 1999). In addition, tricuspid teeth were also recovered from the Maastrichtian of Blasi-2 and referred to an indeterminate lizard (possibly an iguanid) (Fig. 5A–B in Blain et al. (2010). However, the specimen from Serrat del Rostiar-1 mostly resembles those from Laño and L'Espinau (see below). For its part, the lizard from Blasi-2 shows more acute central and lateral cusps than the former ones.

Squamata indet.
Fig. 7I–K.

Material: One tooth-bearing bone (IPS-85009) and one ischium (IPS-85016).

Description: A tooth-bearing bone fragment (1.21 mm long) preserving two cylindrical and straight teeth without their crown (IPS-85009; Fig. 7I). A replacement tooth is rising at the base of one of them (Fig. 7J) and is slightly displaced from the centre of the erupted tooth. The ischium (IPS-85016) is fragmentary, but the proximal part is well preserved (Fig. 7K). It shows the ischiatic portion of the acetabulum, which is formed by the three pelvic bones (ischium, ilium and pubis). The proximal part of the bone is divided into two rectangular facets for the contact with the ilium dorsally and the pubis anteroventrally, and it comprises the posteroventral third of the acetabulum. The ischium is constricted distally to the acetabulum. The distal edge of this bone is not preserved.

Discussion: The pleurodont implantation of the teeth suggests squamate affinities, and the tooth morphology indicates that this tooth-bearing element represents a lizard and not a snake or amphisbaenian. However, it is not possible to assess if these remains belong to one of the taxa described above, or, alternatively, if they conform a different squamate type. Even more, it is not possible to know if the jaw fragment and the ischium belong to the same taxon. The absence of more complete and diagnostic material prevents a more detailed comparison and assignment.

4.2. L'Espinau

Class: Amphibia Linnaeus, 1758
Subclass: Lissamphibia Haeckel, 1866
Order: Allocaudata Fox and Naylor, 1982.
Family: Albanerpetontidae Fox and Naylor, 1982.
Albanerpetontidae indet.
Fig. 3D–H.

Material: A partial premaxilla (IPS-85020), a fragment of ? maxilla (IPS-85021), five fragments of dentaries (IPS-85024, IPS-85027, IPS-86067, IPS-85029a, IPS-85029b) and a proximal epiphysis of humerus (IPS-85028).

Description: Two specimens consist of a partial left premaxilla (IPS-85020, Fig. 3D) preserving three teeth, and a tooth-bearing bone fragment (IPS-85021; Fig. 3E) preserving only one tooth. The tooth implantation is pleurodont; the crowns are labiolingually compressed and show three small cusps, which are characteristic of albanerpetontids. The cusps are eroded in IPS-85020 (Fig. 3D), but it is evident that they increase in length to the medial margin of the premaxilla.

Specimens IPS-85024 and IPS-85027 are fragments of left and right dentaries (Fig. 3F, G, respectively), both bearing five tooth positions. Both are fragments corresponding to an anterior position. They are broader caudally and narrow rostrally, broken at both edges and lack the interlocking symphysis. The bones narrow and curve medially in their anterior portion. In IPS-85024 (Fig. 3F), one tooth is lost and three teeth have broken crowns, being only partially preserved in the parapet. The only complete tooth shows three small cusps. Teeth are not completely preserved in IPS-85027 (Fig. 3G). In both dentary fragments, the implantation is pleurodont, the Meckelian canal is closed and the labial surfaces are smooth. IPS-85028 is a proximal fragment of a humerus (Fig. 3H). The proximal epiphysis shows a large groove in the medial surface for the articulation of the scapular girdle. The proximal end of the epiphysis is broken.

Discussion: The specimen IPS-85020 is similar to the albanerpetontid premaxillae from Blasi-2 (Fig. 2A–D in Blain et al., 2010). The pleurodont implantation and the closed Meckelian canal of IPS-85024 and IPS-85027 are diagnostic characteristics of Albanerpetontidae (i.e., Blain et al., 2010). Based on morphology alone, the assignment to one of the genera within this family cannot be assessed because the absence of more complete and diagnostic material. However, other similar dentaries were recovered from Laño, Blasi-2 and Chera localities (Duffaud and Rage, 1999; Blain et al., 2010; Company and Szentesi, 2012). The albanerpetontid material recovered from Blasi-2 was referred to *Albanerpeton* aff. *nexuosum* Estes (Blain et al., 2010). Specimens from L'Espinau might belong to the same genus, given the close geographical and chronological proximity of both localities, and the lack of evident morphological differences. IPS-85029a, IPS-85029b and IPS-86067 are more fragmentary than IPS-85024 or IPS-85027.

Order: Anura Fischer von Waldheim, 1813
Family: Alytidae Fitzinger, 1843
Subfamily: Alytinae Fitzinger, 1843
Alytinae indet.
Fig. 4H–K.

Material: Two sacral vertebrae (IPS-85019, IPS-85030) and two partial ilia (IPS-85032, IPS-85034).

Description: Both sacral vertebrae (IPS-85019, IPS-85030, Fig. 4H, I) preserve one anterior and two posterior condyles. The anterior condyle is divided into two halves by a longitudinal groove. Anterior and posterior condyles are similar in size in both vertebrae (0.76 mm and 0.57 mm, respectively, in IPS-85019, and 0.72 mm and 0.68 mm, respectively, in IPS-85030). IPS-85032 and IPS-85034 are fragmentary left and right ilia, respectively (Fig. 4J, K). Both ilia preserve part of the acetabulum and the *pars descendens*. They lack the dorsal crest (vexillum) over the proximal part of the iliac shaft. The *tuber superius* is low and rounded in outline, situated slightly anteriorly to the acetabulum. The acetabulum seems to be in relief compared to the acetabular area.

Discussion: A similar size of the sacral anterior and posterior condyles is a feature of the Alytidae (i.e., Blain et al., 2013). The sacral vertebrae resemble those from the Serrat del Rostiar-1 (IPS-86062, Fig. 4E), also referred to Alytidae. However, IPS-85019 shows a deeper groove in the anterior condyle than IPS-85030 and IPS-86062 (Fig. 4H, I and E, respectively). IPS-85030 also differs from the others in having a more conspicuous outline. The ilia are very similar to IPS-85013, which was recovered from the Serrat del Rostiar-1 locality (Fig. 4G). The morphology of the *tuber superius* also resembles those of the extant genus *Alytes* (i.e., Bailon, 1999). However, as mentioned above, the morphology of the ilia also resembles those of the *K. antiqua* Nessov (Fig. 37 in Sanchiz, 1998) from the Turonian to Santonian of Uzbekistan.

Family: Palaeobatrachidae Cope, 1865
Palaeobatrachidae indet.
Fig. 5C.

Material: Two humeral epiphyses (IPS-85017, IPS-85025).

Description: All the specimens consist of distal epiphyses (1.8–2.5 mm long) of left humeri. The shafts are subtriangular in the cross section, and the *fossa cubitus ventralis* is absent in all cases. Ulnar and radial epicondyles are well-developed, with the humeral ball being slightly laterally shifted (Fig. 5C).

Discussion: The absence of the *fossa cubitus ventralis* and the strong development of both epicondyles characterise the humeri of members within the family Palaeobatrachidae. Similar humeri of indeterminate palaeobatrachids were reported from the localities of Laño (Duffaud and Rage, 1999) and Serrat del Rostiar-1 (this study).

Family: Pelobatidae Bonaparte, 1850 or Gobiatidae Roček and Nessov, 1993.
?Pelobatidae or ?Gobiatidae indet.
Fig. 6C, D.

Material: One maxilla (IPS-85022).

Description: A fragment of maxilla preserves part of the *crista dentalis* and ten tooth positions. Teeth are lacking, but they were probably very small. The *crista dentalis* is proportionally low, and the *lamina horizontalis* is relatively wide (Fig. 6C). In the labial view, the bone is ornamented with several ridges and grooves (Fig. 6D).

Discussion: This ornamentation is common in pelobatids and gobiatids (Borsuk-Białynicka, 1978; Roček, 1982, 2008, 2013; Špinar and Tatarinov, 1986; Roček and Nessov, 1993; Henrici, 1994). IPS-85022 is similar to an anuran maxilla from Chera described by Company and Szentesi (2012), although several characters might suggest a different taxon. The *crista dentalis* is proportionally longer, and the *lamina horizontalis* is shorter but more conspicuous in the Chera specimen. The ornamentation is also more marked in the Chera specimen. However, both specimens could be included in the same Family. Company and Szentesi (2012) suggested a pelobatid condition, because the gobiatids were restricted to Asia during the Late Cretaceous (see also Roček, 2013). However, the probable presence of Asian immigrants in our Maastrichtian assemblages from the north-eastern Iberian Peninsula (as alytines, see discussion below) prevents, in our opinion, a definitive reference to either of these two families.

Anura indet.
Fig. 6E–K.

Material: one prearticular (IPS-85023), fragmentary vertebrae (IPS-86064, IPS-86066, IPS-85035, IPS-85036), one urostyle (IPS-85033), one coracoid (IPS-86069), one partial radioulna (IPS-85031), one humeral epiphysis (IPS-85026) and six fragments of tibiobifulae (IPS-86065).

Description: Fragmentary vertebrae (IPS-86064, IPS-86066, IPS-85035, IPS-85036) are abundantly recovered from L'Espinau locality. Vertebral condyles are subspherical and are separated from the centra by a straight lateromedial sulcus (Fig. 6E). The prearticular (IPS-85023) is incomplete, only preserving a probable coronoid process and the sulcus for Meckel's cartilage (Fig. 6F). IPS-85031 is a proximal epiphysis of a radioulna with a well-developed olecranon cavity (Fig. 6G). A probable fragment of coracoid (IPS-86069) consists of only its wider anterior end (*pars epicoracoidalis*), and it is strongly narrower at the mid-length (Fig. 6H). IPS-85033 is the proximal edge of a urostyle (Fig. 6I). Two cotylar cavities for articulation with the sacral vertebra are located anteriorly and separated by a vertical septum. The ventral surface of the bone is nearly plane. The upper part of the dorsal crest is not preserved, revealing the floor of the neural canal. The humeral distal epiphysis (IPS-85026) shows that the ulnar and radial epicondyles are well-developed, and the humeral ball is nearly symmetrically placed (Fig. 6J). This morphology resembles a palaeobatrachid condition; however, IPS-85026 also shows a small *fossa cubitus ventralis*, unlike Palaeobatrachidae. This fossa is laterally shifted. Shaft fragments of tibiofibulae (IPS-86065) are also abundant in this locality (Fig. 6K).

Class: Diapsida Osborn, 1903
Superorder: Lepidosauria Haeckel, 1866
Order: Squamata Oppel, 1811
Suborder: Iguania Cuvier, 1817
Family: Iguanidae Gray, 1827
Iguanidae indet.
Fig. 7L.

Material: One tooth-bearing bone (IPS-85018).

Description: IPS-85018 is an indeterminate tooth-bearing fragment of jaw, showing a single tooth (Fig. 7L). The tooth is pleurodont, with a cylindrical shaft (1.43 mm long) and a spatulate tricuspid apex (0.57 mm). The apex is labiolingually compressed, and bears a wide central cusp and two smaller secondary anterior and posterior cusps. On the lingual surface, the small cusps are separated from the central one by poorly developed grooves.

Discussion: Similar teeth were described from Laño, and were classified as Iguanidae (Figs. 1 and 2 in Rage, 1999). This form is similar to the taxon with tricuspid teeth from Serrat del Rostiar-1 (IPS-85002, Fig. 7H) described above, and both clearly differ from the tricuspid form from Blasi-2 (Fig. 5A, B in Blain et al., 2010).

4.3. Serrat del Pelleu

Class: Amphibia Linnaeus, 1758
Subclass: Lissamphibia Haeckel, 1866
Order: Allocaudata Fox and Naylor, 1982.
Family: Albanerpetontidae Fox and Naylor, 1982.
Albanerpetontidae indet.

Material: A proximal epiphysis of humerus (IPS-86070).

Description and discussion: The partial humerus consists of a proximal epiphysis showing a large groove in the medial surface for the articulation of the scapular girdle. The specimen is similar in shape to IPS-85010b (Fig. 3B), and it is the single remain referred to Albanerpetontidae from this locality.

Order: Anura Fischer von Waldheim, 1813
Family: Alytidae Fitzinger, 1843
Subfamily: Discoglossinae Günther, 1858
Discoglossinae indet.
Fig. 4L.

Material: One prearticular (IPS-86073), three distal epiphyses of humeri (IPS-86072) and six fragments of tibiofibulae (IPS-86071).

Description: This prearticular (IPS-86073) is partially preserved. It is an anterior fragment, which only shows the sulcus for the Meckelian cartilage. The three portions of humeri (IPS-86072) consist of different sized distal epiphyses. The condylar ball is well-developed, almost spherical, and shifted laterally. The ulnar epicondyle is larger than the radial. The *fossa cubitus ventralis* is asymmetrical (Fig. 4L). All the tibiofibulae (IPS-86071) are fragments of the shafts ending in nearly complete epiphyses. They are elongated bones, divided by a proximodistal sulcus into two tubular halves.

Discussion: The different development of both epicondyles, the shifted humeral ball and the asymmetric *fossa cubitus ventralis* are characters observed in Alytidae. The morphology of the humeri resembles those referred to discoglossine alytids from the Serrat del Rostiar-1 site. The partial prearticular and six tibiafibulae lack diagnostic characters. However, these remains are tentatively assigned to discoglossine Alytidae due to the absence of other anuran remains in the Serrat del Pelleu site.

4.4. Camí del Soldat

Class: Amphibia Linnaeus, 1758
Subclass: Lissamphibia Haeckel, 1866
Order: Anura Fischer von Waldheim, 1813
Anura indet.

Material: One urostyle (IPS-86075) and two partial vertebrae (IPS-86074).

Only one urostyle and two fragmentary vertebrae testify the presence of anurans at the Camí del Soldat locality. These bones are characteristic of anurans; however, they lack diagnostic characters to assess a more detailed comparison.

5. Discussion

Two of the four new localities, Serrat del Rostiar-1 and L'Espinau, have yielded a relatively diverse record of microvertebrates (Table 1). From the former, albanerpetontids, anurans and squamates were recovered. Anurans are represented by two different alytids (alytines and one discoglossine) and palaeobatrachids. Squamates are the most diverse group in this site; they comprise from between 4 and 6 different taxa, including scincomorphs, iguanids, anguids and possibly gekkotans. The L'Espinau locality also yielded albanerpetontids, anurans (alytines, palaeobatrachids and pelobatids or gobiatids) and squamates (iguanids). The anuran assemblage from L'Espinau, unlike other sites reported in this paper, includes a probable pelobatid or gobiatid frog. It is interesting to note that the squamate diversity from this site is significantly lower than that from Serrat del Rostiar-1. However, both sites largely contrast with the scanty microvertebrate records from Camí del Soldat and Serrat del Pelleu. A few remains testify to the presence of albanerpetontids and alytid anurans at Serrat del Pelleu, and indeterminate anurans at Camí del Soldat. The size of the samples of sediment taken from Serrat del Pelleu and Camí del Soldat were nearly similar to the sample from Serrat del Rostiar-1 and to half of the sample from L'Espinau, suggesting that the limited diversity in such microvertebrate assemblages is not related to insufficient sampling.

The taxonomic composition of amphibians from the studied sites is similar to other Campanian-Maastrichtian localities from eastern Iberia. Albanerpetontid remains, present at Serrat del Rostiar-1, L'Espinau and Serrat del Pelleu, resemble *Albanerpeton* aff. *nexuosum* from Blasi-2 (Blain et al., 2010), but not the

Table 1
List of amphibians and squamates from Tremp Formation sites (Early-Late Maastrichtian).

	Serrat del Rostiar-1	L'Espinau	Serrat del Pelleu	Camí del Soldat
Lissamphibia				
Allocaudata				
Albanerpetontidae indet.	X	X	X	
Anura				
Alytidae				
Discoglossinae indet.	X		X	
Alytinae indet.	X	X		
Palaeobatrachidae indet.	X	X		
Pelobatidae or Gobiatidae indet.		X		
Anura indet.	X	X		X
Lepidosauria				
Squamata				
Gekkota indet.	X			
'Scincomorpha' indet.	X			
Anguidae indet.	X			
Iguanidae indet.	X	X		
Squamata indet.	X			

indeterminate albanerpetontid from Laño (Duffaud and Rage, 1999). Unlike Laño, none of the studied sites have produced any remains of Caudata. The discoglossine anurans from Serrat del Rostiar-1 are similar to the indeterminate alytid from Laño [named discoglossid by Duffaud and Rage (1999)] and aff. *Paradiscoglossus* from Blasi-2 (Blain et al., 2010). The palaeobatrachids from Serrat del Rostiar-1 and L'Espinau are also reminiscent of those of both Laño and Blasi-2 localities, whereas neither Laño nor Blasi-2 contain pelobatid or gobiatid remains. Similar remains have previously been reported only from Chera, and referred, with doubts, to Pelobatidae (Company and Szentesi, 2012). However, the anuran from L'Espinau does not likely correspond to the same form. More interesting is the presence of alytine anurans in the Serrat del Rostiar-1 and L'Espinau localities, which might represent their first Mesozoic record in Europe. Up to now, the oldest record of alytine anurans on this continent came from the Lower Miocene of Germany (Sanchíz and Schleich, 1986; Roček, 2013). The alytine remains from the Pyrenean localities would extend downwards the stratigraphic range of this subfamily in Europe into the Maastrichtian. The close relationships between these alytines and *K. antiqua* from the Turonian-Santonian of Uzbekistan might suggest dispersal events of Asian anurans during the Late Cretaceous, as hypothesised by Roček (2013). In this sense, Iberian (and probably Indian) alytines might be early immigrants from Asia. This evidence also makes possible the presence of gobiatid anurans in the L'Espinau locality, although it cannot be discarded that the referred material (IPS-85022) belongs to Pelobatidae.

Like amphibians, the squamate composition of assemblages from the studied sites match those from other uppermost Cretaceous localities of eastern Iberia, but also shows some peculiarities. The spatulate tricuspid teeth of the iguanid from the Serrat del Rostiar-1 and L'Espinau resemble those of an iguanid from Laño (Rage, 1999), but not the iguanid from Blasi-2 (Blain et al., 2010). On the contrary, the anguid present at the Serrat del Rostiar-1 is similar to that of Blasi-2 (Blain et al., 2010). An interesting frontal is assigned, with doubts, to Gekkota (Fig. 7A), which would represent the only Mesozoic record for the group in the Iberian Peninsula and possibly in Europe (see Daza et al., 2014). The earliest gekkotans previously identified with confidence in the Iberian Peninsula are of Eocene age (Rage and Augé, 2003; Bolet and Evans, 2013). Finally, despite the presence of other bicuspid forms in the Upper Cretaceous of the Iberian Peninsula and other regions of Europe, a form with bicuspid teeth presenting a very well-developed second cusp may represent a new 'scincomorph' (Fig. 7B–D). The absence of borioteiioid lizards, a well-represented group in Late Cretaceous assemblages from Eastern Europe, and of snakes at these new localities is intriguing, but our knowledge of squamate Iberian faunas from this period is still too poor to provide an explanation for these anomalies. In fact, some taphonomic bias is possible. The top of squamate diversity of these new Pyrenean localities has probably not been evidenced yet, and the low diversity of other Cretaceous assemblages (e.g., Laño and Blasi-2) compared to Eocene sites suggests that other forms might be identified in the Upper Cretaceous of the Iberian Peninsula in the near future. The identification of a multicusped iguanid and a pythonomorph at the upper Campanian-lower Maastrichtian locality of Lo Hueco (Narváez and Ortega, 2010; Houssaye et al., 2013), and an anguimorphan with possible xenosaur affinities and a terrestrial mosasauroid at Armuña (Pérez-García et al., this volume) point to a hidden diversity of Iberian Late Cretaceous lizards; knowledge of which should be improved upon in the coming years. For now, we can only state that iguanids, 'scincomorphs' and anguimorphs are represented in the best sampled localities from the Iberian Upper Cretaceous, whereas other taxa seem to have a more restricted distribution or are, at least, lacking in part of the assemblages. The composition of these late Campanian-Maastrichtian assemblages strongly contrasts with that of the better-known squamate faunas from the Jurassic and Lower Cretaceous of the Iberian Peninsula, which include paramacellodids, dorsetisaur anguimorphs and several forms of uncertain position, but often considered as basal squamates or basal scincogekkonomorphs (Bolet and Evans, 2010, 2011, 2012) suggesting a strong faunal replacement between the Early and Late Cretaceous. In turn, Late Cretaceous anuran assemblages do not differ from those of the Early Cretaceous, except for the presence of gobiatid or pelobatid anurans (Roček, 2013). Unlike squamates, available data at the Family level suggest that there is no evidence of faunal turnover in amphibians through the Cretaceous of the Iberian Peninsula.

The new localities with herpetofaunal remains reported here represent different environments where deposition occurred in low activity periods: meandering rivers (Serrat del Pelleu, Camí del Soldat) and floodplains (Serrat del Rostiar-1), and areas close to lacustrine settings undergoing flooding periods (L'Espinau) (this study and Battista et al., 2014). The other Campanian-Maastrichtian localities previously studied in the Iberian Peninsula represent braided river systems with channels, interchannel pools and sandflats (Laño, Astibia et al., 1990; Pereda-Suberbiola et al., 2015) and small ephemeral lakes and ponds in coastal mangrove-like wetlands (Blasi-2 (Blain et al., 2010) and Chera (Company and Szentesi, 2012)). In addition, these localities represent a timespan of about six million years, from the upper Campanian-lower Maastrichtian localities of Laño and Chera to the upper Maastrichtian of Blasi-2, L'Espinau, Serrat del Pelleu and Camí del Soldat (Pereda-Suberbiola et al., 2000; Blain et al., 2010; Company and Szentesi, 2012; this study). Albanerpetontids, alytids, palaeobatrachids, anguids and iguanids are present in all these environments throughout this timespan, while pelobatids or gobiatids seem to be more restricted to small ephemeral lakes in coastal settings (i.e., Chera and L'Espinau sites) and 'scincomorphs' to fluvial environments (i.e., Laño and Serrat del Rostiar-1). Additionally, environmental preferences could also be assessed among the anurans. At Laño, palaeobatrachid remains are much more abundant (about 70% of the lissamphibian assemblage) than alytids, whereas alytids are dominant taxa at Blasi-2, Serrat del Rostiar-1 and L'Espinau (Csiki-Sava et al., 2015 and references therein). On the other hand, Serrat del Rostiar-1, L'Espinau and Serrat del Pelleu are freshwater environments with some marine influence. In this sense, palaeobatrachids might be restricted to freshwater fluvial environments, but they also seem to be able to live in low-salinity water. It is important to note that the fragile nature and the lack of evidence for significant abrasion suggest that microvertebrate remains herein studied were shortly transported and corresponded to animals that lived in or nearby the depositional settings.

As a whole, the faunas of the studied sites are mostly represented by cosmopolitan ('scincomorphans') or Laurasian elements (albanerpetontids, discoglossines, ?pelobatids and anguids), but they also include possible Asian immigrants (?gobiatids and alytines). Gondwanan taxa seem to be absent in the Maastrichtian fluvial settings of north-eastern Iberia, unlike the upper Campanian-lower Maastrichtian of Laño, in which matsoiid snakes were reported by Rage (1999). This would suggest extinction processes affecting Gondwanan elements in the herpetofaunas from north-eastern Iberia during the Maastrichtian. Thus, environmental preferences and extinction processes might explain the presence or absence of some taxa in determinate localities, although taphonomic biases cannot be discarded.

6. Conclusions

Amphibian and squamate remains were recovered from four new sites within the Tremp Formation. These sites represent fluvial environments with some marine influence. Two of them, Serrat del Rostiar-1 and L'Espinau, yielded a high diversity of anurans (discoglossines, alytines, palaeobatrachids and probable pelobatids or gobiatids) and lizards (gekkotans, 'scincomorphans', anguids and iguanids). Remains of albanerpetontids are also commonly recovered from these sites. The faunal composition is quite similar to other Upper Cretaceous localities from the Iberian Peninsula such as Laño and Blasi-2. However, the studied localities show some peculiarities. Remains of alytines and gekkotans would represent the oldest records of these groups in Europe. The presence of alytines in Serrat del Rostiar-1 and L'Espinau sites could also suggest early immigrants from Asia related to *K. antiqua*. The pelobatid or gobiatid anuran from L'Espinau is only comparable to that recovered from the Chera site. The 'scincomorph' with bicuspid teeth from Serrat del Rostiar-1 differs from other 'scincomorphans' reported from other Cretaceous sites in Europe, and may represent a new species. Gondwanan taxa are absent in all the new fluvial sites. Their absence might correspond to an extinction event during the early Maastrichtian instead of environmental preferences.

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Chapter 7. LATE CRETACEOUS (MAASTRICHTIAN) CROCODYLIFORMS FROM NORTHEASTERN IBERIA

Art by Aina & Agnès Amblàs (ICRA)

ALLODAPOSUCHUS PALUSTRIS SP. NOV. FROM THE UPPER CRETACEOUS OF FUMANYA (SOUTH-EASTERN PYRENEES, IBERIAN PENINSULA): SYSTEMATICS, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY OF THE ENIGMATIC ALLODAPOSUCHIAN CROCODYLIANS

PLoS One, 9(12), e115837 (I.F.: 3,234; Q1 2014, Multidisciplinary sciences)

En este trabajo llevé a cabo la clasificación taxonómica y descripción del material postcraneal perteneciente al holotipo de esta nueva especie de cocodrilo en colaboración con un especialista en cocodrilos eusuquios (Dr. Eduardo Puértolas Pascual, Universidad de Zaragoza), así como una parte importante de los análisis filogenéticos, la redacción de las secciones de Introducción, Material y Métodos, Discusión, Conclusiones, la parte correspondiente de la Paleontología Sistemática, y la creación de las Figuras 2-8. Al incluir este espécimen de cocodrilo parcialmente completo en esta tesis doctoral se pretende mejorar el conocimiento de la diversidad de eusuquios en los ecosistemas del Cretácico Superior, para facilitar la posterior clasificación y descripción de los morfotipos compuestos por restos dentales aislados.

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RESEARCH ARTICLE

Allodaposuchus palustris sp. nov. from the Upper Cretaceous of Fumanya (South-Eastern Pyrenees, Iberian Peninsula): Systematics, Palaeoecology and Palaeobiogeography of the Enigmatic Allodaposuchian Crocodylians

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Abstract

The controversial European genus *Allodaposuchus* is currently composed of two species (*A. precedens, A. subjuniperus*) and it has been traditionally considered a basal eusuchian clade of crocodylomorphs. In the present work, the new species *A. palustris* is erected on the base of cranial and postcranial remains from the lower Maastrichtian of the southern Pyrenees. Phylogenetic analyses here including both cranial and postcranial data support the hypothesis that *Allodaposuchus* is included within Crocodylia. The studied specimen suggests little change in postcranial skeleton along the evolutionary history of crocodylians, except for some bone elements such as the axis, the first caudal vertebra and the ilium. The specimen was found in an organic mudstone corresponding to a coastal wetland environment. Thus, *A. palustris* from Fumanya is the first *Allodaposuchus* reported in lacustrine-palustrine settings that expand the ecological range for this genus. The S-DIVA palaeobiogeographic reconstruction of ancestral area suggests that early members of Crocodylia rapidly widespread for the Northern Hemisphere landmasses no later than the Campanian, leading the apparition of endemic groups. In that way ''Allodaposuchia'' represents an endemic European clade probably originated in the Ibero-Armorican domain in the late Campanian and dispersed by the Southern European archipelago prior to the early Maastrichtian.

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Introduction

The clade of eusuchian crocodylomorphs is composed of several stem taxa and the crown Crocodylia containing the three major extant lineages: Crocodyloidea, Alligatoroidea and Gavialoidea [1–4]. Eusuchia probably originated in the northern continents (North America and Europe) at the beginnings of the Early Cretaceous [5]. By the Late Cretaceous, eusuchians began to diversify, a process that prolonged until the Eocene, but for some time they shared terrestrial biotas with other crocodylomorphs such as dyrosaurids, pholidosaurids, notosuchians and some relics of typical faunas of the Early Cretaceous (e.g. atoposaurids and goniopholidids) [1].

During the Late Cretaceous, eusuchians were widespread in Europe [6]. Among them, there were members of the sister taxa of Crocodylia, such as Hylaeochampsidae (e.g. the English *Hylaeochampsa vectiana* Owen, the Italians *Pietraroiasuchus ormezzanoi* Buscalioni *et al.* and *Acynodon adriaticus* Delfino *et al.*, the Iberian *Acynodon iberoccitanus* Buscalioni *et al.* and the Hungarian *Iharkutosuchus makadii* Ösi *et al.*) and the genus *Allodaposuchus* (according to Puértolas-Pascual *et al.* [5]). The crown Crocodylia was represented by the Spanish crocodyloid *Arenysuchus gascabadiolorum* Puértolas-Pascual *et al.*, and by basal alligatoroids like the French *Massaliasuchus affluvelensis* Martin & Buffetaut and the Spanish *Musturzabalsuchus buffetauti* Buscalioni *et al.* However, new phylogenetic hypotheses only recognize *Arenysuchus* and *Musturzabalsuchus* as closely related to the crown group [5, 6]. Hence, current classification should be revised as more complete specimens are recovered. On the other hand, several species of basal gavialoids attributed to the genus *Thoracosaurus* have been described from the Late Cretaceous of France, Netherlands and Crimea [6].

The systematic emplacement of some basal eusuchians is controversial, especially due to their fragmentary nature and the lack of postcranial remains for the majority of species. This is particularly true of the European genus *Allodaposuchus*. For instance, while some analyses place it as a sister taxon of Crocodylia [5–8], others suggest that it was related to the clade Alligatoroidea + Crocodyloidea [4] or included within Alligatoroidea [9]. Nopcsa [10] erected the genus *Allodaposuchus*, and its type species *A. precedens*, on the basis of some cranial and limited postcranial material from Vălioara (Haţeg Basin, Romania) and Valdonne (Fuveau Basin, France) localities. Later on, Buscalioni *et al.* [7] performed a revision of these materials and included new fragmentary remains from Spain and France, based on characters widely distributed in basal eusuchians. Subsequently, Martin and Buffetaut [11], after reviewing the French material from Valdonne, erected the new taxon *Massaliasuchus affuvelensis*. More recently, Delfino *et al.* [8] described a new complete skull from Oarda de Jos (Romania) that was ascribed to *Allodaposuchus precedens*, and also argued that specimens from Western Europe should be considered as a different taxon from *A. precedens*. Finally, Puértolas-Pascual *et al.* [5] erected *Allodaposuchus subjuniperus* on the base of a nearly complete skull from Huesca (NE Spain). Accordingly, nowadays the genus *Allodaposuchus* includes two formal species, the

Romanian *A. precedens* Nopcsa and the Spanish *A. subjuniperus* Puértolas-Pascual *et al.*, and other remains with ambiguous attribution at species level.

In this paper, we describe new remains of an eusuchian crocodylomorph found in the Tremp Formation beds exposed at the Fumanya Sud locality (lower Maastrichtian, northeastern Iberian Peninsula, Fig. 1). They are attributed to the genus *Allodaposuchus* and consist of partial skull and numerous postcranial elements belonging to both axial and appendicular skeletons. Thus, it represents the most complete postcranial material known for *Allodaposuchus* so far and it is relevant to understanding the evolution of postcranial skeleton in eusuchians. The aims of the work are: 1) describe the postcranial skeleton of *Allodaposuchus* and compare it with other stem and crown eusuchians, 2) enhance the phylogeny of basal eusuchians and, especially, shed light on the conflicting phylogenetic relationships of the genus *Allodaposuchus*, 3) describe the habitat and palaeoecology of the new specimen, and 4) provide new data on the species diversity and palaeobiogeography of Late Cretaceous eusuchians in Europe.

Geological setting

The Tremp Formation [12] consists of transitional and continental materials deposited in an E–W foreland trough and following a marine regression that began near the Campanian–Maastrichtian boundary [13]. After the uplift of the Pyrenean range, these deposits were separated into four main synclines which are, from the east to west: Vallcebre, Coll de Nargó, Tremp and Àger. In the south-central and south-eastern Pyrenees, Rosell *et al.* [14] divided the Tremp Formation, or the so-called 'Garumnian' facies [15], into four lithologic units, which are from the base to the top: i) a transitional 'grey unit' (marls, coals, limestones, and sandstones), ii) a fluvial 'lower red unit' (mudstones, sandstones, oncoids, and paleosols), iii) the lacustrine 'Vallcebre limestone and laterally equivalent strata' and, iv) a fluvial 'upper red unit' (mudstones, sandstones, conglomerates and limestones). At the Vallcebre Syncline, the two former units are Maastrichtian in age whereas the two later are Paleocene, according to charophyte biostratigraphy [16] and magnetostratigraphy [13].

In the Fumanya Sud locality (Vallcebre Syncline), the studied specimen was found approximately 30 meters above the base of the Tremp Formation within a 45 meter thick sequence of alternating dark mudstones, limestones and lignites (Figs. 1 and 2). The sequence is included in the 'grey unit' of Rosell *et al.* [14], more specifically within the 'middle grey garumnian' of Villalba-Breva *et al.* [17]. The sedimentological analysis and the palaeontological content (charophytes, coals, rooting structures and brackish to freshwater mollusks) of this part of the sequence suggest a lacustrine-palustrine environment [17], as part of a more extensive lagoon [13, 14, 18]. Magnetostratigraphy indicates an early Maastrichtian age for the site, within the C31r [13].

The crocodylomorph fossils occurred at the lower part of a dark organic-matter-rich mudstone (about 40 centimeters in thickness. Fig. 2A). It corresponds to the F2 facies of Oms *et al.* [13] and overlays a 10-cm thick limestone with

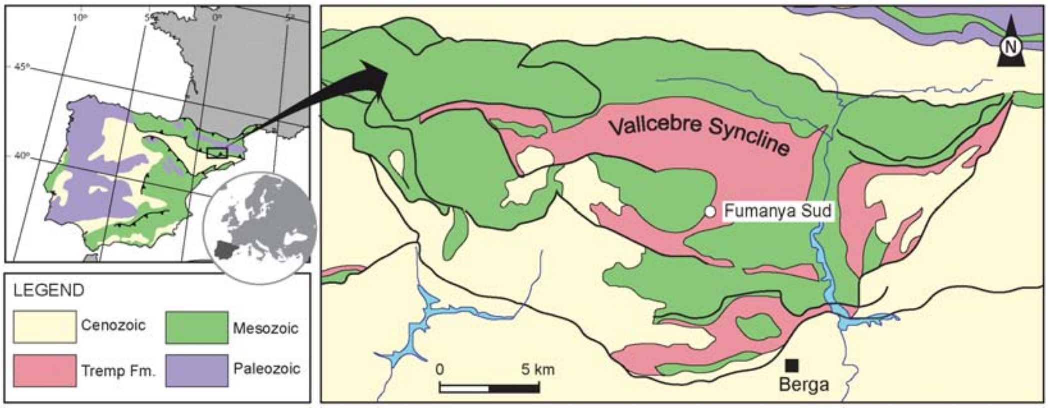

Fig. 1. Geological setting of the Fumanya Sud locality within the Iberian Peninsula.

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synsedimentary microkarstification that evidences probable sporadic subaerial exposure. Forty centimeters below the limestone there is a 10-cm thick black mudstone, usually mistaken with coal. The absence of root marks suggests parautochthonous accumulation of organic matter in coals overlaying black mudstones.

Materials and Methods

Studied material

The studied material consists in a disarticulated specimen (MMC829 - MMC894, B-FUM017-62, B-FUM107-71) housed at the Museu de les Mines de Cercs (Sant Corneli, Barcelona, Spain). The Departament de Cultura de la Generalitat de Catalunya issued the permission for the studied locality. All necessary permits were obtained for the described study, which complied with all relevant regulations.

The specimen herein described was discovered by one of the authors (B.V.) during prospecting works conducted in 2004 at the Fumanya Sud locality and was excavated during three subsequent field campaigns, between 2004 and 2008, under the permission of the Government of Catalonia. Small hand tools facilitated exposure of the bones that were then consolidated and mapped using a metric grid and graph paper, within a digging transect of about 2.5 m long and 30 cm thick (Fig. 2B). Final works at the site consisted in the removal of the contiguous upper sediments around the bone accumulation in order to rule out the presence of more fossils at deeper levels. During the fieldwork, a stratigraphic section was drawn for a 1.5 m-thick interval that contained the crocodylomorph bones. After

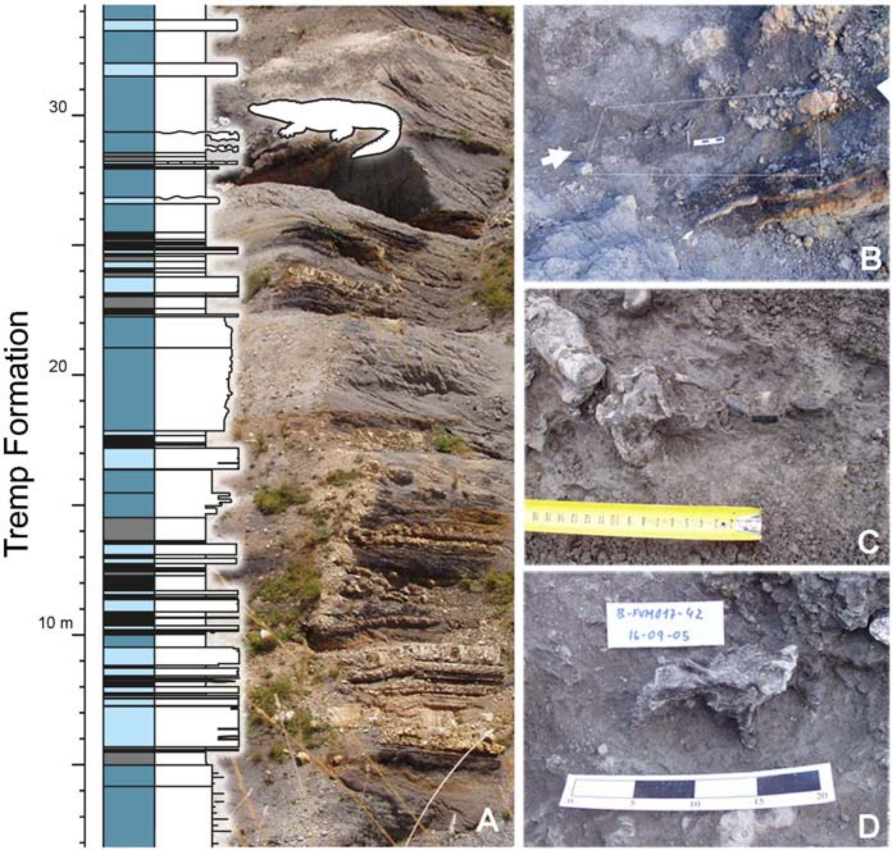

Fig. 2. Stratigraphic location and field aspect of the crocodilian fossils at the Fumanya Sud locality. A, stratigraphic log and outcrop view of the sequence of alternating dark mudstones, limestones and lignites in the 'grey unit' with indication of the bone-bearing horizon. B, metric grid used to mapping the fossils along a digging transect of about 2.5 m long and 30 cm thick. C, field aspect of a lumbar vertebra, a partial tibia and some rib fragments. D, Dorsal vertebra (D5) preserving the centrum and parts of the apophyses in connection with the neural arch, as found in the outcrop. Scale bars in centimeters.

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preparation, crocodylomorph fossils were housed at the Museu de les Mines de Cercs.

Morphological characters of the Fumanya specimen were compared with basal eusuchians (*Isisfordia duncani*, in Salisbury *et al.* [19]), hylaeochampsids (*Pietraroiasuchus ormezzanoi*, in Buscalioni *et al.* [2]), related species of genus *Allodaposuchus* (*A. precedens* [8]; *A. subjuniperus* [5]) and *Arenysuchus gascabadiolorum* [4], gavialoids (*Gavialis gangeticus* Gmelin, in Brochu [20]), basal alligatoroids (*Diplocynodon hantoniensis* Wood, in Brochu [20]; *Musturzabalsuchus buffetauti*, in Buscalioni *et al.* [21], *Massaliasuchus affluvelensis* [11] and crocodyloids (*Crocodylus acutus* Cuvier, in Mook [22]). In addition, postcranial skeletons of extant crocodyloids (*Crocodylus niloticus* Laurenti (MZB 2003-1423), *Osteolaemus tetraspis* Cope (MZB 2006-0039) and alligatoroids (*Alligator mississipiensis* Daudin, MZB 92-0231, MZB 2006-0613), housed at the collection of the Museu de Ciències Naturals de Barcelona, were used for comparisons and measurements.

Cladistic analysis

Phylogenetic relationships of the specimen from Fumanya were explored using the dataset of Brochu [3]. However modifications in some operational taxonomic units (OTUs) and characters were carried out (see S1 Information).

The whole dataset resulted in 85 OTUs, which were coded for a total of 181 craniodental and postcranial characters. The taxon *Bernissartia fagesii* Dollo was used as outgroup. Two matrices were used for analyses. The first one included both craniodental and postcranial characters and the second one included craniodental characters only (see S2 and S3 Information). Datasets were analysed with TNT v1.1 (Willi Hennig Society Edition, [23]). Tree-space was searched using a heuristic search algorithm (traditional search method) with tree-bisection-reconnection branch swapping and 1,000 random addition replicates holding 10 most parsimonious trees for each replicate. All characters were equally weighted and multistate characters were unordered. Bremer supports and bootstrap frequencies (1,000 bootstrap replicates searched) were used to assess the robustness of the nodes.

Palaeobiogeographic analysis

In recent times, the development of mathematical models to infer the ancestral area of origin for a certain taxonomic group has improved our understanding on how speciation patterns work in both present and past times. These types of biogeographical analyses rest upon phylogenetic relationships, known geographical distribution of the taxa, and their time-range. In order to explore the historical palaeobiogeography of Crocodylia and especially to establish the role that *Allodaposuchus* played in the early radiation of the group, we reconstruct the ancestral area by using the Statistical Divergence-Variance methodology (S-DIVA) developed by Yu *et al.* [24]. The phylogenetic matrix employed in the phylogenetic study was implemented in RASP 2.1 software [25]. Geographic distribution of extant and fossil taxa used in the analysis, which was gathered from the literature, was established according to major continental landmasses, those including Europe, North America, South America, Asia, Africa, and Australia. Combination of two geographically close related areas (i.e., North America + Europe or Asia + Europe) was also considered for the present analysis.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub: 74D0FF1E-4095-4E07-A11A-31DFCE17B51E. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Systematic Palaeontology

Superorder CROCODYLOMORPHA
Order CROCODYLIFORMES Hay, (*sensu* Benton and Clark)
Suborder EUSUCHIA Huxley,
Unranked CROCODYLIA Gmelin, (*sensu* Benton and Clark)
Genus *Allodaposuchus* Nopcsa,

Emended diagnosis for the genus

Allodaposuchus differs from all other eusuchians by the exclusive combination of the following synapomorphies: margin of the orbits upturned; quadrate and squamosal not in contact on the external surface of the skull, posteriorly to the external auditory meatus; caudal margin of otic aperture not defined and gradually merging into the exoccipital; dermal bones roof overhang rim of supretemporal fenestra; cranioquadrate passage or canalis quadratosquamosoexoccipitalis laterally open and represented by a sulcus (broader than in *Hylaeochampsa vectiana* [26]), with the exoccipital between the squamosal and the quadrate posterior to otic aperture. Ventral process of the exoccipital not involved in the basioccipital tubera; quadrate foramen aereum on dorsal surface.

Allodaposuchus palustris sp. nov.

(Figs. 3–7)
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Etimology

palustris, from Latin ‘‘palus’’, swamp.

Diagnosis

Lack of shallow fossa in the rostromedial margin of the supratemporal fenestra; frontoparietal suture slightly concavoconvex; exoccipital without boss on

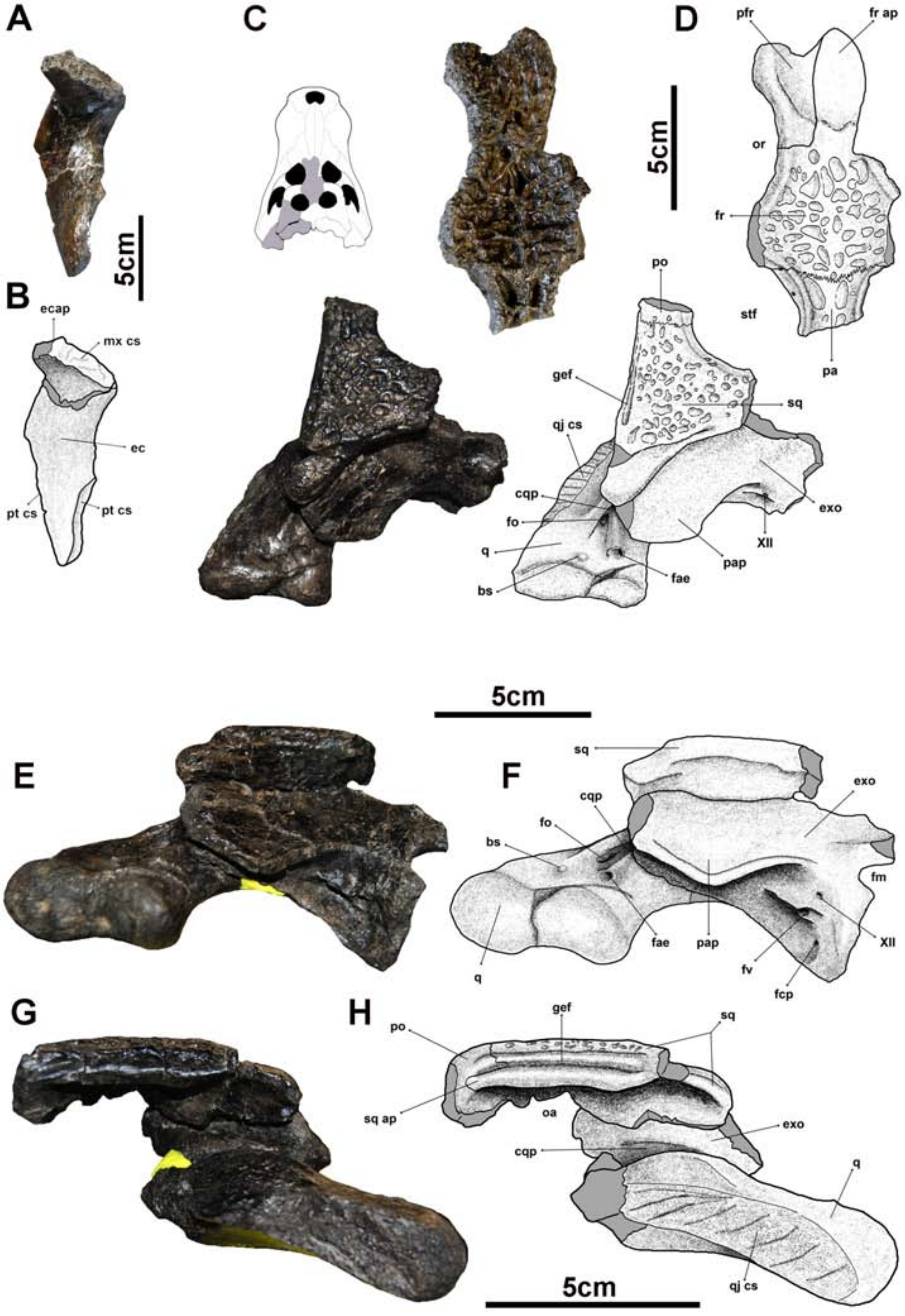
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Fig. 3. Cranial remains of *Allodaposuchus palustris* sp. nov. from the Fumanya locality. A, ectopterygoid; B, interpretative drawing of A; C, reconstruction of the skull table and left posterior part of the skull in dorsal view with original bones (marked in grey in the small skull drawing); D, interpretative drawing of C; E, squamosal, exoccipital and quadrate in posterior view; F, interpretative drawing of E; G, H, the same bones and interpretative drawing in lateral view. Abbreviations: XII, foramen for cranial nerve XII; bs, boss; cqp, canalis quadratosquamosoexoccipitalis; ec, ectopterygoid; ecap, ectopterygoid anterior process; exo, exoccipital; fae, foramen aërum; fcp, carotid foramen; fm, foramen magnum; fo, foramen; fr, frontal; fr ap, frontal anterior process; fv, foramen vagi; gef, groove for ear flap; mx cs, maxillar scar; oa, otic aperture; or, orbit; pa, parietal; pap, paropcipital process; pt cs, pterygoid scar; pfr, prefrontal; po, postorbital; q, quadrate; qj cs, quadratojugal contact surface; sq, squamosal; sq ap, anterior process; stf, supratemporal fenestra.

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paraoccipital process; large foramen aereun in quadrate; short and robust teeth with two very marked longitudinal grooves close to the carinae; teeth with strong ornamentation developing false-ziphodont crenulations; anterior process of the ilium more developed.

Ambiguous autapomorphies: neural spine of the axis with a medial depression; keel of the axis occupies completely the ventral side of the centrum; iliac blade with very rounded and wrinkled superior border, and elevated posterior process; large distal end of the calcaneum. We prefer coding all these autapomorphies as ambiguous, due to the absence of postcranial remains in other species of *Allodaposuchus*. New discoveries may reveal if they are autapomorphies of the genus.

Holotype

The holotype is a partial skeleton (housed in the Museu de les Mines de Cercs, Barcelona) that comprises 9 isolated teeth (MMC-829a, MMC-829b, MMC-846, MMC-850, MMC-851, MMC-854, MMC-856, MMC-879, FUM017-62), one fragmentary dentary (MMC-857, MMC-870, MMC-876, MMC-881), left prefrontal and fused frontals (MMC-892), left squamosal (MMC-859), left ectopterygoid (MMC-864), left quadrate (MMC-862), 2 articulars (MMC-834, MMC-871), left exoccipital (MMC-866), 4 cervical vertebrae (MMC-849, MMC-865, MMC-875, MMC-883), 7 dorsal vertebrae (MMC-839, MMC-853, MMC-869, MMC-872, MMC-873, MMC-882, MMC-890), 2 lumbar vertebrae (MMC-835, MMC-888), 3 caudal vertebrae (MMC-843, MMC-886, FUM017-71), 2 well preserved ribs (MMC-840, MMC-842), one right humerus (MMC-861, MMC-894), one left radius (MMC-889), one left ilium (MMC-838), one fragment of the left femur (MMC-863), a fragmentary left tibia (MMC-833), left fibula fragments (MMC-830, MMC-844), left calcaneum (MMC-837), left astragalus (MMC-891), and two phalanges (MMC-832 MMC-844).

Locality, age and horizon

Fumanya Sud (North Barcelona, Catalonia), early Maastrichtian (C31r) as determined by charophyte biostratigraphy and magnetostratigraphy [13]. The fossil-bearing horizon is found 29 meters above the top of ''concrete level'', the basis of the Tremp Formation [13].

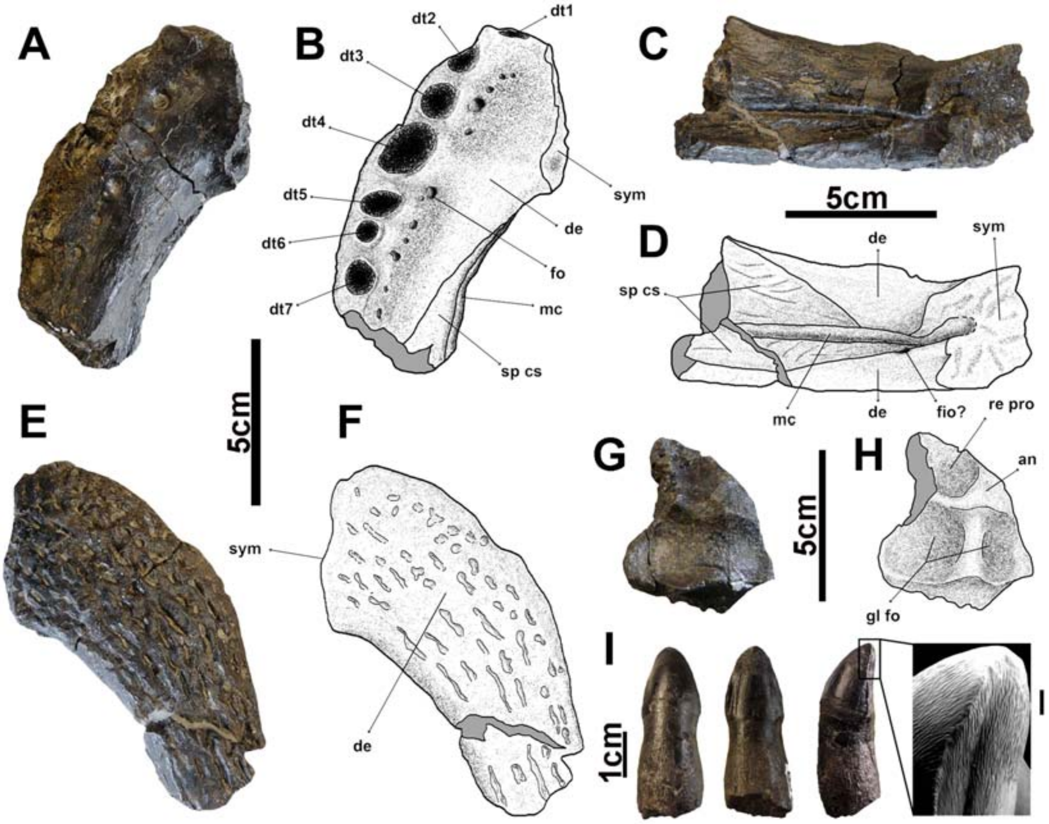

Fig. 4. Mandibular bones and teeth of *Allodaposuchus palustris* sp. nov. from the Fumanya locality. A, C, E, anterior tip of the left dentary in occlusal, lingual and ventral views; B, D, F, interpretative drawings of A, C and E; G, articular; H, interpretative drawing of G; I, a tooth in labial, lingual and lateral views and a detail of the ornamentation of the crown surface (scale 1 mm). Abbreviations: an, angular; dt1-7, tooth alveoli1-7; de, dentary; fim, foramen intermandibularis oralis; fo, foramen; gl fo, glenoid fossa; mc, Meckelian canal; re pro, retroarticular process; sp cs, splenial scar; sym, symphysis.

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Description

Cranial skeleton

The cranial remains were scarce, fragmentary and disarticulated (Fig. 3 and 4). Nevertheless, some identifiable elements have been preserved such as the left anterior region of the dentary and other undetermined parts of the dentary, the left and right articular, several isolated teeth, the left ectopterygoid, the frontal, part of the left prefrontal, the left squamosal, the left exoccipital and the left quadrate. Despite being isolated, these cranial elements, allowed a detailed description of each one and the main morphology of the skull table, left occipital region and part of the skull openings.

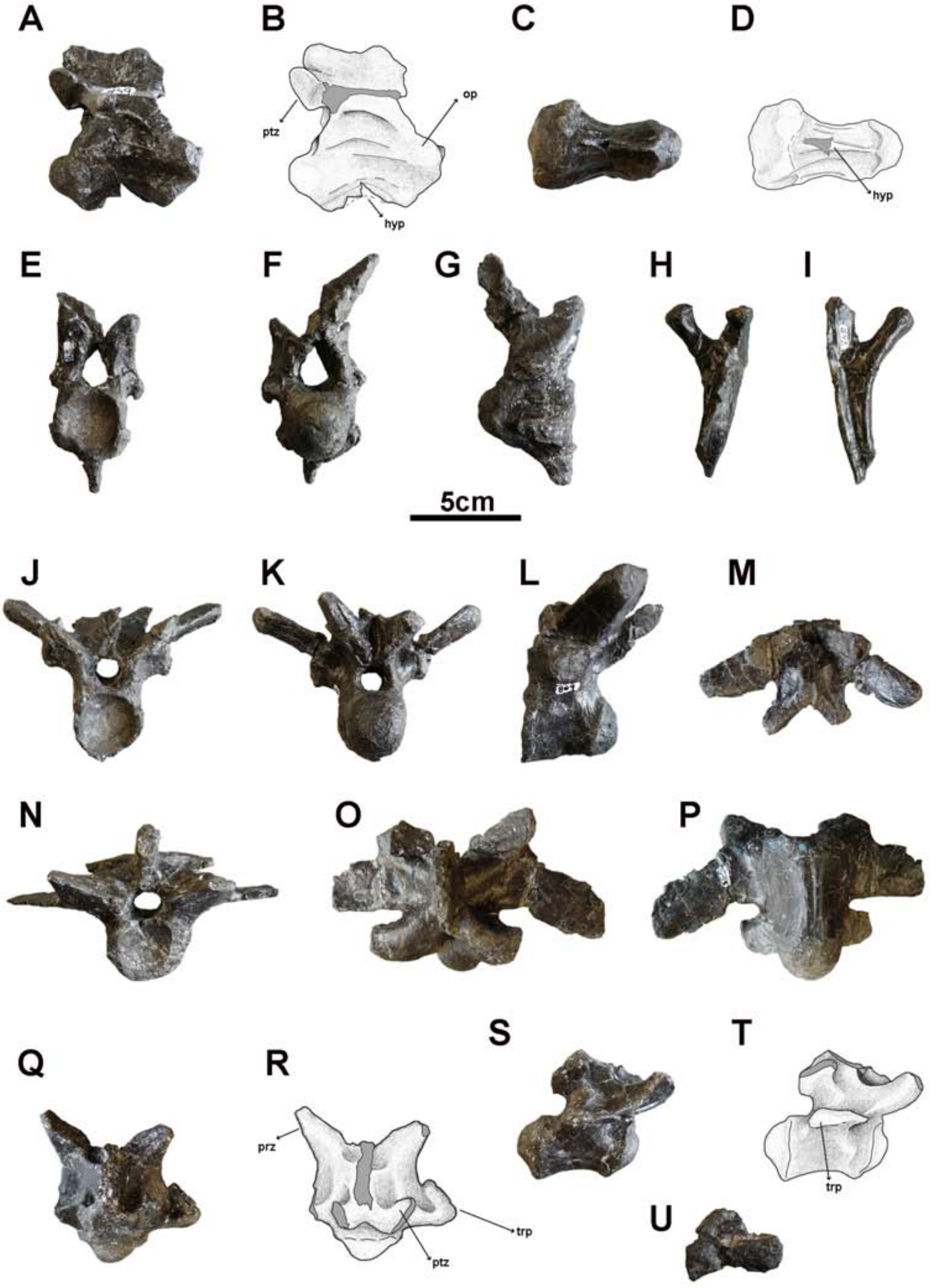
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Fig. 5. Axial skeleton bones of *Allodaposuchus palustris* sp. nov. from the Fumanya locality. A, left side of the axis; B, interpretative drawing of A; C, ventral view of the axis; D, interpretative drawing of C; E–G, 7th cervical in anterior, posterior and lateral views; H–I, proximal part of the eighth cervical rib in lateral and medial views; J–M, 5th dorsal vertebra in anterior, posterior, lateral and dorsal views; N–P, 2nd lumbar vertebra in anterior, dorsal and ventral views; Q, S; first caudal vertebra in dorsal and lateral view; R, T, interpretative drawings of Q and S; U, undetermined caudal vertebra. Abbreviations: hyp, hypapophysis; op, odontoid process; prz, prezygapophysis; ptz, postzygapophysis; trp, transverse process.

doi:10.1371/journal.pone.0115837.g005

Cranial openings

All the medial rim of the left orbit is preserved being able to interpret its general morphology (Fig. 3C). The orbits are relatively large, rounded and slightly elongated rostrocaudally with their rostromedial margin somewhat elevated. In

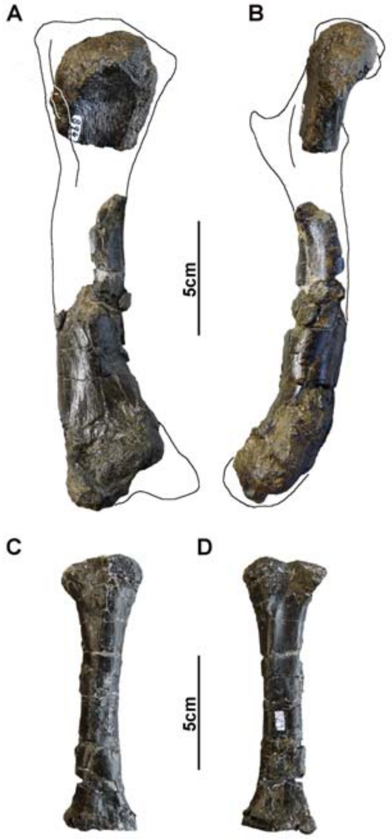

Fig. 6. Forelimb bones of *Allodaposuchus palustris* sp. nov. from the Fumanya locality. A–B, humerus in medial and frontal views; C–D; radius in lateral and medial views.

doi:10.1371/journal.pone.0115837.g006

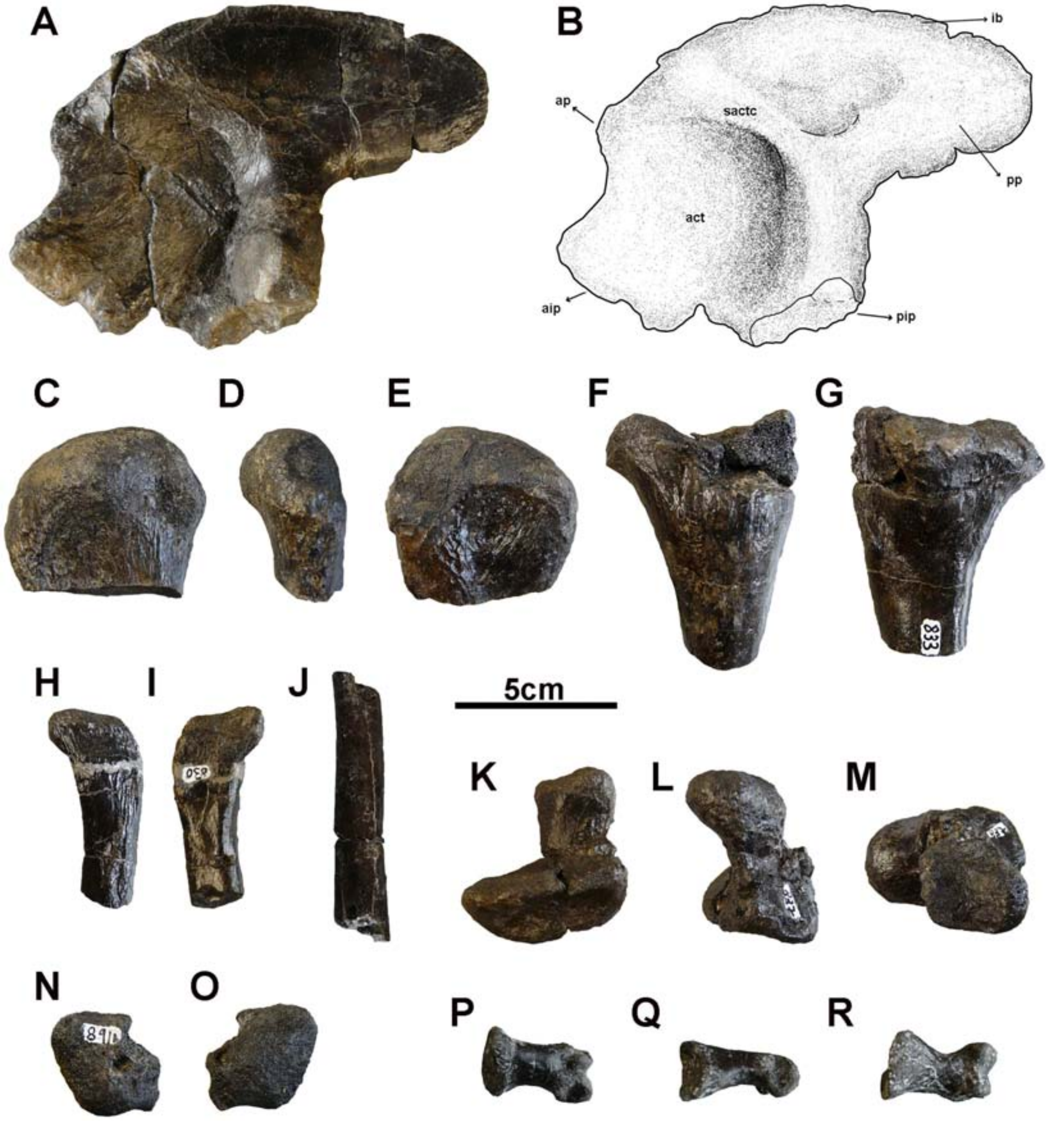

Fig. 7. Pelvic scar and hindlimb bones of *Allodaposuchus palustris* sp. nov. from the Fumanya locality. A, left ilium in lateral view; B, interpretative drawing of A; C–E, proximal epiphysis of the left femur in anterior, lateral and posterior views; F–G, proximal epiphysis of the left tibia in anterior and posterior views; H–J, proximal fragment and diaphysis of the left fibula; K–M, calcaneum in distal, lateral and anterior views; N–O, astragalus in anterior and posterior views; P–R, undetermined phalanx in dorsal, lateral and ventral view. Abbreviations: act, acetabulum; aip, anterior ischiadic process; ap, anterior process; ib, iliac blade; pip, posterior ischiadic process; pp, posterior process; sactc, supracetabular crest.

doi:10.1371/journal.pone.0115837.g007

lateral view, the prefrontal-frontal suture in the medial wall of the orbit is vertical. There are several foramina in the medial wall of the orbit, the largest is placed in the prefrontal and there are five smaller foramina rostrocaudally aligned in the frontal.

Only the rostromedial and caudolateral margins of the left supratemporal fenestra are preserved (Fig. 3C). The supratemporal fenestra is circular and smaller than the orbits. The skull roof overhangs the fenestra in the medial and caudolateral rims. There is no shallow fossa forming a step or notch in the rostromedial margin of the supratemporal fenestra, being this wall almost vertical. There are two foramina in the rostromedial and medial wall of the supratemporal fenestrae, one is located on the frontoparietal suture and the second one is placed in the parietal.

The quadrate, the squamosal and the exoccipital are fully preserved and it is possible to reconstruct the partial morphology of some structures related with the otic region (Fig. 3C–H). The otic aperture does not have a sharp posterior rim, and the cranioquadrate passage forms a caudolaterally open sulcus called canalis quadratosquamosoexoccipitalis [7, 8, 27]. The squamosal and the quadrate are not in contact posteriorly to the otic opening, being the exoccipital between these two bones (Fig. 3G–H).

Ectopterygoid

The left ectopterygoid (MMC-864) is fully preserved (Fig. 3A–B). It is very broad and robust, with the anterior process strongly ventrolaterally twisted. However, this region is partially broken and glued, and this torsion may be a deformation effect. Because the ectopterygoid was recovered isolated, the exact contact relationships with the maxilla and the pterygoid are unknown, and the overall shape of the suborbital fenestra cannot be interpreted.

Frontal

The frontals are fused into a whole single bone (MMC-892) and part of the left prefrontal is also preserved (Fig. 3C–D). The anterior process of the frontal is separated from its main body approximately in the middle of the medial margin of the orbits. This anterior process is heavily ornamented with pits and grooves and it is lanceolate in shape being probably shorter than the prefrontal. The preserved part of the prefrontal is upturned forming a transverse ridge in the rostromedial margin of the orbits. The main body of the frontal is slightly concave. The frontal forms the caudomedial corners of the orbits and part of the rostromedial edges of the supratemporal fenestrae. The frontoparietal suture is slightly concavo-convex and enters the rostromedial margins of the supratemporal fenestrae.

Squamosal

Only the left squamosal (MMC-859) has been preserved and it is almost complete (Fig. 3C–D). The squamosal forms the caudolateral margin of the supratemporal fenestra overhanging it. Its dorsal surface is flat, horizontal and fully ornamented with circular pits. The lateral margins of the skull table appear to be straight rather than curved or convex. The posterior region is formed by a squamosal prong that projects caudoventrally to contact the exoccipital, the squamosal and the quadrate are not in contact in this region (Fig. 3E–H). This prong lacks ornamentation and is not laterally projected. In lateral view there are two nearly parallel rims that form the groove for the attachment of musculature for the ear valve (Fig. 3G–H). The squamosal has a lobular anterior process that extends ventrally to the caudodorsal end of the postorbital (Fig. 3G–H).

Quadrate

The left quadrate (MMC-862) is almost fully preserved (Fig. 3C–H). The surface of the quadrate is smooth, without ornamentation. Its dorsal surface has a sulcus caudolaterally directed from the otic aperture that forms the ventral margin of the canalis quadratosquamosoexoccipitalis. This canalis is laterally delimited by a marked crest and the medial margin of the canalis is delimited by the exoccipital (Fig. 3E–H). At the end and within the canalis there is a foramen, and posterior to this foramen there is a marked circular boss (Fig. 3D, F). Medially to the foramen and boss, there is a large foramen aërum on the dorsal surface of the quadrate (Fig. 3D, F). Both quadrate hemicondyles are slightly dorsoventrally expanded. The lateral hemicondyle is larger, and both hemicondyles are rounded (Fig. 3C–F). The ventral surface of the quadrate is very smooth without well-marked crests.

Exoccipital

Only the left exoccipital (MMC-866) has been preserved (Fig. 3E–F). The ventrolateral region of the paroccipital process forms a well-marked crest caudoventrally directed, but there is no boss on paroccipital process. The paroccipital process is short and just slightly surpasses laterally the caudolateral aperture of the canalis quadratosquamosoexoccipitalis, which remains laterally opened. In posterior view, although the basioccipital is not preserved, it seems that the ventral process of the exoccipital is short, smooth and not involved in the basioccipital tubera. This is due to none rugose posterior expansion is observed in this region (Fig. 3E–F). Below the paroccipital process there is a concave region crossed by ridges that surround the large foramen vagi. The foramen for the XII cranial nerve and the carotid foramen are smaller and difficult to distinguish.

Mandible

The most anterior tip of the left dentary (MMC-876) has been preserved. Furthermore, undetermined parts of the mandible (MMC-857, 870, 881) and part of the left (MMC-871) and right articulars (MMC-834) have also been recovered. The anterior region of the dentary has the alveolar margin at the same dorsal height. The first seven alveoli of the dentary are preserved (Fig. 4A–B) and they are slightly dorsolaterally projected. The largest tooth alveolus is the fourth, being almost twice as large as the other preserved alveoli. The ventrolateral surface of the dentary (Fig. 4E–F) is densely vascularized with elongated grooves. The dentary symphysis is short and extends back to the level of the fourth dentary alveolus

(Fig. 4A–D). The dorsomedial surface of the dentary is broad and smooth between the symphyseal surface and the tooth row. Medially to the tooth alveoli, the dentary is strongly vascularized with small and aligned foramina (Fig. 4A–B). The splenial is not preserved, but its attachment scar on the medial surface of the dentary can be observed. The splenial does not enter in the symphysis and its anterior tip is ventrally placed to the Meckelian canal (Fig. 4C–D). There is a foramen in the anterior most tip of the splenial-dentary contact, but we cannot know if the splenial was perforated by the intermadibularis oralis foramen. The left and right articulars have been partially preserved but they provide little information due to their fragmentary nature (Fig. 4G–H).

Dentition

Several isolated teeth have been preserved (MMC-829, 846, 850, 851, 854, 856, 879, and FUM017-62). All teeth have a similar morphology and only vary in size and elongation degree. The teeth are conical to lanceolate, relatively short and robust, with the labial surface more convex than the lingual surface (Fig. 4I). They show a slight constriction in the base. The carinae are well developed in the anterior and posterior views of the teeth. In the lingual surface two very marked longitudinal grooves close to the carinae are developed. The teeth have strong ornamentation composed of numerous and fine longitudinal ridges, conspicuous to the apex, that present a strong anastomosis that crosses the carinae developing false-ziphodont crenulations.

Axial skeleton

Axis

The axis (MMC-849) is a characteristic vertebra (Fig. 5A–B). The neural arch is low. It is 4.8 cm high at its posterior end and the spine is low and elongated craniocaudally. The anterior border of the spine is slightly rugose and slightly thickened compared to the posterior one. At its middle part, the spine makes a small depression, which is concave in lateral view. The spine projects caudally beyond the postzygapophyses. The anterior end of the neural arch is broken and the shape of the prezygapophyses is not clearly recognisable. The postzygapophyses face obliquely ventrolaterally. Tubercular and capitular facets are located in the odontoid process (Fig. 5A). The neural arch and the odontoid process are completely sutured to the centrum, suggesting an adult specimen. The centrum is 7.05 cm long and ventrally keeled. The keel (hypapophysis) is a thin layer and completely occupies the ventral side of the centrum (Fig. 5C–D), which is slightly convex ventrally in lateral view forming an obtuse angle of 145°.

Remaining cervical vertebrae

The third (MMC-875), fifth (MMC-865) and seventh (MMC-883) (Fig. 5E–G) cervicals are also preserved. They are higher than wide. The neural spine is lost in all the three vertebrae. Along the cervical series, the diapophyses are progressively oriented from ventral to perpendicular to the sagital plan. Therefore, the tubercular facets, located in the diapophyses, face ventrolaterally in the third and fifth cervicals, whereas are nearly flat in the seventh cervical. Zygapophyses are oriented craniocaudally, nearly parallels to the longitudinal axis. The centra are procoelous and cranially keeled in the ventral side, but the keel is only completely preserved in MMC-883 (Fig. 5E–G). Their lengths are similar (~4.7 cm) along the series, but their diameters increase progressively from 3.0 to 3.7 cm. In the three vertebrae, the capitular facets are located in the parapophyses, in a lower position within the centrum.

Dorsal vertebrae

The preserved dorsal vertebrae have been sorted based on the presence/absence of keels as well as their shape, and the location of the parapophyses. The first, third and fifth dorsal vertebrae (MMC-873, 872 and 869 respectively) and other four dorsals of uncertain position (MMC-853, MMC-882, MMC-839, MMC-890) have been recovered. The shape of the first and third dorsals resembles that of the cervicals. The spines are relatively high, the keel is prominent, and the capitular facets are located in the parapohyses, but in an upper position within the centrum. The fifth dorsal (Fig. 5J–M) is not much different, but it presents a vestigial keel. It also has lost the parapophyseal processes and the capitular facets are located at the base of diapophyses (Fig. 5L). The neural arch and spine seem to progressively increase in high and bend caudally. It is about 4.8 cm high in D1 but incomplete in the others. Diapophyses also increase in size caudally (7.9 to 10.8 cm in D1 and D5, respectively). Zygapophyses are broader than those of the cervicals and dorsomedially oriented. The centra are procoelous and similar in length (~5 cm) and diameter (~ 3.7 cm) to the last cervical.

The last four vertebrae are too eroded to perform a detailed description. They are believed to be equal or posterior to the sixth dorsal position, based on the morphology of the diapophyses, the position of the parapophyses and the absence of the keel. Some of them preserve a part of the neural arch and the postzygapophyses, but none is complete. Zygapophyses are broader than those from the anterior dorsals and cervicals, and are laterally oriented. Neither the parapophyses nor the keel are present in the centrum. In addition, the centra are slightly longer (up to 5.8 cm) than those from the anterior dorsals.

Lumbar vertebrae

The first (MMC-888) and second (MMC-835) lumbar vertebrae are present (Fig. 5N–P). These two lumbar vertebrae are similar in shape, but L1 is slightly smaller in size. They are slightly eroded. The neural spines are craniocaudally wide and lower (1.6 cm high) than those of the dorsals and cervicals. Transverse processes and zygapophyses are elongated and broad (~12.5 cm wide in L2). The centra are procoelous and longer (~7.5 cm in L2) than those of the anterior vertebrae. The L2 has a longitudinal groove ventral to the centrum (Fig. 5P).

Caudal vertebrae

Only three caudal vertebrae have been recovered (MMC-843, MMC-886, FUM017-71). The left transverse process, postzygapophyses and the end of the neural spine are not preserved in the largest caudal (MMC-843, Fig. 5Q–T). Its right transverse process is very short (1.5 cm long) and thick (Fig. 5Q–R). Prezygapophyses are oriented craniolaterally, and their articular surfaces are wide, long and face medially. MMC-843 is identified as the first caudal vertebrae based on the biconvex centrum, unique through the complete axial skeleton of eusuchians (Fig. 5S–T). The centrum is similar in size (~7 cm long) to the lumbars. The MMC-886 is interpreted as a middle to posterior caudal vertebra (Fig. 5U). No transverse process is present and the lateral surface is smooth. The centrum is elongated, 4.6 cm long, and the neural spine is broken and eroded. The FUM017-71 is a more posterior caudal vertebra. It is similar in shape to MMC-886, but smaller in size (4.4 cm long).

Ribs

MMC-842 and MMC-840 are C8 and D1 left ribs, respectively. The ribs of the eighth cervical are intermediate in form between the cervical and dorsal ribs (Fig. 5H–I). The anterior process of the shaft of a typical cervical rib is present in the rib of C8. The process is thin, extends cranially from the shaft, below the capitulum and tuberculum. These two articular processes are similar in length, width and angle respect to the shaft, making a symmetrical shape for the proximal part of the bone. The shaft is flattened, and presents a long groove in the ventral side. The rib of the first dorsal vertebra is similar in shape, but its anterior process is vestigial and the ventral grove is lesser. The distal end of the shaft is broken for the two ribs. Other rib fragments were recovered, but their location is uncertain due to their fragmentary nature.

Appendicular skeleton

Humerus

The right humerus was recovered in two fragments (Fig. 6A–B). MMC-894 is the proximal end. The anterior and posterior surfaces of the bone fragment, immediately distally to the proximal articular surface, are greatly roughened. This is consistent with the attachment of strong ligaments. The bone is broken or eroded before the deltopectoral crest, so no description is possible for this structure. MMC-861 is the distal half of the same bone. The cortical bone in both articular surfaces is also eroded, but the general shape can be observed. The articular surface of the distal end shows two condyles and faces caudoventrally (i.e. the distal part of the bone is slightly ventrally curved) (Fig. 6B). The lateral surface of the humerus is slightly convex and the medial slightly concave.

Radius

MMC-889 is a slender bone, 12.3 cm long, expanded at both proximal and distal ends, which is interpreted as a left radius (Fig. 6C–D). The distal expansion is fore and aft only whereas the proximal end is both fore and aft and laterally expanded. The shaft is elliptical in cross-section. A soft groove can be observed in the medial side of the proximal end (Fig. 6D).

Ilium

The ilium (MMC-838) is very irregular in outline, 10.4 cm high (from posterior ischian process to dorsal blade) and 14.5 cm long (from anterior ischian process to posterior tip of the blade) (Fig. 7A–B). It is extended caudally into a conspicuous posterior process. The anterior end of the blade does not extend cranially than the anterior process which articulates with the ischium. The superior border of the iliac blade is very rounded and wrinkled. The anterior process of the ilium is sharp and extends craniodorsally, near the anterior end of the blade. The posterior process is in a very elevated position. Its external surface is smooth. The posterior tip of the blade is slightly blunt. The ilium has two distinct articulations with the ischium and none for the pubis. Both ischiadic surfaces are situated on stout processes anteriorly separated by a thin wall bone. The anterior ischian process is orientated in a right angle respect to the posterior process. This latter is laterally expanded. The external surface of the ilium is deeply concave between these two ischiadic processes constituting a closed acetabulum. The internal surface of the iliac crest is mainly smooth, but there are wrinkled areas at the superior margin and in the posterior end. The inferior portion of the same internal surface is also occupied by rough surfaces which articulated with the supposed two sacral vertebrae. These areas are separated from each other by a prominent vertical ridge.

Femur

The bone (MMC-863) is interpreted as a proximal articular surface of the left femur (Fig. 7C–E). It is craniocaudally flattened (Fig. 7D) and 6.2 cm wide. The articular surface of the head is large, round and very rough. The cranio-medial border near the proximal end is convex (Fig. 7C). The caudal surface is concave, with a ridge in the middle, under the articular surface (Fig. 7E). The bone is broken before the fourth trochanter position.

Tibia

The bone (MMC-833) is massive and interpreted as the proximal end of the left tibia (Fig. 7F–G). The articular surface is subtriangular in outline, with the apex of the triangle cranially directed and slightly concave. The proximal portion of the shaft is stout and triangular in section, ornamented with fine longitudinal striations. It is laterally constricted near the anterior side, and it presents a small ridge in its caudolateral side (Fig. 7G). The central portion of the shaft is much more slender than the proximal end. Its section is elliptic.

Fibula

They are elongated and slender bones (Fig. 7H–J). The MMC-830 (Fig. 7H, I) is a left proximal end and MMC-844 is a broken shaft (Fig. 7J). The proximal end is expanded and at the same time flattened. In the external side, there is a conspicuous wrinkled area for the attachment of ligaments (Fig. 7H). In the inner side, near the proximal end, there is a smooth surface for the articulation with the tibia showing a rugosity below it within a conspicuous groove (Fig. 7I). The external surface of the partial shaft is smooth, without rugosity. The central portion of the shaft is cylindrical in cross-section.

Calcaneum

This bone (MMC-891) extends medially with a very short shaft of 3.8 cm and has an expanded distal end (Fig. 7K–M). This expanded end is very elongated (5.2 cm), robust and conform the larger side of the bone. It contacted with the distal edge of the fibula in its proximal end and the astragalus at the middle of the shaft.

Astragalus

MMC-891 is a massive irregular bone 3.2 cm long and 3.4 cm high. The articular surfaces with the tibia and fibula are eroded, but bone is almost complete (Fig. 7N–O), including the fossa for the calcaneum.

Phalanges

Two indeterminate phalanges were recovered. MMC-844 is 3.3 cm long and its proximal end is incomplete. It probably is a first phalange. MMC-832 (Fig. 7P–R) is 3.1 cm long and may be a second phalange. It is not possible to elucidate if they belong to the manus or pes.

Comparison

Cranial remains were compared with species within genus *Allodaposuchus*, hylaeochampsids, *Massaliasuchus*, *Musturzabalsuchus* and *Arenysuchus*. Postcranial bones were compared with available postcranial skeletons of extant crocodylids, alligatorids, gavialids and of the extinct *Diplocynodon*, *Pietraroiasuchus ormezzanoi* and *Isisfordia duncani*.

The external otic region suggests relationship of the specimen from Fumanya (*Allodaposuchus palustris*) with hylaeochampsids and the genus *Allodaposuchus*. The caudal margin of the external otic aperture is different from that of modern crocodylians and most of fossil crocodylomorphs. In the same way as *Hylaeochampsa*, *Allodaposuchus* and *Goniopholis*, the otic aperture of *A. palustris* has not a sharp posterior rim, and the cranioquadrate passage forms the canalis quadratosquamosoexoccipitalis. The quadrate of the studied specimen lacks a dorsal projection medially to the canalis contacting the base of the squamosal at the otic aperture, and the medial margin of the canalis is delimited by the exoccipital. Quadrate foramen aereum is comparatively large than *A. subjuniperus*, *A. precedens* or *A. subjuniperus*. Both quadrate hemicondyles are more dorsoventrally expanded than in other basal eusuchians such as *A. subjuniperus*, *A. precedens* or *Hylaeochampsa*. Nevertheless, the hemicondyles do not show the typical expansion observed in most crocodyloids.

The Fumanya specimen shows some skull and jaw characters related to *Allodaposuchus* species. However, it differs in other features from this genus and hylaeochampsids. Unlike other basal eusuchians from the upper Cretaceous of Europe such as *A. precedens*, *A. subjuniperus*, *Arenysuchus* or *Hylaeochampsa*, there is no shallow fossa in the rostromedial margin of the supratemporal fenestra, being this wall almost vertical. The anterior process of the frontal is much shorter and ornamented compared with *Arenysuchus*, in which it is clearly smooth. Unlike other eusuchians from the upper Cretaceous of Europe, this process in the Fumanya specimen is wider, being its maximum width more than half of the width of the main body of the frontal in the interorbital region. The interorbital region is much narrower than in *A. subjuniperus*. The main body of the frontal is slightly concave as in *A. precedens* or *Arenysuchus*, but without the sloping present in *Hylaeochampsa* or *Acynodon*, and it is different to the condition presented in *A. subjuniperus* whose skull table is totally planar. Frontoparietal suture is concavoconvex in the Fumanya eusuchian. In contrast to *A. precedens*, *A. subjuniperus* or *Hylaeochampsa*, there is no tubercle or boss on the dorsal surface of the convexity of the paroccipital process of the exoccipital, being totally smooth.

The anterior region of the dentary does not show any festooned outline having the alveolar margin at the same dorsal height, as it has been observed in the genus *Acynodon*. On the contrary, in *Musturzabalsuchus* or in the basal eusuchians from Lo Hueco site in Cuenca (Spain) the dentary is higher at the level of the fourth tooth [21, 28–31]. In the Fumanya specimen, *Musturzabalsuchus* and the eusuchians from Lo Hueco the fourth tooth alveolus is the largest, being almost twice as large as the other preserved alveoli. This condition is different in *Acynodon* whose teeth are smaller and similar in size. The tooth morphology resembles to that of *Musturzabalsuchus* [21, 28] and differs from *A. precedens*, *A. subjuniperus* and *Arenysuchus* [4, 5, 8] whose teeth are longer, with smooth or less ridged surfaces and carinae without false-ziphodont crenulations.

All recovered vertebrae are procoelous, with the exception of the first caudal vertebra that is biconvex. This character clearly indicates that the Fumanya specimen belongs to the clade Eusuchia [19]. The axial skeleton of the Fumanya specimen reveals important differences with extinct and extant taxa, especially in the axis, the first caudal and cervical ribs. The centrum of the axis of the Fumanya eusuchian is completely keeled. This feature clearly differs from other taxa such as *C. acutus*, *C. niloticus*, *O. tetraspis* and *A. mississipiensis* in which only the cranial end of the axis is keeled, or the basal *Isisfordia duncani*, in which the keel is absent. In addition, all of the compared taxa show straight instead of curved centra. The dorsal edge of the neural spine of the axis is horizontally oriented as in *Crocodylus*, *Gavialis* or *Diplocynodon*. In the Fumanya specimen, it is concave in lateral view, without crest, in contrast to all the compared taxa. Complete sutured neural arch and odontoid process suggest an adult specimen.

The preserved presacral vertebrae, except the axis, are similar in shape to those of *C. acutus*, *C. niloticus* and *A. mississipiensis*. Cervical and dorsal vertebrae are similar in size, but the last lumbar and the first caudal are clearly bigger. However, the first caudal is different in shape to all compared taxa. Transverse process of the first caudal is uncommonly shorter and wide.

The cervical rib of the eighth vertebrae is also characteristic. Its articular processes are different in size, length and angle compared to *C. acutus, C. niloticus* and *A. mississipiensis*. These extant taxa show curved instead of straight and symmetrical rib.

The appendicular skeleton seems more conservative in fossil and living taxa. The main differences have been found in the ilium and calcaneum comparing the Fumanya eusuchian with extant taxa. The humerus is similar in shape to those of *C. acutus*, *C. niloticus*, *O. tetraspis*. *A. mississipiensis*, or *Pietraroiasuchus omezzanoi*. It is similar in size (based on the width of distal condyles) to those of *C. niloticus* and *A. mississipiensis* but scars of the ligaments are more numerous, bigger and conspicuous in *A. palustris*. The radius is slightly bigger but similar in shape to *C. niloticus* and *A. mississipiensis*. However, the medial groove of the radius is not present in any of taxa used for comparison.

The ilium is different in form to *C. acutus*, *C. niloticus*, *O. tetraspis* or *A. mississipiensis*, being more rounded, longer and much taller. However, it is similar in size to the ilium of *A. precedens* reported by Buscalioni *et al.* [7]. The general shape, especially dorsal curvature of the blade, is similar to that of *Diplocynodon* but its caudal tip is not as deep. The posterior tip of the blade of *A. palustris* is similar to that of *Gavialis*. The anterior process is proportionally developed, unlike other compared taxa, including remains assigned to *Allodaposuchus*. The posterior process is stout as in *A. precedens*, but the latter has a blade with straight dorsal margin.

The head of the femur is proportionally larger in *A. palustris* than in *C. niloticus*, or *A. mississipiensis*. It is similar in shape, but the scars of the ligaments are bigger and conspicuous. The tibia is slightly broader and similar in shape to all the other taxa used in comparisons, but the lateral ridge is not seen in any of them, as well as the medial groove of the fibula. The fibula has also conspicuous scars of the ligaments. The calcaneum is larger in *A. palustris* than in the other taxa. Its distal end is uncommonly long, unlike other taxa used in comparisons.

Phylogenetic Relationships

The composite analysis of cranial and postcranial data resulted in 1110 equally parsimonious cladograms of 590 steps (CI = 0.388; RI = 0.814; RC = 0.316). The strict consensus tree topology (Fig. 8A) showed relevant differences with previous works [2–9, 32]. In our analysis, the clade (*Allodaposuchus* + *Arenysuchus*) was included within Crocodylia, placed in a more derived position than Gavialoidea, and forming a polytomy with *Borealosuchus*, Planocraniidae and the clade Brevirostres (Crocodyloidea + Alligatoroidea). Nevertheless, this result is consistent with the phylogeny proposed by Puértolas *et al.* [4] in which *Allodaposuchus* is considered the sister taxa of Brevirostres. However in that analysis, *Arenysuchus* and *Allodaposuchus* were not closely related. Relationships within the clade (*Allodaposuchus* + *Arenysuchus*) were weakly resolved (Fig. 8A). There, *A. palustris*, the Fumanya eusuchian, was basal to the clade (*A. precedens* + *A. subjuniperus* + *Arenysuchus*), which form a polytomy.

To elucidate the effects of postcranial characters in the phylogenetic position of the clade (*Allodaposuchus* + *Arenysuchus*), the analysis of cranial characters (excluding postcranial data) was also performed (Fig. 8B). It resulted in 1550 equally parsimonious cladograms of 463 steps (CI = 0.378; RI = 0.825; RC = 0.312). In the cranial analysis, the clade (*Allodaposuchus* + *Arenysuchus*) was also placed within Crocodylia but formed a polytomy with planocraniids, *Borealosuchus*, gavialoids, crocodyloids and alligatoroids.

Taphonomy

Remains of *A. palustris* from Fumanya correspond to a 2.3 m-long bone accumulation found within an organic mudstone (Figs. 2 and 9). The bone elements were disarticulated, tightly concentrated in about 1m-long central accumulation with most bones in close contact one to each other, within a centimetric range. In spite of its apparent disarticulation, the bone distribution showed a non-random, anatomical-like arrangement. Thus, the skull fragments and teeth located in the northern edge of the accumulation, the cervical and dorsal vertebrae and ribs in the central part, and some few lumbar and caudal vertebrae in the southern region (Fig. 9). Fragments of the limb bones (phalanges, fibula, femur, tibia, calcaneous) seemed to be randomly distributed throughout the accumulation. Because no duplication of bones belonging to the same side (left or right) existed, we consider the specimen as a single individual.

Bones have no signals of crushing, significant abrasion, weathering or mineralogical crusts nor show superficial scratches or tooth marks. The skull is only represented by partial fragments (quadrates, squamosal, articular, frontal, ectopterygoid, exoccipital, and dentary), which were concentrated together with dentition. Skull fragments exhibit no abrasion. Most of the teeth preserve the enamel, the tip, the root, and delicate and small pseudo-denticles; some teeth are still attached to the enclosing bone. Most of the vertebrae (notably exemplified in MMC-873, MMC-869, MMC-888 and MMC-835) preserve the centrum and parts of the apophyses in connection with the neural arch (Fig. 2D, 5). Limb bones show a variable state of preservation: from partially (humerus, tibia, femur, fibulae) to completely preserved (radius, calcaneous, astragalus, phalanges). The only pelvic element available, the ilium, is completely preserved.

The tight concentration of the bones and the absence of bone sorting suggest an autochthonous accumulation. After death, its body was exposed for a time until the carcass decayed. Bones were probably exposed in the muddy swamp for a time favoring their disarticulation and partial breakage. After that, superficial water currents would have reworked the bones with absent or minimum transport. Final burial of bones was probably produced in the phreatic zone under reducing conditions, as indicated by the organic-matter-rich feature of the embedding

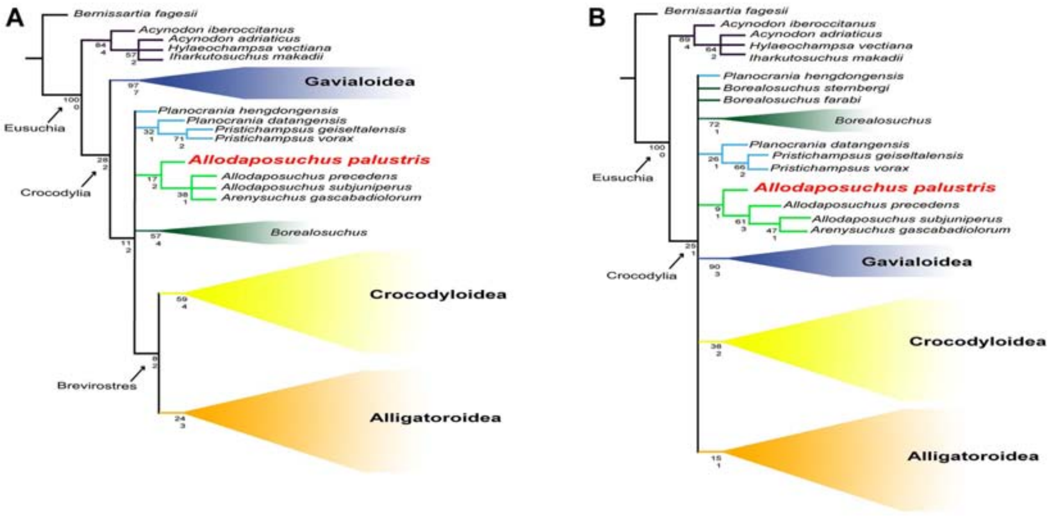

Fig. 8. Strict consensus tree of composite data (cranial + postcranial) (left) and cranial only (right). Bootstrap (above) and Bremer (below) values are indicated.

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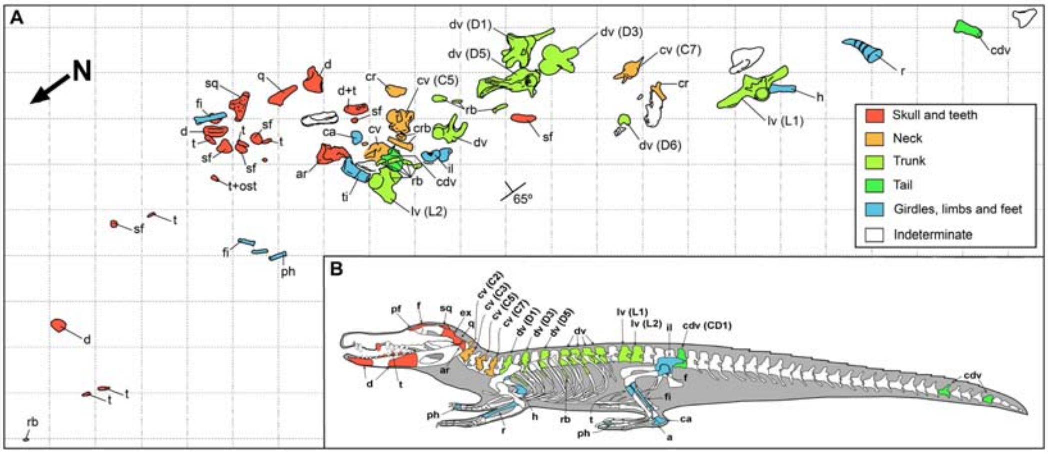

Fig. 9. Mapping of the crocodylian bones at the Fumanya Sud locality and their anatomical location. A, distribution of the fossils along a 2.3 m-long accumulation with indication of the type of bone (see legend). Grid square is 10 centimeters. B, anatomical location of the recovered bones. Abbreviations: a, astragalus; ar, articular; ca, calcaneum; cdv, caudal vertebra; cr, cervical rib; cv, cervical vertebra; d, dentary; dr, dorsal rib; dv, dorsal vertebra; eo, exoccipital; ept, ectopterygoid; f, frontal; fi, fibula; fm, femur; h, humerus; il, ilium; lv, lumbar vertebra; ost, osteoderm; pa, parietal; pf, prefrontal; ph, phalanx; q, quadrate; r, radius; rb, rib; sf: skull fragment; sq, squamosal; t, tooth; ti, tibia; ul, ulna.

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black mudstone (after Oms *et al.* [13]). Fossils are black in colour and it probably results from the high hydrocarbon components of the embedded carbonaceous mudstone, a typical trait of swampy environments [33].

The depositional setting of this organic-matter-rich mud is related with a peat-forming environment within a swampy area of an extensive lagoon [13, 17]. In this context, the fossils of *A. palustris* were found in muddy sediments near the area where plant detritus accumulated (i.e., the coal layer about 60 cm below the studied specimen; Fig. 1). Taphonomic evidence suggests that the depositional setting was the same place where the individual inhabited (i.e. swampy areas from coastal wetlands). Although not very common, vertebrate remains have been documented in peat-forming/swampy environments [34, 35]. At Fumanya area, solemydid turtles have been described as inhabitants of related lagoon environments (transitional brackish mudflat [36]).

Discussion

Systematics of genus *Allodaposuchus* and the Fumanya eusuchian

The most parsimonious hypothesis obtained in our analyses suggests that the clade (*Allodaposuchus* + *Arenysuchus*) belongs to Crocodylia (Fig. 8). Even though the Bremer and bootstrap values were low, the clade Crocodylia, including (*Allodaposuchus* + *Arenysuchus*), was better supported in the complete analysis (bootstrap = 28, Bremer index = 2) than in the cranial analysis (bootstrap = 25, Bremer index = 1) (Fig. 8). In this sense, the genus *Allodaposuchus* might represent more derived eusuchian crocodylomorph than previously thought [2, 5, 7, 8], but not as derived as in Martin [9]. This hypothesis is supported by several cranial and vertebral characters. According to Brochu [20], the inclusion of the clade (*Allodaposuchus* + *Arenysuchus*) within Crocodylia would be supported by the following synapomorphies: 1) anterior dentary teeth project anterodorsally, 2) retroarticular process projects posterodorsally, 3) exoccipital lacks boss on paraoccipital process, and 4) hypapophyseal keels are present on the eleventh vertebrae behind the atlas. Absence of the boss in paraoccipital process, only in *A. palustris*, would be an ancestral state reverted in the other members of the clade (*Allodaposuchus* + *Arenysuchus*). The following synapomorphies related *Allodaposuchus* with *Borealosuchus* + Planocraniidae + Brevirostres (*sensu* Brochu [20]): 1) slender postorbital bar, 2) ventral margin of postorbital bar inset from lateral jugal surface, 3) skull table surface planar at maturity, 4) neural arch of the axis lacking lateral processes (diapophyses), 5) wide posterior half of the axis neural spine, 6) axial hypapophysys without deep fork. All these characters except the two former can be observed in *A. palustris*. However, postcranial data are incomplete or lacking for most fossil taxa. Thus, the new phylogenetic location for the genus *Allodaposuchus* should be taken as an alternative hypothesis to be tested with future findings of new complete fossil crocodylomorphs.

Both phylogenetic trees recognized the clade (*Allodaposuchus* + *Arenysuchus*), in which *A. palustris*, the Fumanya eusuchian, was included (Fig. 8). In this sense, the new unranked clade 'Allodaposuchia' is proposed. The inclusion of the Fumanya eusuchian within genus *Allodaposuchus* is well supported by the phylogenetic analyses (Fig. 8) and qualitative data. For instance, some skull features of *A. palustris* are found in taxa within genus *Allodaposuchus*: the canalis quadratosquamosoexoccipitalis of the external otic region, quadrate foramen aereum on dorsal surface, the concave surface of the frontal, the margin of the orbits upturned, the squamosal-quadrate suture, the exoccipital between the squamosal and the quadrate posterior to otic aperture, the ventral process of the exoccipital.

Allodaposuchus palustris shows some significant differences compared to other members of the clade 'Allodaposuchia'. The frontal bone and its anterior process are clearly different from *Arenysuchus* in ornamentation, length and concavity (see comparison for details). The interorbital region is much narrower than in *Allodaposuchus subjuniperus*. The Fumanya eusuchian also differs from this latter species and *A. precedens* in the following characters: the surface of the rostromedial margin of the supratemporal fenestra and the elongation of quadrate hemicondyles. The tooth features are very relevant. In *A. palustris*, the teeth are strongly ornamented developing false ziphodont crenulations on the carinae. This ornamentation is lacking in *A. precedens*, *A. subjuniperus* and *Arenysuchus*. All these differences justify the assignment of the specimen from Fumanya to a different species within *Allodaposuchus*.

Comments on the evolution of postcranial skeleton in eusuchians

Postcranial material is almost unknown for many fossil eusuchians. In the present study, these data were only available for the basal eusuchian *Isisfordia duncani*, the hylaeochampsid *Pietraroiasuchus omezzanoi* and the alligatoroid *Diplocynodon darwinii*. In contrast, postcranial skeletons of several crown taxa were used for comparisons including gavialoids (*Gavialis gangeticus)*, alligatoroids (*Alligator mississipiensis*) and crocodyloids (*Crocodylus niloticus, C. acutus, Osteolaemus tetraspis*). Because of the incompleteness of the database, conclusions regarding to the evolution of postcranial skeleton in eusuchians are preliminary. However, some patterns can be extracted from the available data. In a general view, the postcranial skeletons seem mostly uniform comparing *Allodaposuchus palustris* with taxa within Brevirostres. This is especially evident for most of vertebrae and appendicular skeleton. Major differences were found in the shape of the axis, the first caudal, cervical ribs, the ilium and the calcaneum. These differences might be associated to skull-neck kinesis and locomotion.

Palaeobiology and palaeoecology of the Fumanya eusuchian

Relatively large size of the lumbar vertebrae, ilium and the astragalus; medial grooves present in the radius and fibula; and more developed attachment of the ligaments in the humerus, femur and fibula suggest a robust crocodile with well-developed musculature. The specimen was probably an adult based on the completely sutured neural arch and odontoid process to the centrum of the axis [37]. According to the measurements of the cranial width and following Verdade [38], the total length inferred for *A. palustris* from Fumanya is 3.72 meters. As it was suggested for *A. precedens* from Oarda de Jos (Romania) [8], the specimen from Fumanya can be considered a generalised predator based on the tooth morphology (robust but pointed teeth) and the absence of bulbous crushing posterior crowns. Following Erickson *et al.* [39], the inferred body mass is of 211 kg and could develop 6788.63 N in its bite force. These magnitudes are similar to those reported [39] for extant typical large crocodylians such as *Crocodylus palustris* Lesson or *Crocodylus intermedius* Graves. For analogy, *A. palustris* might predate small-sized sauropods, which are reported from Fumanya sites [40].

Sedimentology and taphonomy indicate that the habitat of *A. palustris* was a wetland area partially covered by shrubby vegetation (probably abundant cheirolepidiaceous conifers of the genus *Frenelopsis* and a variety of ferns) and tree palms of *Sabalites longirhachis* [17]. The presence of freshwater charophytes and mesohaline (*Saccostrea* oysters) to freshwater (unionids) molluscs indicates changes in the salinity through a set of freshwarer lakes and marshes near the edges of an extensive brackish mudflat [17, 41]. However, related eusuchians from the Maastrichtian of the Pyrenees, such as *Allodaposuchus subjuniperus* and *Arenysuchus gascabadiolorum*, have been found associated to fluvial environments (floodplain deposits laterally close to coastal lagoon), also in the Tremp Formation [4, 5]. *Allodaposuchus precedens* from Oarda de Jos (Romania) was discovered in pond deposits at the base of a series interpreted as a braided fluvial system [8]. This suggests that genera *Allodaposuchus* and *Arenysuchus* were composed of generalist taxa living in both fluvial inner and more coastal lacutrine-palustrine environments.

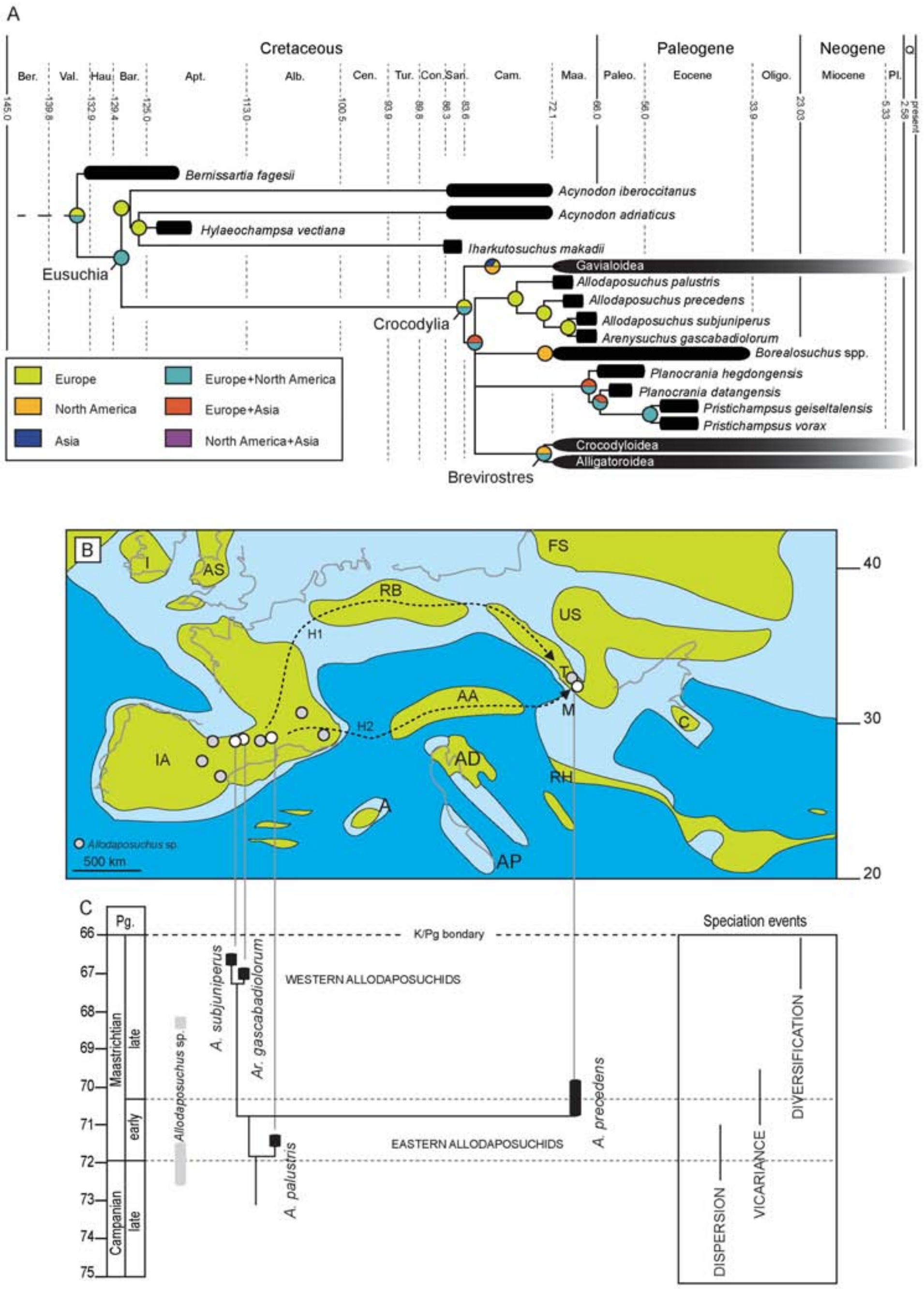
Palaeobiogeographic implications

It is widely accepted that Eusuchia originated in between Europe and North America during the Early Cretaceous [2, 4, 42], and the same geographical region is proposed as the most likely candidate to host the first members of the order Crocodylia (Fig. 10A). As a whole, the S-DIVA results reported here agree with previous interpretations but also point at a complex early radiation of the clade Crocodylia during the Campanian, involving several dispersal and vicariant events through out the Northern Hemisphere landmass, giving rise to the three main extant superfamilies of crocodiles (Gavialoidea, Crocodyloidea and Alligatoroidea). Because the phylogenetic analyses of the present study cannot resolve the basal polytomy within Crocodylia, there is not a single linage that can unambiguously claim to be the origin of the group. Nevertheless, our results offer a much more complex scenario about the geographical distribution of the first crocodilians than previously thought. If so, first members of Crocodylia would spread through the Northern Hemisphere no later than the Campanian and, by processes of isolation, endemic taxa could rise on different geographical regions, such as *Allodaposuchus* in Europe, or *Borealosuchus* in North America. Less clear it seems to be the ancestral area of the clade Brevirostres, which probably make its firstly apparition somewhere in the Euroamerican region.

During the Late Cretaceous, Europe was divided into a set of islands that formed an archipelago of great palaeobiogeographical and evolutionary interest. Between North America and the European archipelago, palaeogeographical bridges sporadically connected the two continents and permitted faunal exchange between them [43, 44]. Moreover, the layout of Europe as an archipelago fostered endemism and vicariant evolution in terrestrial vertebrates such as crocodylomorphs and dinosaurs [42, 45, 46]. The clade ''Allodaposuchia'' seems to be endemic of the southern European archipelago where it was widely distributed _from the Transylvanian domain, at the east, to the Ibero-Armorican domain, at the west_ during the Campanian–Maastrichtian (Fig. 9B). Through its geographic and temporal range, the clade diverged into a set of taxa. *Allodaposuchus palustris*, *A. subjuniperus* and *Arenysuchus gascabadiolorum* seem to be endemic of the Ibero-Armorican Island. The presence of *A. precedens* in this island is dubious and based on the specimen MDE/CM-616 studied by Martin [9] and additional fragmentary material. On the contrary, this last species seems endemic the Transylvanian domain [8].

Considering that the oldest remains of the genus *Allodaposuchus* are known from the late Campanian of both Iberian Peninsula [7, 31, 42] and France [7, 47], it seems likely to suggest that this genus could originate elsewhere in the Ibero-Armorican domain, no later than the middle Campanian, and then it dispersed to other European islands. The specimen from Fumanya, together with older findings in the Campanian-Maastrichtian of Armuña (Segovia, Spain) [7], also suggests that the radiation of the genus *Allodaposuchus* might have occurred in wetland environments from the early Maastrichtian of Iberia before a rapid expansion to the remaining archipelago. This is supported by the major diversity of taxa reported in the Ibero-Armorican domain. In this sense, the resulting S-DIVA model suggests a phenomenon of speciation by vicariance for explaining the occurrence of different allodaposuchian species in different European islands, an event that could take place prior to the early-late Maastrichtian boundary (Fig. 10C). This vicariance model may also explain the high degree of endemism of the European faunas. For instance, Weishampel *et al.* [46] postulated that although at high taxonomic level (i.e. family level or higher) Romanian faunas were nearly equal to those from other European regions, but the geographic isolation of the islands during the Late Cretaceous favoured the occurrence of several endemic taxa, such as *Allodaposuchus* species.

Even accepting previous scenario, the route that *Allodaposuchus* could have taken to move from the Ibero-Armorican Island to the Transylvanian one still remains unclear. Given the palaeogeographic configuration and intermittent connection between diverse European islands during the latest Cretaceous (Campanian-Maastrichtian), two dispersal routes arise to be the most likely (Fig. 9B). One possibility is that *Allodaposuchus* could leave the Ibero-Armorican


A
Cretaceous
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Q
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Bar.
Apt.
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Cen.
Tur.
Con.
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Cam.
Maa.
Paleo.
Eocene
Oligo.
Miocene
Pl.
145.0
139.8
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129.4
125.0
113.0
100.5
93.9
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86.3
83.6
72.1
66.0
56.0
33.9
23.03
5.33
2.58
present
Bernissartia fagesii
Acynodon iberoccitanus
Acynodon adriaticus
Hylaeochampsa vectiana
Iharkutosuchus makadii
Gavialoidea
Allodaposuchus palustris
Allodaposuchus precedens
Allodaposuchus subjuniperus
Arenysuchus gascabadiolorum
Borealosuchus spp.
Planocrania hegdongensis
Planocrania datangensis
Pristichampsus geiseltalensis
Pristichampsus vorax
Crocodyloidea
Alligatoroidea
Eusuchia
Crocodylia
Brevirostres
Europe
North America
Asia
Europe+North America
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B
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Allodaposuchus sp.
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Maastrichtian
late
early
Campanian
late
Allodaposuchus sp.
K/Pg bondary
A. subjuniperus
Ar. gascabadiolorum
WESTERN ALLODAPOSUCHIDS
A. precedens
A. palustris
EASTERN ALLODAPOSUCHIDS
Speciation events
DISPERSION
VICARIANCE
DIVERSIFICATION

Fig. 10. Palaeobiogeographical history of *Allodaposuchus*. A, Time-calibrated phylogram of the Crocodylia based on the phylogenetic hypothesis shown in Fig. 8. The circles at each node represent the relative probabilities for the ancestral areas inferred using the Statistic Divergence-Vicariance Analysis method (S-DIVA). B, Palaeobiogeographical distribution of ''Allodaposuchia'' showing the two most likely routs for the dispersion of the genus along the European archipelago during the latest Cretaceous. Map modified from Dalla Vecchia [51]. C, Time-calibrated phylogram of ''Allodaposuchia'' species and their hypothetical speciation events.

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Island taking a northern way to the Renish-Bohemian Island and then move south to the Transylvanian Island. The advantage that this hypothesis offers rests upon the fact that hemipelagic seas separated those islands, with possible intermittent land bridge connection between them. On the other hand, the shortest way for an Ibero-Armorican taxon to reach the Transylanian basins could be that via the Adriatic-Australpine domain. However, according to palaeogeographic reconstructions those areas were separated for eupelagic basins with no possible land connection between them [48–50].

Nevertheless, the occurrence of several fossil taxa in the Adriatic-Australpine domain with close phyletic relationship to Ibero-Armorican and Transylvanian faunas, such as dinosaurs [45, 51–55], constitutes an irrefutable evidence of the faunal exchange between these areas. How these faunas reached these regions is still matter of debated but ''island hopping'' dispersion has been proposed [51, 54]. Future findings will shed light on these questions. Finally, with all current phyletic and palaeobiogeographic data at hand, ''Allodaposuchia'' represents the last truly Europe lineage of crocodilians previous to the end-Cretaceous mass extinction.

Conclusions

The genus *Allodaposuchus* was traditionally considered a basal eusuchian clade of crocodylomorphs that has historically been comprised of two species (*A. precedens* and *A. subjuniperus*). On the basis of the studied material from the Fumanya Sud locality (southern Pyrenees) we erect the new *Allodaposuchus palustris* species that is diagnosed by the following characters: lack of shallow fossa in the rostromedial margin of the supratemporal fenestra; frontoparietal suture slightly concavoconvex; exoccipital without boss on paraoccipital process; large foramen aereun in quadrate; short and robust teeth with two very marked longitudinal grooves close to the carinae; teeth with strong ornamentation developing false-ziphodont crenulations; anterior process of the ilium more developed. The herein described species add postcranial characters in the cladistical analysis, and provides a new phylogenetic interpretation. Several cranial and vertebral characters are shared with *Borealosuchus* + Planocraniidae + Brevirostres (Crocodyloidea + Alligatoroidea), and suggest a more derived position of *Allodaposuchus* than gavialoids, within Crocodylia. Taphonomic analysis suggests that the studied specimen inhabited coastal wetlands, and thus indicates that the genus *Allodaposuchus* was present in both coastal and fluvial settings. Palaeographical analysis suggests that allodaposuchians diverged in the Ibero-Armorican domain between the middle Campanian and the early Maastrichtian before expanding to the remaining European archipelago.

Supporting Information

S1 Information. Modifications carried out in operational taxonomic units (OTUs) and characters of the dataset of Brochu, to explore phylogenetic relationships of the specimen from Fumanya Sud locality.
doi:10.1371/journal.pone.0115837.s001 (DOC)

S2 Information. Modified dataset of Brochu to explore phylogenetic relationships, including both craniodental and postcranial characters.
doi:10.1371/journal.pone.0115837.s002 (TNT)

S3 Information. Modified dataset of Brochu to explore phylogenetic relationships, including craniodental characters only.
doi:10.1371/journal.pone.0115837.s003 (TNT)

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Author Contributions

Conceived and designed the experiments: AB JM EPP AGS BV. Performed the experiments: AB EPP AGS BV JM. Analyzed the data: AB EPP AGS. Contributed reagents/materials/analysis tools: BV JM. Wrote the paper: AB EPP JM BV AGS.

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A NEW SPECIES OF *ALLODAPOSUCHUS* (EUSUCHIA, CROCODYLIA) FROM THE MAASTRICHTIAN (LATE CRETACEOUS) OF SPAIN: PHYLOGENETIC AND PALEOBIOLOGICAL IMPLICATIONS

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Mi trabajo consistió en la clasificación taxonómica y descripción del material craneal y postcraneal perteneciente al holotipo de esta nueva especie de cocodrilo, así como llevar a cabo los análisis filogenéticos, la redacción de las secciones de Introducción, Material y Métodos, Paleontología Sistemática, Descripción, Resultados, Discusión, y parte de las figuras. Al incluir este espécimen de cocodrilo parcialmente completo en esta tesis doctoral se pretende mejorar el conocimiento de la diversidad de eusuquios en los ecosistemas del Cretácico Superior, para facilitar la posterior clasificación y descripción de los morfotipos compuestos por restos dentales aislados.

A new species of *Allodaposuchus* (Eusuchia, Crocodylia) from the Maastrichtian (Late Cretaceous) of Spain: phylogenetic and paleobiological implications

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ABSTRACT

Background. The Late Cretaceous is a keystone period to understand the origin and early radiation of Crocodylia, the group containing all extant lineages of crocodilians. Among the taxa described from the latest Cretaceous of Europe, the genus *Allodaposuchus* is one of the most common but also one of the most controversial. However, because of its fragmentary record, several issues regarding its phylogenetic emplacement and its ecology remain unsolved or unknown. The discovery of a single specimen attributed to *Allodaposuchus*, represented by both cranial and postcranial remains, from the Casa Fabà site (Tremp Basin, NE Spain) in the lower red unit of the Tremp Fm. (early Maastrichtian, Late Cretaceous) offers a unique opportunity to deepen in the phylogenetic relationships of the group and its ecological features.
Methods. The specimen is described in detail, and CT scan of the skull is performed in order to study the endocranial morphology as well as paratympanic sinuses configuration. In addition, myological and phylogenetic analyses are also carried out on the specimen for to shed light in ecological and phylogenetic issues, respectively.
Results. The specimen described herein represents a new species, *Allodaposuchus hulki* sp. nov., closely related to the Romanian *A. precedens*. The CT scan of the skull revealed an unexpected paratympanic sinuses configuration. *Allosaposuchus hulki* exhibits an "anterodorsal tympanic sinus" not observed in any other extant or extinct crocodilian. The caudal tympanic recesses are extremely enlarged, and the expanded quadratic sinus seems to be connected to the middle-ear channel. Phylogenetic analyses confirm the emplacement of the informal taxonomic group 'Allodaposuchia' at the base of Crocodylia, being considered the sister group of *Borealosuchus* and Planocraniidae.
Discussion. Although this is a preliminary hypothesis, the unique paratympanic configuration displayed by *A. hulki* suggests that it could possess a high-specialized auditory system. Further, the large cranial cavities could help to reduce the weight of the cranium. Concerning the postcranial skeleton, *Allodaposuchus hulki* shows massive and robust vertebrae and forelimb bones, suggesting it could have a bulky

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body. The myological study performed on the anterior limb elements supports this interpretation. In addition, several bone and muscular features seem to point at a semi-erected position of the forelimbs during terrestrial locomotion. Taking all the above results into consideration, it seems plausible to suggest that *A. hulki* could conduct large incursions out of the water and have a semi-terrestrial lifestyle.

Subjects Animal Behavior, Paleontology, Taxonomy, Zoology
Keywords Crocodylia, Endocranial morphology, Locomotion, *Allodaposuchus*, Paleoecology, Late Cretaceous

INTRODUCTION

The Late Cretaceous is a crucial period for understanding the rise and radiation of Crocodylia. At this time, the three main lineages of modern crocodilians made their appearance, and started their dominance upon other crocodilian faunas (*Puértolas, Canudo & Cruzado-Caballero, 2011*). Thus, any new find regarding the Eusuchia record is worthwhile because it provides new information to the puzzling origin of modern crocodilians.

In this way, the fossil record of Late Cretaceous crocodylomorphs from Europe offers an exceptional opportunity to approach such questions, because it contains both basal Eusuchians and members of all groups involved in the radiation of Crocodylia. In the uppermost Cretaceous strata of SW Europe, basal Eusuchia are represented by the hylaeochampsids *Iharkutosuchus*, *Ősi, Clarck & Weishampel, 2007*, *Acynodon Buscalioni, Ortega & Vasse, 1997*, and *Musturzabalsuchus Buscalioni, Ortega & Vasse, 1997* (see also *Narváez et al., 2014*). In turn, the clade Alligatoroidea is represented by the genera *Massaliasuchus Martin & Buffetaut, 2008*, whereas *Thoracosaurus Leidy, 1852* is included within Gavialoidea (see *Laurent, Buffetaut & Le Loeuff, 2000*), and *Arenysuchus Puértolas, Canudo & Cruzado-Caballero, 2011* is considered a basal crocodyloid.

Allodaposuchus Nopcsa, 1928 was one of the most common taxa during the latest Cretaceous of Europe, but is also considered one of the most controversial. Mainly represented by fragmentary skull remains, this genus currently comprises three different species (*Allodaposuchus precedens Nopcsa, 1928*, *Allodaposuchus subjuniperus Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*, and *Allodaposuchus palustris Blanco et al., 2014*) reported from Spain (*Buscalioni et al., 2001*; *Blanco et al., 2014*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*), France (*Martin, 2010*), and Romania (*Nopcsa, 1928*; *Delfino et al., 2008*). From a phylogenetic point of view, *Allodaposuchus* has been considered for a long time to be a sister taxon of the family Hylaeochampsidae (see *Buscalioni et al., 2001*; *Delfino et al., 2008*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*), but has also been included within Alligatoroidea (*Martin, 2010*) or more recently treated as a basal crocodylian (*Blanco et al., 2014*).

In addition, until the discovery of *A. palustris* (*Blanco et al., 2014*), the features of the postcranial elements of this genus were never studied in detail. The recovery of new

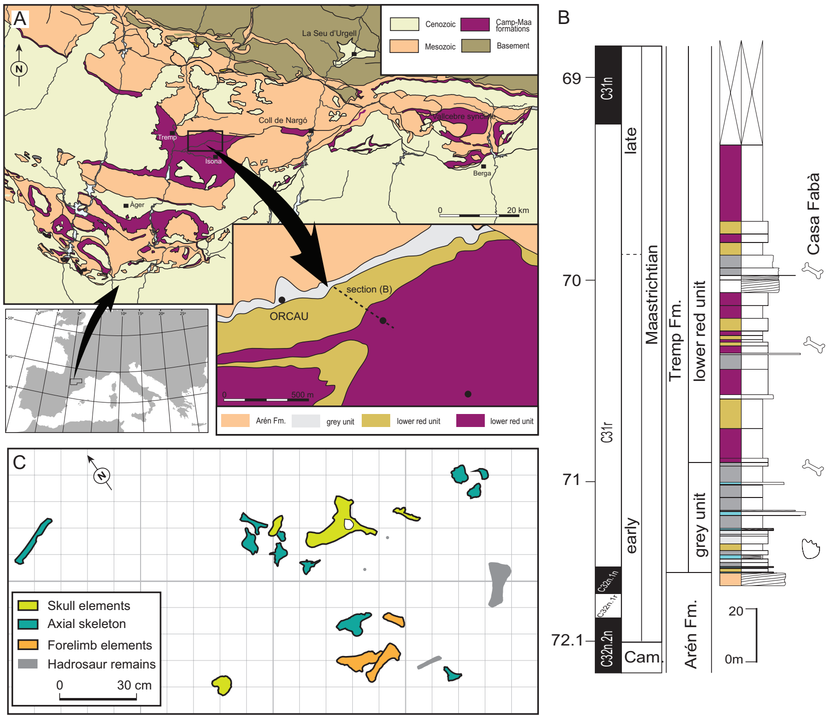

Figure 1 Geographical and geological location of the Casa Fabà site. (A) Geological map of the Tremp Basin (modified from *López-Martínez & Vicens, 2012*); (B) stratigraphical section performed near the Casa Fabà site (modified from *Riera et al., 2009*); (C) mapping of the crocodilian bones at the Casa Fabà locality.

cranial and abundant postcranial material ascribed to *Allodaposuchus* from Casa Fabà site (Tremp Basin Southern Pyrenees; Fig. 1), not only sheds light on the anatomical characteristics of this genus, but also provides new clues for its systematic placement and paleobiological traits.

GEOLOGICAL SETTING

The Casa Fabà locality is one of the dozens of Late Cretaceous continental fossil sites located within the Tremp Basin (Southern Pyrenees, Catalonia; *Riera et al., 2009*). Discovered by Ana María Bravo and Rodrigo Gaete in 2001, the Casa Fabà site is located about 500 m east of the village of Orcau (Pallars Jussà, Catalonia, Spain), in a ravine area known as Les Olives (Fig. 1A). At the end of the Cretaceous, the southern Pyrenean region (NE Iberian Peninsula) consisted of an elongated E-W foreland trough connected to the Atlantic Ocean. In this basin, sedimentation occurred in marine settings up to the Campanian-Maastrichtian boundary. Since then, the sedimentary environment gradually evolved to more continental conditions. As a result of an uplift of successive thrust-sheets involved in the formation of the Pyrenean range (*Muñoz, Martínez & Vergés, 1986*; *Puigdefàbregas & Souquet, 1986*), four synclines can now be distinguished from the east to the west: the Vallcebre syncline, the Coll de Nargó syncline and the Tremp and Àger synclines.

In the Tremp syncline, the uppermost Cretaceous non-marine deposits have received diverse terminology (see *Gaete et al., 2009* for a review). In the present study, we refer to the transition to fully continental materials deposited from the early Maastrichtian to the Thanetian as the Tremp Formation. This formation was divided into four lithological units by *Rosell, Linares & Llompart (2001)*, which are from the base to the top: (1) a transitional 'grey unit' (marls, coals, limestones, and sandstones), (2) a fluvial 'lower red unit' (mudstones, sandstones, oncoids, and paleosols), (3) the lacustrine 'Vallcebre limestone' and laterally equivalent strata, and (4) a fluvial 'upper red unit' (mudstones, sandstones, conglomerates and limestones).

Although the Casa Fabà site is mostly covered by abundant vegetation, the outcrop consists of a surface of about 4 m^2 of a sandstone layer with carbonate matrix inter-bedded between grey marl strata. These sediments are characteristic of the 'lower red unit'. The occurrence of the charophyte *Microchara punctata* in those marl deposits would indicate a Maastrichtian age according to recent results of *Vicente et al. (2015)*. These authors described a local *Microchara punctata* biozone ranging from the middle part of chron C31r to the lower part of chron C30n in the Vallcebre Basin. These results concur with the stratigraphic and biostratigraphic data of the site, which indicate an early Maastrichtian age, within the C31r chron (*Riera et al., 2009*; *Díez-Canseco et al., 2014*).

MATERIAL AND METHODS

Material

The recovered material was found in a 2 m^2-area (Fig. 1C) including both cranial and postcranial elements (Figs. 2–6). Because no duplication of bones existed, and bones are connected or coherent in size, we consider the specimen to be a single individual. The skull is represented by the left premaxilla, a fragment of the right dentary, the right jugal and quadratojugal, most of the skull-table, and a damaged fragment of the jaw. The postcranial skeleton is also preserved and includes a right scapula, a fragmentary right humerus, a complete right ulna, a right dorsal rib, a proximal part of an indeterminate rib, an anterior dorsal vertebra and three lumbar vertebrae.

The holotype of *Allodaposuchus palustris* (*Blanco et al., 2014*) and several extant crocodile skeletons were used as material of comparison, including one specimen of *Crocodylus niloticus* *Laurenti, 1768* (MZB2003-1423), two of *Alligator mississippiensis* *Daudin, 1802* (MZB2006-0613, MZB92-0231) and one *Osteolaemus tetraspis* *Cope, 1861* (MZB2006-0039). In addition, we gathered both cranial and postcranial information from the literature about extant and extinct crocodylomorphs: *Crocodylus acutus* *Cuvier, 1807* (see *Mook, 1921*), *Sebecus icaeorhinus* *Simpson, 1937* (see *Pol et al., 2012*), *Allodaposuchus precedens* (*Buscalioni et al., 2001*; *Delfino et al., 2008*) and *Allodaposuchus subjuniperus* (*Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*).

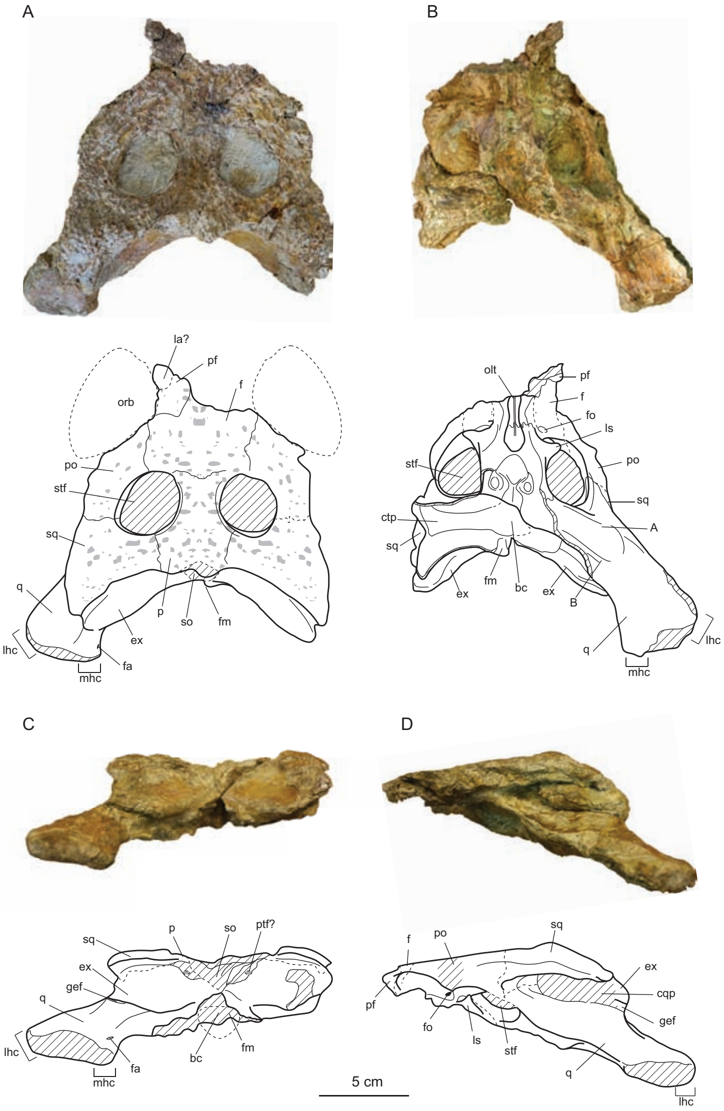

Figure 2 **Skull of *Allodaposuchus hulki* sp. nov.** (MCD5139) and interpretative diagrams in (A) dorsal, (B) ventral, (C) caudal, and (D) left lateral view. Abbreviations: bc, basicranium; ctp, *cavum tympanicum propium*; cqp, cranioquadrate passage; ex, exoccipital; f, frontal; fa, *foramen aëreum*; fm, *foramen magnum*; fo, foramen; gef, groove for ear flap; la, lacrimal; lhc, lateral hemicondyle; ls, laterosphenoid; mhc, medial hemicondyle; olt, olfactory track; orb, orbit; p, parietal; pf, prefrontal; po, postorbital; ptf, postemporal fenestrae; q, quadrate; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra. A and B are muscle scars on the quadrate.

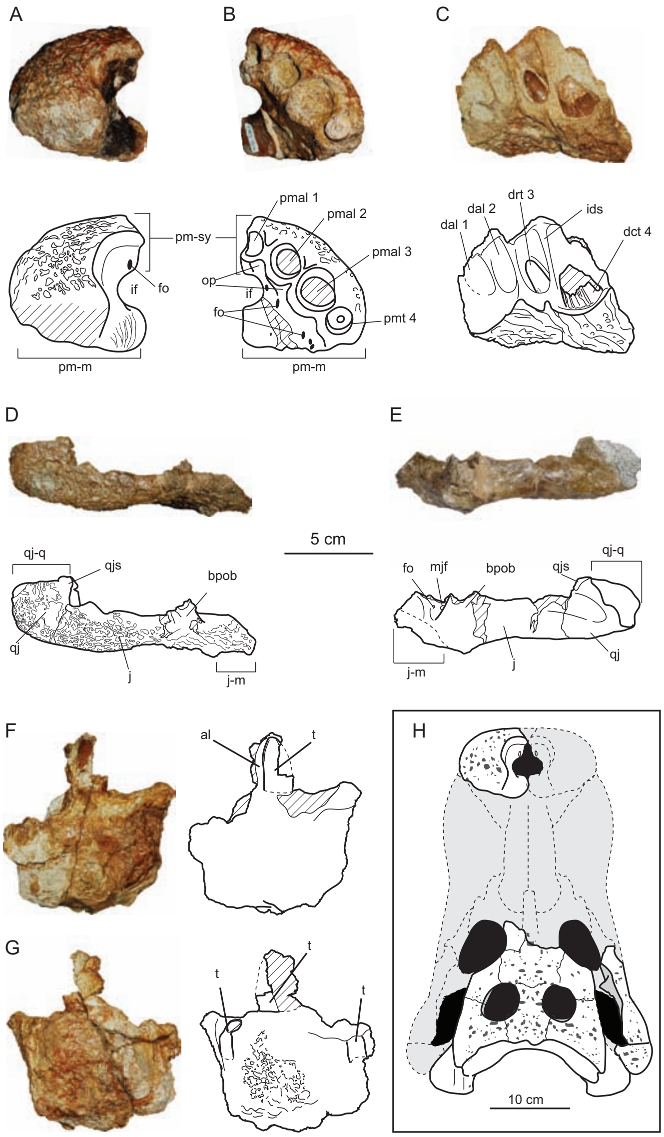

Figure 3 **Cranio-mandibular elements of *Allodaposuchus hulki* and interpretative diagrams.** Left premaxilla (MCD4763) in (A) dorsal, and (B) ventral view. Right dentary fragment (MCD5134) in (C) labial view. Right pair jugal-quadratojugal (MCD5129) in (D) dorsolateral and (E) ventromedial view. Indeterminate jaw fragment (MCD4758a) in (F) labial and (G) mesial view. (continued on next page...)

Figure 3 (...continued)
Reconstruction of the skull of *Allodaposuchus hulki* (H). Abbreviation: al, alveoli; bpob, base of the postorbital bar; dal, dentary alveolus; dct, dentary caniniform tooth; drt, dentary replacement tooth; fo, foramen; ids, interdentary septum; if, incisive foramen; j, jugal; j-m, jugal-maxilla suture; mjf, medial jugal foramen; op, occlusion pits; pmal, premaxillary alveoli; pm-m, premaxilla-maxilla suture; pmt, premaxillary tooth; pm-sy, premaxilla symphysis; qj, quadratojugal; qj-q, quadratojugal-quadrate suture; qjs, quadratojugas spine; t, tooth.

Anatomical nomenclature

The description of the cranial osteology of the new material follows the terminology used in those works concerning the genus *Allodaposuchus* (*Buscalioni et al., 2001*; *Delfino et al., 2008*; *Blanco et al., 2014*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*), whereas postcranial elements are described following *Mook (1921)* and *Brochu (2011)*. In addition, the terminology used to describe appendicular myological features is according to *Meers (2003)*.

Phylogenetic analyses

Phylogenetic relationships of the specimen from Casa Fabà were explored using the dataset of *Brochu (2011)*. However modifications in some operational taxonomic units (OTUs) and characters were carried out (see Supplemental Information S1).

The entire dataset resulted in 86 OTUs coded for a total of 181 craniodental and postcranial characters (see Supplemental Information S2). The taxon *Bernissartia fagesii* *Dollo, 1883* was used as outgroup. The dataset was analysed with TNT v1.1 (Willi Hennig Society Edition, *Goloboff, Farris & Nixon, 2008*). Tree-space was explored using a heuristic search algorithm (traditional search method) with tree-bisection-reconnection branch swapping and 1,000 random addition replicates holding 10 most parsimonious trees for each replicate. All characters were equally weighted and multistate characters were unordered. Bremer supports and bootstrap frequencies (1,000 bootstrap replicates searched) were used to assess the robustness of the nodes.

Inner structural exploration

A Computed Tomography scanner (CT-scan) was used to explore the morphology and the inner structure of the cranial elements. The remains were scanned by multi-detector computer tomography (Sensation 16; Siemens) at Hospital Universitari Mútua de Terrassa (Terrassa, Spain). The material was scanned at 140 kV and 300 mA with an output of 512 × 512 pixels per slice, with an interslice space of 0.3 mm obtaining a pixel size of 0.586 mm and processed with the Avizo 7.0 software (FEI VSG Company). This process allows the recognition of inner cranial structures.

Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work

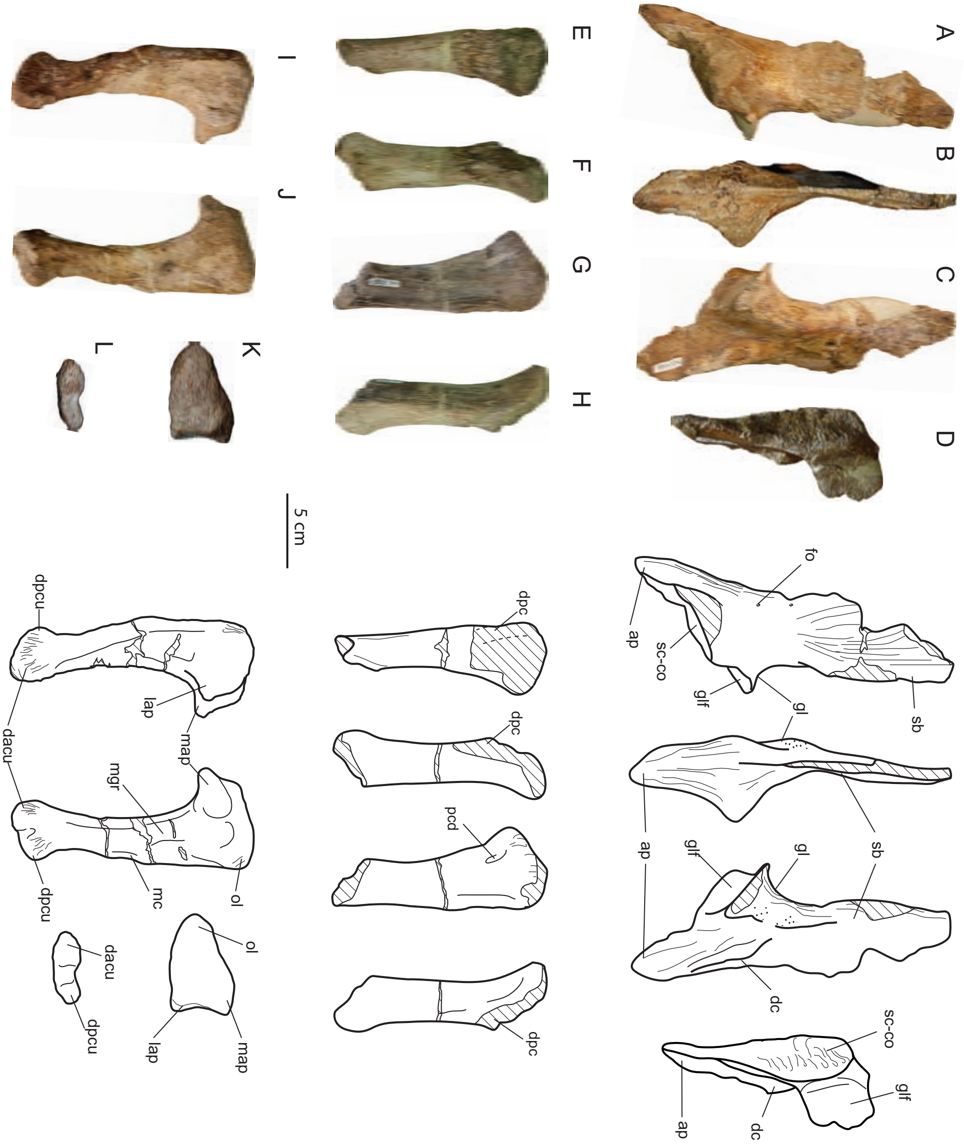

Figure 4 **Appendicular forelimb elements of *Allodaposuchus hulki* and interpretative diagrams.** Right scapula (MCD4765) in (A) medial, (B) anterior, (C) lateral, and (D) ventral view. Right humerus (MCD4758b) in (E) ventral, (F) medial, (G) dorsal, and (H) lateral view. Right ulna (MCD4760) in (I) lateral, (J) medial, (K) proximal, and (L) distal view. Abbreviation: ap, anterior process; dacu, distal anterior condyle of the ulna; dc, deltoid crest; dpc, deltopectoral crest; dpcu, distal posterior condyle of the ulna; fo, foramen; gl, glenoid; glf, glenoid fossa; lap, lateral anterior process; map, medial anterior process; mc, medial crest; mgr, medial groove; ol, olecranon; pcd, posterior circular depression; sb, scapular blade; sc-co, scapula-coracoid suture.

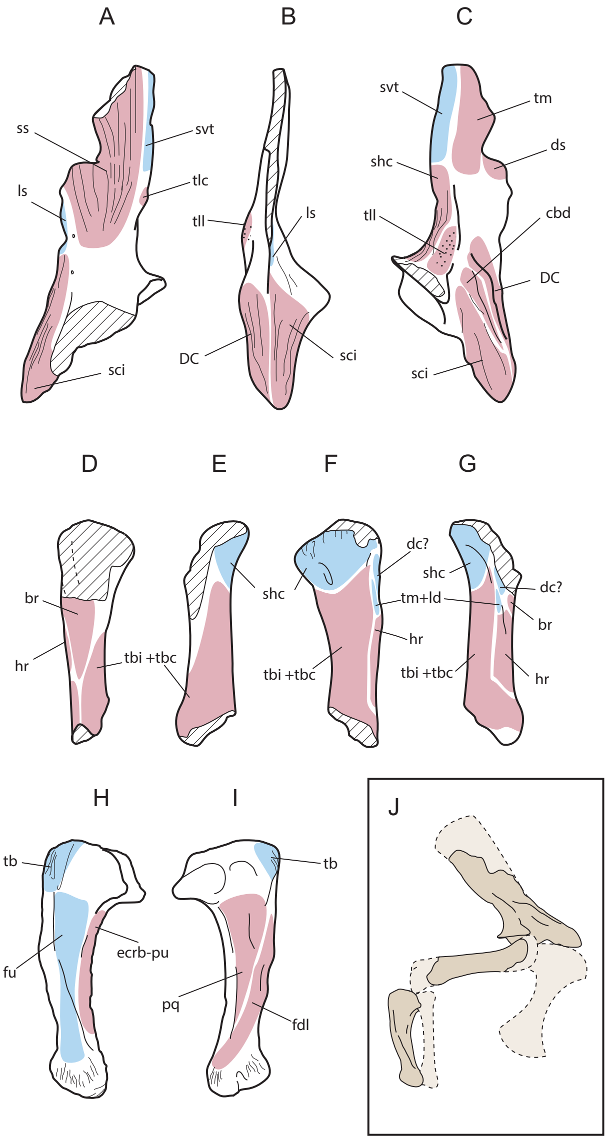

Figure 5 **Muscular map of the forelimb bones of *Allodaposuchus hulki*.** Right scapula (MCD4765; A-medial, B-anterior, C-lateral), right humerus (MCD4758b, D-ventral, E-medial, F-dorsal, G-lateral), right ulna (MCD 4760, H-lateral, I-medial); and reconstruction of the anterior limb configuration (J). Muscle origins are indicated in pink and insertions in blue. (continued on next page...)

Figure 5 (...continued)

Abbreviations: br, *M. brachialis*; cbd, *M. coracobrahialis brevis dorsalis*; dc, *M. deltoideus clavicularis*; DC, deltoid crest; ds, *M. deltoideus scapularis*; ecrd-pu, *M. extensor carpi radialis brevis-pars ulnaris*; fdl, *M. flexor digitorum longus*; fu, *M. flexor ulnaris*; hr, *M. humeroradialis*; ld, *M. latissum dorsi*; ls, *M. levator scapulae*; pq, *M. pronator quadratus*; shc, *M. scapulohumeralis caudalis*; sci, *M. supracoracoideus intermedius*; ss, *M. subscapularis*; svt, *M. serratus ventralis thoracis*; tb, *M. triceps brachii*; tbc, *M. triceps brevis caudalis*; tbi, *M. triceps brevis intermedius*; tlc, *M. triceps longus caudalis*; tm, *M. teres major*; tll, *M. triceps longus lateralis.*

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SYSTEMATIC PALEONTOLOGY

Order CROCODYLIFORMES *Hay, 1930* (*sensu* *Benton & Clark, 1988*),
Suborder EUSUCHIA *Huxley, 1875*,
Unranked CROCODYLIA *Gmelin, 1789* (*sensu* *Benton & Clark, 1988*),
Genus *Allodaposuchus* *Nopcsa, 1928*,
Allodaposuchus hulki sp. nov.

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(Figs. 2–6).

Etymology: *hulki*, from the character of Marvel, Hulk; due to the strong muscle attachments of the bones.

Differential diagnosis: *Allodaposuchus* differs from all other Eusuchians by the presence of the *canalis quadratosquamosoexoccipitalis*, or cranioquadrate passage, laterally open and represented by a sulcus (broader than in *Hylaeochampsa vectiana* *Owen, 1874*). *Allodaposuchus hulki* differs with *Allodaposuchus palustris* in having a linear frontoparietal suture, a prominent boss on paraoccipital process of the exoccipital, a small *foramen aëreum*, and lacking false-ziphodont teeth. *Allodaposuchus hulki* differs from *A. subjuniperus* by having the incisive foramen abutting the premaxillary tooth row, located between the first and second alveoli, the premaxillary-maxillary suture does not reach the incisive foramen, external naris opened in aterodorsal direction, no elevation around the rim of the external naris, absence of interorbital ridge, a very large medial jugal foramen, quadratojugal spine nearly absent and located near of the ventral angle in the infratemporal fenestra, medial articular hemicondyle of the quadrate without ventral expansion, and teeth without longitudinal grooves in the lingual side. *Allodaposuchus hulki* differs from *A. precedens* by having the premaxilla wider than long with four teeth positions, the third being the largest, a smaller and keyhole-shaped external naris, no elevation around the rim of the

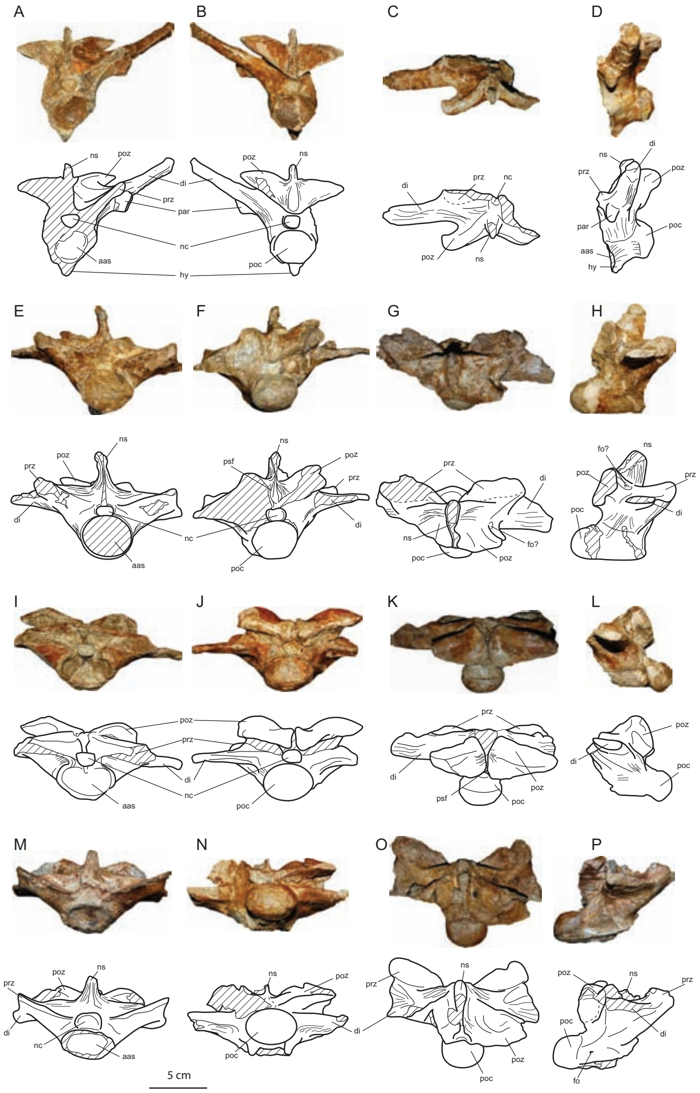

Figure 6 **Axial elements of *Allodaposuchus hulki* and interpretative diagrams.** Anterior dorsal vertebra (MCD5131) in (A) anterior, (B) posterior, (C) dorsal, and (D) left lateral view; first lumbar vertebra (MCD5136) in (E) anterior, (F) posterior, (G) dorsal, and (H) left lateral view; second lumbar vertebra (MCD4769) in (I) anterior, (J) posterior, (K) dorsal, and (L) left lateral view; third lumbar vertebra (MCD5126) in (M) anterior, (N) posterior, (O) dorsal, and (P) left lateral view. Abbreviations: aas, anterior articular surface; di, diapophysis; fo, foramen; hy, hypapophysis; nc, neural canal; ns, neural spine; par, parapophysis; poc, posterior condyle; poz, postzygapophysis; prz, prezygapophysis; psf, post-spinal fossa.

external naris, incisive foramen located between the first and second alveoli, dermal bones of skull roof overhanging supratemporal fenestra rim, two crests in the ventral surface of the quadrate without association of any tubercle, and capitate processes of laterosphenoid anteroposteriorly oriented, and teeth with smooth enamel.

Allodaposuchus hulki shows the following autapomorphies: Quadratojugal does not extend along the infratemporal fenestra; absence of fossa or shelf at anteromedial corner of the supratemporal fenestra; teeth bear smooth enamel, low-developed mesial and posterior carinae, and absence of longitudinal grooves in the lingual side.

Aside the previous characters, *A. hulki* has the following ambiguous autapomorphies: Spine of quadratojugal significantly reduced; no ridge surrounds the *foramen aëreum*; anterolateral, anteromedial and olecranon processes of the ulna well developed; ulnar shaft lateromedially compressed with lateral and medial grooves; distal condyles of the ulna turned lateroposteriorly, causing a lateral crest in the shaft. These features are ambiguous autapomorphies because these characters cannot be scored in other species of *Allodaposuchus*. Additionally, variability might affect the ridge surrounding the ridge surrounding the *foramen aëreum*. New discoveries may reveal whether they are autapomorphies of *A. hulki* or synapomorphies of the genus.

Holotype: MCD4757 (rib fragment), MCD4758a (jaw fragment), MCD4758b (right humerus), MCD4760 (right ulna), MCD4763 (left premaxilla), MCD4765 (right scapula), MCD5127 (dorsal rib), MCD5129 (right jugal and quadratojugal), MCD5131 (dorsal vertebra), MCD5134 (dentary fragment), MCD5139 (skull-table, exoccipitalis and left quadrate), MCD4769, MCD5126 and MCD5136 (lumbar vertebrae).

Locality, age and horizon: Casa Fabà site, Tremp Basin (NE Spain); lower part of the 'lower red unit' of the Tremp Fm; C31r of the early Maastrichtian (Late Cretaceous).

DESCRIPTION

Cranial skeleton

The cranial remains consist of an isolated left premaxilla (MCD4763), jaw fragments (MCD5134 and MCD4758a), an isolated right jugal and quadratojugal (MCD5129), and a posterior cranial fragment (MCD5139) that preserves frontal, left prefrontal, parietal, both squamosals, postorbitals, exooccipitals, left quadrate and laterosphenoid in connection (Figs. 2 and 3). The preserved portion of the skull table is markedly medially concave, with nearly horizontal sides and displays roughly straight margins. The supratemporal fenestrae are filled with sediment (Figs. 2A–2B). We estimated a total width ranging from 27 cm (from both lateral hemicondyles of the quadrates) to 34 cm (from both lateral edges of the quadratojugals).

Cranial openings

The external naris is undivided and keyhole-shaped (Figs. 3A–3B). It is 3.2 cm wide and opens in the antero-dorsal direction. In ventral view, there is a small and subcircular incisive foramen (1.7 cm wide), the anterior rim of which is located between the first and second alveoli (Fig. 3B). The medial margin of the left orbit is preserved, being able to interpret its general morphology. The orbits are relatively wide and short, rounded with their rostromedial margin being somewhat elevated. Supratemporal fenestrae are subcircular in shape (4.5 cm maximum width) and filled with sediment. There is no fossa or shelf at the anteromedial corner of the supratemporal fenestrae. The otic aperture is developed between the squamosal, quadrate and exoccipital, and the cranioquadrate passage forms a caudolaterally open sulcus called *canalis quadratosquamosoexoccipitalis* (*Buscalioni et al., 2001*; *Delfino et al., 2008*). The squamosal and the quadrate are not in contact posteriorly to the otic opening.

Premaxilla

The premaxilla is nearly complete and characterized by its robust appearance. The premaxilla is rounded, and wider than long. Its posterodorsal margin is slightly eroded; thus, the presence of a notch or pit in the palatal side of premaxillary-maxillary suture, or the length of the premaxillary process, could not be confirmed. It contacts the maxilla posterolaterally, and probably the nasals medially (Figs. 3A–3B). There is no elevation along the lateral rim of the naris, and none seems to occur posteriorly. The naris opens flush with the dorsal surface of the premaxilla, without the development of any lateral notch. The internal cavity of the naris shows a large foramen in the rostral-most portion of the left surface, and several longitudinal ridges caudally to the incisive foramen, probably for soft tissues or muscle attachment. On the palatal surface, the premaxillary-maxillary suture does not abut the posterior margin of the incisive foramen, with the latter being completely included within the premaxilla. There are four premaxillary alveoli, but only the fourth tooth root is preserved within its socked. The first premaxillary alveolus is the smallest in size, while the second and fourth are similar in size, and the third is the largest (Fig. 3B). There is one occlusal pit between the first and second alveoli, and another between the second and third. No pit is present between the third and fourth alveoli.

Jugal

A complete right jugal bone, not preserving the postorbital bar, has been recovered (Figs. 3D–3E). It displays an elongated morphology and shows an ornamented external surface. Rostral and caudal edges of the jugal are respectively lateromedial turned, keeping an approximately constant lateromedial width. Along the orbit, the jugal dorsal margin is slightly elevated for contact with the lacrimal, making a rounded ventral margin of the orbit. The postorbital bar is lost, but insertion on the jugal can be defined as ‘inset’. In lingual view, an uncommonly large medial jugal foramen can be observed rostrally to the postorbital bar insertion. Another smaller foramen is also present rostrally to the former. Ventrally to these foramina, the articular surface with the maxilla begins and continues to the rostral edge.

Quadratojugal

Quadratojugal is a short and wide bone, forming the posterior angle of the infratemporal fenestra (Figs. 3D–3E). It does not bear any process along the lower temporal bar. It also does not extend to the superior angle of the infratemporal fenestra. The quadratojugal spine is nearly absent and low in position, near to the posterior angle of infratemporal fenestra. In the lateral side, jugal and quadratojugal bear the same ornamentation pattern as the skull table.

Quadrate

Only the left quadrate is complete, being part of MCD5139 (Fig. 2). In lateral view, the quadrate contacts the squamosal rostrally, and the exoccipital caudally, forming the anteroventral margin of the external otic aperture and the ventral limit of the cranioquadrate passage. The quadrate also contacts the postorbital ventrally to the skull table, in the dorsal margin of the infratemporal fenestra. In dorsal view, the quadrate is short caudally to the paroccipital process of the exoccipital bone. Both articular hemicondyles are similar in size, although the medial hemicondyle is slightly smaller and ventrally deflected (Fig. 2C). From the posteroventral corner of the otic aperture, a soft sulcus passes along the quadratoexoccipital suture, in the posterolateral direction, parallel to the cranioquadrate passage, and ends abruptly. The *foramen aëreum* is small and located on the dorsal surface, close to the medial edge of the quadrate. No ridge surrounds the *foramen aëreum*. In ventral view, there are two well-marked crests corresponding to the muscle scars A and B of *Iordansky (1973)*, without the association of any tubercle (Fig. 2B). In contrast, the right quadrate is just broken ventrally to the otic aperture, showing the otic canal, also known as the *cavum tympanicum propium*, filled with sediment.

Frontal

The frontal forms the posteromedial corners of the orbits and the anteromedial corners of the supratemporal fenestrae. It contacts the postorbital laterodorsally and the parietal caudally (Fig. 2A). The frontal prevents contact between postorbital and parietal. The frontoparietal suture is nearly linear and enters the rostromedial margins of the supratemporal fenestrae. The dorsal surface of the frontal is markedly ornamented by subcircular pits that can reach 3 mm in diameter. The main body of the frontal is strongly concave at the centre of the dorsal surface, and the orbital margins are upturned. No interorbital ridge is present. The anterior process of the frontal is not preserved. At least part of the left prefrontal is also preserved in MCD5139 (Figs. 2A–2B).

Parietal

It contacts the frontal anteriorly and the squamosal laterally (Fig. 2A). There is no contact between the parietal and the postorbital in dorsal view. Contact with the supraoccipital could not be assessed due to preservation reasons. The parietal is longer than wide and displays a marked ornamentation on the dorsal surface, consisting of the same subcircular depressions present in the rest of the skull bones. The parietal is medially concave, as part of the general concavity of the skull table. A recess in the parietal communicates with the pneumatic system.

Postorbital

It contacts the squamosal posteriorly and the frontal anteromedially. In MCD5139, both postorbitals are longer than wide, displaying a well-curved contour in dorsal view (Fig. 2A). Postorbital constitutes the anterolateral corner of the supratemporal fenestra, conferring rounded anterior edges to the skull table. It also forms the posterior orbital margin and the anterodorsal corner of the infratemporal fenestra. The ornamentation is the same as that of the rest of the skull table.

Squamosal

The squamosal is a triangular-shaped bone which contacts the postorbital anteriorly, the parietal medially, the quadrate anteroventrally, and the exoccipital posteroventrally, constituting the cranioquadrate passage (Fig. 2D). Posteriorly to the passage, the quadrate and the squamosal are separated by the exoccipital. In lateral view, two rims delimited a longitudinal groove for external ear valve musculature. These dorsal and ventral rims are parallel. In dorsal view, the suture between the squamosal and the postorbital is very posteriorly situated, reaching the caudal-most part of the lateral margin of the supratemporal fenestra. The squamosal develops a significantly posterolateral extension resulting in a horizontal margin of the skull table. In occipital view, the squamosal slopes ventrolaterally over the exoccipital, but the squamosal does not laterally surpass the paroccipital process of the exoccipital.

Supraoccipital

The skull table is damaged coinciding with the supraoccipital location; thus, the morphology of the supraoccipital and its relationships with other bones could not be assessed with confidence.

Exoccipital

It occupies most of the occipital surface, contacting the squamosal dorsally, and the quadrate lateroventrally (Fig. 2). The exoccipital conforms the caudoventral margin of the cranioquadrate passage. The paroccipital process does not extend much laterally, ending in the medial quadrate branch. In occipital view, the exoccipital shows a very prominent boss on the paraoccipital process. The *foramen magnum* is relatively preserved, but the ventral edges of exoccipitals are broken, and the suture with the basioccipital is missing.

Laterosphenoid

In palatal view, the laterosphenoid is situated medially in the braincase, between the supratemporal fenestrae (Fig. 2B). It contacts frontal rostrally and postorbitals laterally, conforming the rostromedial margin of supratemporal fenestra in ventral view. The capitate process of the laterosphenoid is anteroposteriorly oriented.

Dentary

Only a right fragment of the anterior part of the dentary was recovered (MCD5134), which is very fragmentary and incomplete (Fig. 3C). According to the medial curvature of the bone, we have interpreted this as the rostral-most portion of the right dentary, bearing from the first to the fourth alveoli. The lingual surface of the bone is not preserved, showing the alveoli in a section. Only two teeth are preserved *in situ*, the second and fourth, projecting anterodorsally. In the second alveolus, the functional tooth is lost, but there is a replacement non-erupted tooth. In contrast, the fourth tooth is a caniniform.

MCD4758a is an indeterminate fragment of the jaw. For preservation reasons, it is not possible to elucidate its position along the jaw. This fragment preserves three alveoli, bearing one erupted tooth (Figs. 3F–3G).

Dentition

The whole specimen preserves four teeth (one root in the premaxilla, two teeth in the dentary, and one tooth in MCD4758a). The teeth are circular in section and the tooth crowns are slightly blunt. Enamel lacks ornamentation, but several longitudinal ridges appear in the most basal portion of the crown in the lingual side. Anterior and posterior keels are poorly developed, and there are no longitudinal grooves next to the keels in the lingual side. These ridges are weak in MCD4758a, and more developed in the caniniform tooth of MCD5134. Replacement tooth of MCD5134 lacks ridges, probably due to being a non-erupted tooth (Fig. 3C).

Postcranial skeleton

Recovered postcranial skeleton of *Allodaposuchus hulki* is composed of a distal end of the right scapula (MCD4765), right humerus (MCD4758b), right ulna (MCD4760), two dorsal ribs (MCD4757 and MCD5127) and five vertebrae (one dorsal, three lumbar, and fragments of an indeterminate one, MCD5131, MCD5136, MCD4769, MCD5126 and MCD5125, respectively).

Scapula

Only the ventral edge of the scapula is preserved, showing the glenoid fossa, the deltoid crest, the anterior process of the scapula and part of the scapular blade (Figs. 4A–4D). The scapular blade is constricted at its beginning, and seems to flare dorsally. In posterior view, the scapular blade is sinuous. The glenoid is oriented posterolaterally. In lateral view, the posterior end of the scapular blade is straight. The lateral surface of the scapula bears several rugose areas (Fig. 4A). A rugose zone for the insertion of the *M. serratus ventralis thoracis* (*Meers, 2003*) is situated in the posterior edge of the scapular blade. In the same side, but in a more ventral position where the blade is constricted, another rugose area evidences the origins of the *M. scapulohumeralis caudalis*, and just dorsal to supraglenoid buttress a highly-developed rugosity constitutes the origin of the *M. triceps longus lateralis* (*Meers, 2003*). The anterior process of the scapula bears a wide deltoid crest. This crest is the origin of the *M. coracobrachialis brevis dorsalis* and the *M. deltoideus clavicularis*. Ventrally to the deltoid crest, a softer rugose area evidences the origin of the *M. supracoracoideus intermedius* (Figs. 4A–5C; *Meers, 2003*). In medial view, the scapula also shows several rugose areas for muscle attachment (Fig. 4A). The medial surface of the blade shows the origin of *M. subscapularis*, and *M. triceps longus caudalis* (Fig. 5A; *Meers, 2003*). In this view, a small foramen is present at the base of the scapular blade. The anterior process of the scapula also bears a soft rugose area for the origin of *M. supracoracoideus longus* (*Meers, 2003*). In the ventral side, the scapula-coracoid facet is present, and is broader caudally (Fig. 4D). Coracoid is not fused to the scapula. The sutural surface is teardrop-shaped, and the lateromedial width in the posterior portion is much greater than the anterior one.

Humerus

A right humeral diaphysis was recovered (Figs. 4E–4H). The proximal articular surface is eroded. The anterior tuberosity and the humeral head seem to have the same height, and the posterior tuberosity seems to be slightly distally positioned. The deltopectoral crest is missing because of the preservation. In lateral view, the proximal portion of the shaft is dorsally concave, and its distal portion is ventrally turned. The lateral surface of the humerus is slightly concave. In turn, the medial surface of the humerus is slightly convex. The shaft is broken proximally to the distal condyles.

Like the scapula, the humerus also shows several rugous areas around the bone. In posterior view (Fig. 4G), a wide rugous area is situated caudally to the condyles, corresponding to the insertion of the *M. scapulohumeralis caudalis* (Figs. 5D–5G; *Meers, 2003*). The dorsal surface bears a single insertion scar for *M. teres major* and *M. dorsalis scapulae* (according to *Brochu, 2011*), or *M. teres major* and *M. latissimus dorsi* (according to *Meers, 2003*). The shaft shows small and soft ridges completely occupying the dorsal surface. These ridges correspond at least to the origin of the *M. triceps brevis intermedius*, and possibly the *M. triceps brevis cranialis* (*Meers, 2003*), but limits between both muscles are not distinguished. The origins of *M. triceps brevis intermedius* extends to medial side of the shaft (Figs. 5D–5G). The lateral surface of the shaft shows part of the origins of *M. triceps brevis intermedius*, and the origin of the *M. humeroradialis* (*Meers, 2003*). The deltopectoral crest is lost, lacking most of the *M. deltoideus clavicularis* insertion (*Meers, 2003*). A small crest (lineae intermuscularis humeroradialis-brachialis) is situated laterally to the insertion of *M. teres major*. In ventral view (Figs. 5D–5G), descriptions for muscle attachment in the proximal epiphysis could not be made for preservation reasons. However, the shaft shows the end of the origin of *M. triceps brevis intermedius* in medial margin, and the end of the origin of *M. humeroradialis* in the lateral one. At the middle of the shaft, the origin of *M. brachialis* is present (*Meers, 2003*), distally to the deltopectoral crest location.

Ulna

The right ulna is one of the best-preserved bones (Figs. 4H–4K). The proximal end of the ulna is anterioposteriorly expanded. In proximal view, it is triangular-shaped, with a very prominent vertex. The olecranon process is acute, and the articular surface for the radius is concave. There is a very sharp process medially to the articular surface for the radius. The shaft is compressed mediolaterally, and shallow grooves could be discerned in the medial and lateral sides. The distal half of the shaft is prominently oriented anteriorly. Both distal condyles are compressed and anterolateral to mediocaudally oriented. As a result of this torsion, there is a ridge in the lateral side of the distal end of the ulna.

The ulna also shows several muscle attachments. A rugosity abuts the olecranon process in caudal, lateral and medial views, and evidences the insertion of *M. triceps brachi* (*Meers, 2003*). In lateral view (Fig. 4H), the *M. flexor ulnaris* originates in a groove situated just distally to the sharp process of the articular surface of the radius. *M. flexor ulnaris* disposes over the lateral ridge of the ulna. Rostrally to it, a very soft ridge conforms the origin of *M. extensor carpi radialis brevis—pars ulnaris*, close to the anterior margin and facing to the radius (Fig. 5H). In the medial side (Fig. 4I), other groove supports the origin of *M. pronator quadratus* (*Meers, 2003*). A small crest is situated caudally to this groove, in addition to other soft ridges, which comprise the origin of *M. flexor digitorium longus* (Fig. 5I; *Meers, 2003*). There are also very rough areas laterally and medially to the distal condyles for ligament attachments, with the lateral one being more developed than the medial.

Vertebrae

The preserved vertebrae have been sorted based on the presence of the keels and the position of the parapophyses, according to *Mook (1921)*. The fourth dorsal vertebrae (MCD5131) and the first (MCD5136), second (MCD4769) and third (MCD5126) lumbar have been recovered. All vertebrae are strongly procoelus.

MCD5131 (Figs. 6A–6D) is broken at the right side, and prezygapophyses, right diapophysis and parapophysis, and neural spine are lost. Postzygapophyses are elongated lateromedially and short anteroposteriorly, its articular surface faces ventrally and is lateromedially inclined. The left parapophysis is located at the base of diapophysis. The diapophysis is elongated and dorsolaterally oriented, but thin anteroposteriorly. The centrum and the neural arch are completely fused. The centrum is relatively short anteroposteriorly. A well-developed hypapophyseal keel is present ventrally to the centrum. Wide striated areas can be observed at the base of the neural arch, under the diapophyses and postzygapophyses, in the ventral side of the centrum, and dorsally to the neural arch, between the diapophysis, post- and prezygapophysis, and neural spine. These areas are consistent with a strong muscle attachment.

Lumbar vertebrae (MCD5136, MCD4769 and MCD5126; Figs. 6E–6P) are partially broken or eroded. Pre- and postzygapophyses are broader than those of the dorsal, and progressively wider from the first to the third lumbar. Neural spines are partially broken, but they seem to be wide anteroposteriorly and low. Transverse processes are horizontally oriented, and progressively decrease in height with respect to the centrum. They are laterally shorter and anteroposteriorly wider from the first to the third lumbar. There is a longitudinal groove ventrally to the centrum in all lumbar vertebrae. Like the dorsal vertebrae, wide striated areas are present laterally to the neural arch, across the diapophyses, in the ventral side of the centrum, and between the diapophysis, post- and prezygapophysis, and neural spine.

Ribs

Two partial ribs were recovered. One of them comprises only the shaft of a right dorsal rib (MCD5127) lacking its capitular and tubercular processes. It is elongated (19.2 cm long) and lateromedially compressed. In section, it is teardrop-shaped, with its thinner margin cranially, forming an anterior crest of the shaft. Soft ridges for muscle or ligaments attachments are present lateral and medially in the distal-most portion of the shaft. In turn, MCD4757 consists of the capitular and tubercular processes of an anterior-most left dorsal rib, which lacks the shaft.

Comparative anatomy

Cranial remains are comparable to other species of *Allodaposuchus*, especially to the nearly complete skulls of *A. precedens* and *A. subjuniperus* (*Delfino et al., 2008*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*; respectively). However, postcranial remains are only comparable to *A. palustris* (*Blanco et al., 2014*) due to the absence of published material of the others.

Several characters of the premaxilla distinguish *Allodaposuchus hulki* from the other species of the genus. The external naris opens in the antero-dorsal direction like *A. precedens*. In turn, naris of *A. subjuniperus* opens in dorsal direction. The external naris is significantly smaller than *A. precedens* and keyhole-shaped in *A. hulki*. Unlike *A. precedens* and *A. subjuniperus*, there is no elevation along the rim of the external naris. However, no lateral notch develops on the dorsal surface of premaxilla next to the naris opening, like *A. precedens* and *A. subjuniperus*. In palatal view, the incisive foramen is located more anteriorly than *A. precedens* and *A. subjuniperus*. In *A. hulki* the anterior rim of the incisive foramen is located between the first and second alveoli, whereas in *A. subjuniperus*, it reaches the third premaxillary alveolus. The premaxilla is wider than long, like *A. subjuniperus*. However, unlike *A. subjuniperus*, the premaxillary-maxillary suture does not reach the posterior margin of the incisive foramen, like *A. precedens*. The number of premaxillary alveoli is four, with the third alveolus being the largest, like *A. subjuniperus*. The premaxilla of *A. precedens* shows five teeth, and the fourth is the largest. Moreover, *A. hulki* shows a pattern of occlusal pits, different to *A. precedens* and *A. subjuniperus*: there is one occlusal pit between the first and second alveoli, another between the second and third, and no pit between the third and fourth alveoli. In turn, *A. precedens* shows one occlusal pit between the third and the fourth, and another between the fourth and the fifth alveoli, whereas *A. subjuniperus* shows only a large diastema between the first and second alveoli.

In addition, the skull table of *A. hulki* also shows differences from the other species of the genus. The main body of the frontal is concave medially, like *A. palustris* and *A. precedens*, and the orbital margins are upturned. However, this concavity is strongly marked in *A. hulki*, but only slightly in *A. palustris* and *A. precedens*. In contrast, *A. subjuniperus* shows a practically flat frontal with a low transverse interorbital ridge at the beginning of the anterior process. *Allodaposuchus palustris* also shows the interorbital ridge. Nevertheless, no interorbital ridge is present in *A. hulki* and *A. precedens*. The orbits of *A. hulki* are wide and short, like *A. precedens* and *A. subjuniperus*. In contrast, *A. palustris* shows relatively large and elongated orbits. However, the four species of *Allodaposuchus* have an elevated rostromedial margin of the orbits. The frontoparietal suture of *A. hulki* is nearly linear, like *A. subjuniperus* and *A. precedens*. *Allodaposuchus palustris* is the only 'allodaposuchian' that shows a concavo-convex frontoparietal suture. Additionally, *A. hulki* and *A. palustris* are the two species that do not show a fossa or shelf around the supratemporal fenestrae.

Like *A. precedens*, both articular hemicondyles of the quadrate of *A. hulki* are similar in size, although the medial hemicondyle is slightly smaller and ventrally deflected. In turn, *A. subjuniperus* shows a ventral expansion in the medial hemicondyle. The *foramen aëreum* of *A. hulki* is small, like *A. precedens* and *A. subjuniperus*, but large in *A. palustris*. This foramen is located on the dorsal surface, close to the medial edge of the quadrate, in all species of *Allodaposuchus*. However, in *A. hulki,* no ridge surrounds the *foramen aëreum*, unlike the other three species of *Allodaposuchus*. Like *A. subjuniperus*, in ventral view, there are two muscle scars of Iordansky (1973), without the association of any tubercle. *Allodaposuchus precedens* only shows one crest ending abruptly and forming a small tubercle, and *A. palustris* does not show any crest.

The exoccipital of *A. hulki*, *A. subjuniperus*, and *A. precedens* bears a very prominent boss on the paraoccipital process. *Allodaposuchus palustris* is the only 'allodaposuchian' that does not show this boss.

In ventral view, the capitate process of the laterosphenoid is anteroposteriorly oriented in *A. hulki* and *A. subjuniperus*, but is laterally oriented in *A. precedens*.

The quadratojugal of *A. hulki* shows a characteristic shape that represents a few autapomorphies of this taxon. Unlike *A. precedens* and *A. subjuniperus*, the quadratojugal does not extend to the superior angle of the infratemporal fenestra. Moreover, the quadratojugal spine is almost absent and near the ventral angle in the fenestra infratemporal. *Allodaposuchus precedens* and *A. subjuniperus* show the quadratojugal spine in a higher position in the fenestra. This spine is highly developed in *A. subjuniperus*.

The dentition of *A. hulki* also shows several characters that distinguish this form from the other species of the genus. In *A. hulki*, the enamel lacks ornamentation, both anterior and posterior carinae are poorly developed, and there are no longitudinal grooves in the lingual side. In contrast, *A. palustris* and *A. precedens* show ornamented enamel with well-developed carinae, whereas *A. subjuniperus* and *A. palustris* bear well-marked longitudinal grooves in the lingual side.

Concerning the axial skeleton, all recovered vertebrae are procoelous. This character clearly indicates a Eusuchian condition (*Salisbury et al., 2006*). Preserved dorsal and lumbar vertebrae are similar in shape to those of *Crocodylus acutus*, *Crocodylus niloticus*, *Alligator mississipiensis*, *Osteolaemus tetraspis* and *Allodaposuchus palustris*. However, all of the vertebrae of *A. hulki* show wide areas for muscle or ligament attachment, which are absent in those of *A. palustris*.

The appendicular skeleton is poorly comparable to *A. palustris*. This specimen does not preserve the scapula and ulna, but a fragmentary humerus, radius and hindlimb bones (*Blanco et al., 2014*). The scapula of *A. hulki* is similar in shape to those of extant crocodylians. The scapular blade shows a constriction dorsally to the glenoid and anterior process, and flares dorsally. However, in caudal view, the glenoid is more conspicuous and the scapular blade is more sinuous than in extant taxa. In addition, the scapula of *A. hulki* bears more developed scars for the origin of *M. scapulohumeralis caudalis, M. triceps longus lateralis, M. supracoracoideus intermedius* and *M. supracoracoideus longus* than in the other taxa compared. The humerus of *A. hulki* is clearly more robust and also shows more developed origins of *M. humeroradialis* and *M. brachialis* than in *A. palustris* and other extant taxa. In the latest taxa, the humeral surface is mainly smooth, but in *A. hulki* it is completely covered by soft ridges for muscle attachments. However, the humerus of *A. hulki* resembles those of the compared taxa in shape. In contrast, the ulna of *A. hulki* largely differs from the morphology of the extant crocodylians. The proximal epiphysis of the ulna of *A. hulki* has three well-developed processes (the olecranon directed posteriorly, an anteromedial process, and an anterolateral process). These processes are weakly developed in extant crocodylians, but well-developed in *Sebecus* and other terrestrial notosuchians (*Pol et al., 2012*; and references therein). Nevertheless, the general morphology of the proximal surface of the ulna is different between those fossil taxa and the new taxon of *Allodaposuchus*. The shaft of this bone is lateromedially compressed in *A. hulki*, unlike the other compared taxa that show a subcircular shaft in cross-section. Additionally, the torsion of the distal condyles, the crest for the origin of *M. flexor digitorium longus,* and the lateral and medial grooves for the origin of *M. flexor ulnaris* and *M. pronator quadratus*, respectively, have not been seen in other taxa used for comparison.

Thus, given all of the factors discussed above, *Allodaposuchus hulki* seems to be morphologically intermediate to *A. subjuniperus* and *A. precedens*, with several unique characters. In addition, as noted by *Blanco et al. (2014)*, the appendicular skeleton seems to be conservative in fossil 'allodaposuchians' and living taxa. Nevertheless, despite appendicular bones could not be directly compared between *A. hulki* and *A. palustris*, both 'allodaposuchians' show stronger muscle and ligament scars than in other taxa used for comparison.

RESULTS

Endocranial configuration

As typical for archosaurs, the brain did not occupy the entire endocranial cavity (*Witmer et al., 2008*). The 3D reconstruction of the cranial fragment reveals the morphology of some parts of the olfactory bulbs, the cerebral hemispheres, cranial nerves, inner middle ear and tympanic recesses (Fig. 7).

The preserved portion of the endocast shows the typical sigmoid morphology. However, just the most anterior part of the olfactory bulbs are preserved, whereas the cerebral hemisphere is dorsally well preserved but lacking some ventral areas for preservation reasons. Some of the left side cranial nerves are recognisable, in particular the nerve V system, particularly V$_1$, V$_2$ and V$_3$ as well as nerves III, IV and XII. The inner middle ear is present but badly preserved. Moreover, the low pixel resolution of the CT scan avoids assessing its morphology with confidence and is therefore not included in the figures (Fig. 7E).

Of particular interest are the tympanic recesses in the cranial fragment. On the one hand, the intertympanic recess is very developed. In extant crocodilians, such as *Crocodylus johnstoni* *Krefft, 1873* (*Witmer & Ridgely, 2008*), the anterior part of the intertympanic recess presents a semicircular morphology, whereas in the described specimen, a complete circle morphology is found due to the development of an anterior portion. In connection with the intertympanic recess, there is a *cavum tympanicum propium* with a similar morphology to that in other extant crocodilians. However, on the other hand, the quadrate sinus is very wide in comparison with other extant crocodilians (*Witmer et al., 2008*; *Witmer & Ridgely, 2008*) in the reported specimen.

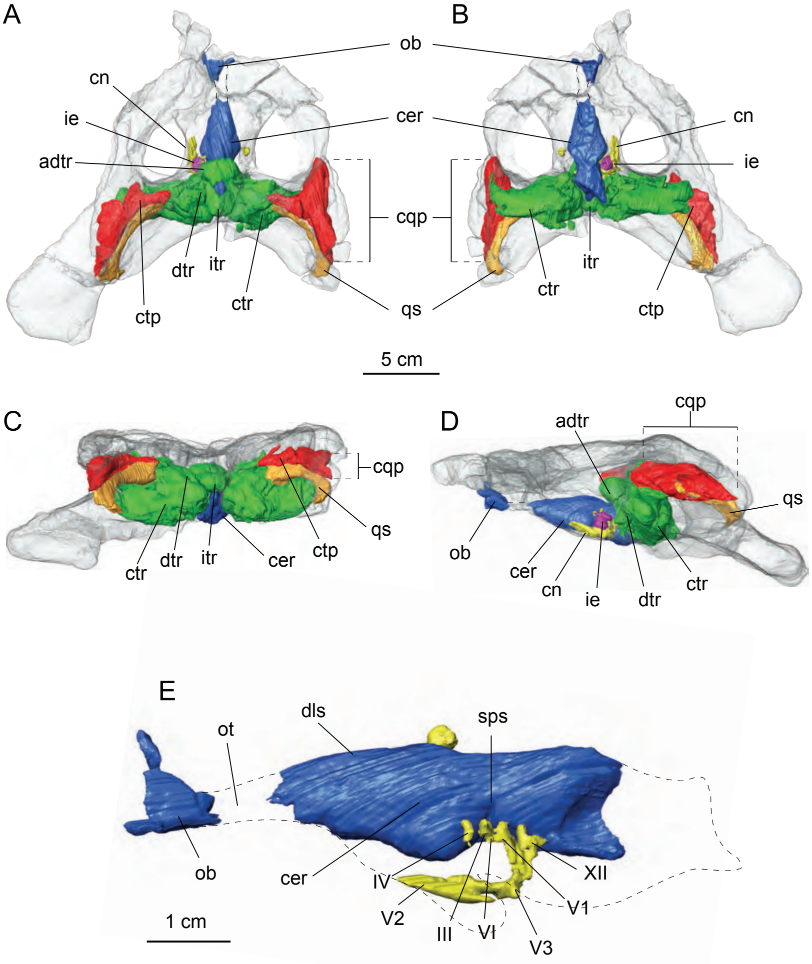

Figure 7 **Cranial endocast and pneumatic sinuses within the semi-transparent body skull of *Allodaposuchus hulki.*** MCD5139 derived from surface rendering of CT scan data in (A) dorsal, (B) ventral, (C) caudal, and (D) left lateral view. (E) Detail of the braincase and cranial nerves; the inner ear is removed because it obscured some endocast details. Abbreviations: adtr, anterodorsal tympanic recess; cer, cerebral hemisphere; cn, cranial nerves; cqp, craniocuadrate passage; ctp, *cavum tympanicum propium*; ctr, caudal tympanic recess; dls, dorsal line dural venous; dtr, dorsal tympanic recess; ie, inner ear; itr, intertympanic recess; ob, olfactory bulb; ot, olfactory track; qs, quadrate sinus; sps, sphenoparietal dural venous. Cranial nerve identification: III, oculomotor nerve canal; IV, trochlear nerve canal; V1, opthalmig nerve canal; V2, maxillary nerve canal; V3, mandibular nerve canal; VI, abducens nerve canal; XII, hypoglossal nerve canal.

Phylogenetic relationships

The cladistic analysis resulted in 1,240 equally parsimonious cladograms of 600 steps (CI = 0.382; RI = 0.811; RC = 0.310), and includes the specimen from Casa Fabà in the genus *Allodaposuchus*. The strict consensus tree (Fig. 8) shows similar topology to the last hypothesis about *Allodaposuchus* emplacement (*Blanco et al., 2014*), in contrast to some previous works that suggest that *Allodaposuchus* is a sister taxa of hylaeochampsids (*Buscalioni et al., 2001*; *Delfino et al., 2008*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*) or derived alligatoroid (*Martin, 2010*). In the present analysis, as in *Blanco et al. (2014)*, the clade 'Allodaposuchia' was included within Crocodylia, placed in a more derived position than Gavialoidea, and forming a polytomy with *Borealosuchus*, Planocraniidae and the clade Brevirostres (Crocodyloidea + Alligatoroidea). However, in the present analysis, the relationships between *Arenysuchus* and *Allodaposuchus* species were better resolved. In *Blanco et al. (2014)*, *A. palustris* is the most basal 'allodaposuchian', whereas *A. precedens*, *A. subjuniperus*, and *Arenysuchus* form a polytomy. Our results suggest that *A. precedens* and the Eusuchian from Casa Fabà are more derived than *A. subjuniperus* and *Arenysuchus*. Both results agreed that *A. palustris* is the most basal crocodylian of the genus, and that *Arenysuchus gascabadiolorum* could be included within the clade 'Allodaposuchia'. However, the relationships of *Arenysuchus* with this genus exceed the aim of this paper, and should be confirmed in detail in future works.

DISCUSSION

Phylogeny

The most parsimonious hypothesis obtained in our analyses suggests that the clade 'Allodaposuchia' belongs to Crocodylia (Fig. 8). Even though the Bremer and bootstrap values were low, the clade 'Allodaposuchia' has similar support to the other clades of Crocodylia. According to *Blanco et al. (2014)*, the genus *Allodaposuchus* might represent more derived Eusuchian crocodylomorphs than previously thought (*Buscalioni et al., 2001*; *Delfino et al., 2008*; *Narváez & Ortega, 2011*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*) but not as derived as in *Martin (2010)*. This hypothesis is supported by several cranial and vertebral characters. According to *Brochu (1997)*, the inclusion of the clade 'Allodaposuchia' within Crocodylia would be supported by the following synapomorphies: (1) anterior dentary teeth project anterodorsally, (2) retroarticular process projects posterodorsally, (3) frontoparietal suture concavo-convex, (4) mature skull table with nearly horizontal sides, and long posterolateral squamosal rami along paraoccipital process, (5) exoccipital lacks boss on paraoccipital process, and (6) hypapophyseal keels are present on the eleventh vertebrae behind the atlas. Absence of the boss in the paraoccipital process, only in *A. palustris*, would be an ancestral state reverted in other members of the clade 'Allodaposuchia' (*Blanco et al., 2014*). The following synapomorphies related *Allodaposuchus* with *Borealosuchus* + Planocraniidae + Brevirostres (*sensu*Brochu, 1997*): (1) slender postorbital bar, (2) ventral margin of postorbital bar inset from lateral jugal surface, (3) skull table surface planar at maturity, (4) frontoparietal suture concavo-convex, (5) neural arch of the axis lacking lateral processes (diapophyses),

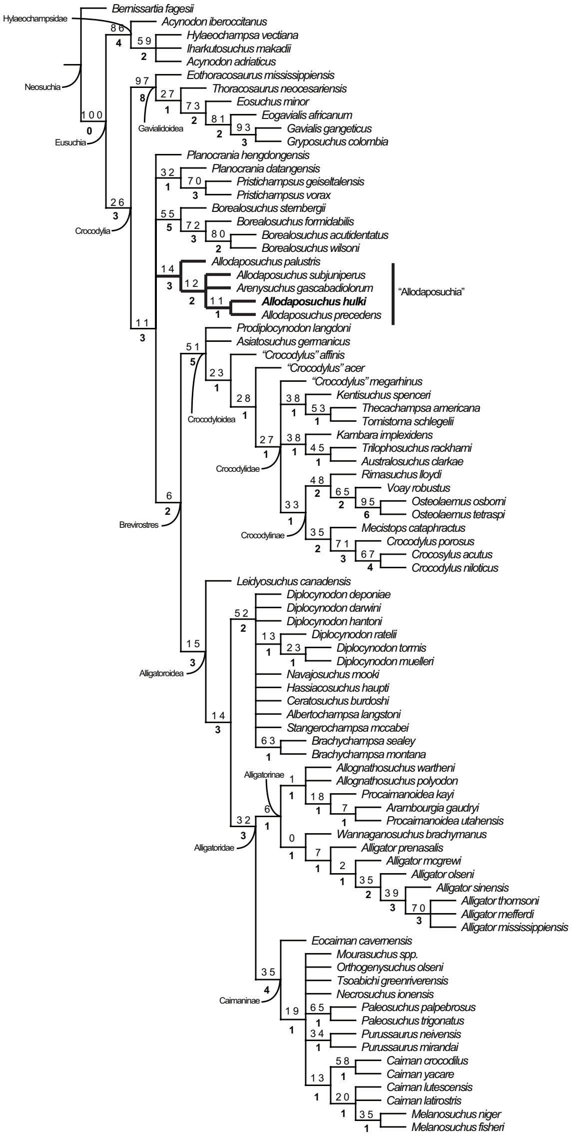

Figure 8 Resulting strict consensus cladogram illustrating the phylogenetic relationship of *Allodaposuchus hulki* and the basal position of 'Allodaposuchia' within Crocodylia. Values above nodes represent bootstrap percentage, whereas values under nodes represent Bremer support.

(6) wide posterior half of the axis neural spine, (7) axial hypapophysys without deep fork, and (8) M. *teres major* and M. *dorsalis scapulae* inset with common tendon on humerus. The concavo-convex frontoparietal suture, only in *A. palustris*, would be a reverted state in the other members of the clade 'Allodaposuchia' (*Blanco et al., 2014*).

The inclusion of Casa Fabà Eusuchian within the genus *Allodaposuchus* is well supported by the phylogenetic analyses (Fig. 8) and qualitative data (see above). *Allodaposuchus* differs from all other Eusuchians by the exclusive combination of the following synapomorphies (*Blanco et al., 2014*): margin of the orbits upturned; quadrate and squamosal not in contact on the external surface of the skull, posteriorly to the external auditory meatus; caudal margin of otic aperture not defined and gradually merging into the exoccipital; dermal bones roof overhang rim of supratemporal fenestra; cranioquadrate passage or *canalis quadratosquamosoexoccipitalis* laterally open and represented by a sulcus (broader than in *Hylaeochampsa vectiana*), with the exoccipital between the squamosal and the quadrate posterior to otic aperture. The ventral process of the exoccipital is not involved in the basioccipital tubera; the quadrate *foramen aëreum* on the dorsal surface. When preserved, all of the characters found in the specimen of Casa Fabà are in agreement with the synapomorphies of *Allodaposuchus*.

Allodaposuchus hulki, A. precedens and *A. subjuniperus* share a linear frontoparietal suture [C. 151 (1)], the presence of a shallow fossa or shelf at anteromedial corner of supratemporal fenestra [C. 153] (posteriorly reverted in *Allodaposuchus hulki* [C. 153 (1)]), and the exoccipital with very prominent boss on the paraoccipital process [C. 174 (0)].

Allodaposuchus hulki and *A. precedens* share the incisive foramen abutting the premaxillary tooth row [C. 89 (1)], external naris opened in aterodorsal direction [C. 81 (0)], and a very large medial jugal foramen [C. 102 (1)]. Such foramen is larger in *A. hulki* than in *A. precedens*, and consequently than in any other *Allodaposuchus*.

Allodaposuchus hulki shows some autapomorphies compared to other members of the clade 'Allodaposuchia': the quadratojugal that does not extend along the infratemporal fenestra [C. 145 (1)], the absence of fossa or shelf at anteromedial corner of supratemporal fenestra [C. 153 (1)], and teeth with characteristic morphology. In contrast, *A. precedens* shows dermal bones of the skull roof not overhanging supratemporal fenestra rim [C. 152 (0)], and capitate processes of laterosphenoid that are laterally oriented [C. 166 (0)]. In addition to the characters provided in the phylogenetic matrix, several qualitative morphological characters could be added to the phylogenetic results (see above). All of these differences justify the assignment of the specimen from Casa Fabà to a different species within *Allodaposuchus*.

Cranial pneumaticity and paratympanic recesses

In recent times, the virtual reconstruction of cranial cavities of extant and extinct archosaurs has provided an enormous advance in knowledge about the configuration and evolution of the brain regions and the surrounding bony recesses. Most of these studies focus on the endocast morphology as well as the inner ear disposition and its paleobiological implications (e.g., *Witmer & Ridgely, 2009*; *Kley et al., 2010*; *Fernández et al., 2011*; *Bona, Degrange & Fernández, 2013*, and references therein).

Despite lacking most of its ventral and posterior-most parts, the general shape of the cranial endocast of *Allodaposuchus hulki* (Fig. 7) is similar to those of extant crocodilians (e.g., *Gavialis gangeticus* *Gmelin, 1789*, *Crocodylus johnstoni*, *Alligator mississipiensis*; see *Wharton, 2000*; *Witmer et al., 2008*; *Witmer & Ridgely, 2009*; *George & Holliday, 2013*, respectively). Furthermore, the overall configuration of the cranial endocast of the specimen resembles that of many other crocodylomorphs such as notosuchians (e.g., *Anatosuchus* *Sereno et al., 2003*, *Araripesuchus* *Price, 1955*, and *Simosuchus* *Buckley et al., 2000*; see *Sereno & Larsson, 2009*; *Kley et al., 2010*, respectively) and metriorhynchids (*Fernández et al., 2011*). The curvilinear dorsal counter of the endocast exhibited by *Allodaposuchus hulki* is more similar to those observed in Neosuchia (*Witmer & Ridgely, 2008*; *George & Holliday, 2013*; Fig. 7A) than the characteristic spade-shape outline showed by notosuchians (*Sereno & Larsson, 2009*; *Kley et al., 2010*). In sagittal view, the shape of the cranial cavity indicates that most of the braincase elements were arranged in a planar configuration (Figs. 7D and 7E), in contrast to the sigmoidal organisation of most of the extant crocodylians *Witmer et al., 2008*; *Witmer & Ridgely, 2009*; *George & Holliday, 2013*. Another significant feature of the braincase of *Allodaposuchus hulki* is that in dorsal view, the cerebrum exhibits a rhomboid shape, which is more elongated rostrally than extant crocodilians, and shows a gentle transition to the olfactory track (Figs. 7A and 7B).

In comparison to works analysing braincase morphology, there are few studies focusing on the system of pneumatic cavities surrounding the main endocranial body (*Witmer et al., 2008*; *Witmer & Ridgely, 2009*; *Witmer & Ridgely, 2010*; *Bona, Degrange & Fernández, 2013*). In extant crocodilians, the paratympanic system is divided in the three main parts: (1) two caudal tympanic recesses connected by (2) the inner tympanic recess, which also links (3) the dorsal tympanic recesses located at each side of the endocranial cast (*Witmer et al., 2008*). The same configuration is observed in the Miocene caimanine *Mourasuchus nativus* *Gasparini, 1985* (*Bona, Degrange & Fernández, 2013*). *Dufeau & Witmer (2007)* noted several ontogenetic changes in the tympanic cavities along the life history of *Alligator mississippiensis*. The authors stated that these changes could also be phylogenetically tracked within the crurotarsia linage, as basal taxa show the young alligator condition, whereas more crownward taxa resemble the adult one. In this regard, *A. hulki* shows endocranial features of both juvenile (i.e., large quadrate sinuses) and adult alligators (i.e., well-developed dorsal tympanic recesses).

In addition, *Allodaposuchus hulki* exhibits some important differences in the tympanic system configuration observed in extant adult crocodilians. First, it shows a well-developed pneumatic cavity connecting anteriorly both dorsal tympanic recesses. This sinus, herein referred as anterodorsal tympanic recess, covers part of the sphenoparietal dural venous sinus but leaving a circular opening at the level of the occipital dural venous sinus (Fig. 7A). In some ways, it resembles the frontal recess observed in the *Struthio camelus* Linnaeus (*Witmer & Ridgely, 2009*), but not so developed in *Allodaposuchus*. Although variations in the paratympanic system are reported in more derived archosaurs (i.e., some non-avian theropods exhibit supraoccipital pneumatic sinus connected to the tympanic pneumaticity, and birds have enlarged both dorsal and caudal tympanic recesses; *Witmer & Ridgely, 2009*; *Witmer & Ridgely, 2010*), nothing like the anterodorsal tympanic recess of *A. hulki* has been recognised so far. In addition, another distinctive feature of the tympanic system of the new species is the caudolateral expansion of the caudal tympanic recesses; which excavate a large cavity within the exooccipital bones. Such caudal tympanic sinus configuration is not present in any extant crocodilomorph, neither has it been reported previously from any extinct one, but it resembles that of large non-avian theropods (*Witmer et al., 2008*; *Witmer & Ridgely, 2009*; *Witmer & Ridgely, 2010*).

The external ear of the genus *Allodaposuchus* is distinguished by a broad cranioquadrate passage, a feature shared with the basal Eusuchian *Hylaeochampsa* (*Buscalioni et al., 2001*; *Delfino et al., 2008*; *Blanco et al., 2014*; *Puértolas-Pascual, Canudo & Moreno-Azanza, 2014*). Although its external morphology has been described in detail by several authors, here we provide the first tridimensional reconstruction of this cranial cavity and its relationship with the tympanic sinus and the braincase (Fig. 7). The cranioquadrate passage of *Allodaposuchus hulki* opens to a well-developed *cavum tympanicum proprium* that is lateromedially directed (Fig. 7A), which connects to the tympanic complex at the level of the dorsal tympanic recesses. In *Crocodylus johnstoni,* the *cavum tympanicum proprium* is more medioventrally directed (*Witmer et al., 2008*), a condition that is also noted in the caimaninid *Mourasuchus* (*Bona, Degrange & Fernández, 2013*). It is worth commenting that the *cavum tympanicum proprium* of *Allodaposuchus hulki* is ventrally connected to a large quadratic sinus (Fig. 7C).

In fact, the large size of the quadratic sinus is another highlighted feature of *Allodaposuchus*. In *Crocodylus johnstoni*, the quadratic sinus is also located above the *cavum tympanicum proprium* but it is smaller than that of the *A. hulki* and extends posterodorsally to the pharingotympanic recess (*Witmer et al., 2008*). A long and thin siphonial tube (see *Witmer et al., 2008*: Fig. 6.6.A-B) runs along the quadrate connecting the quadratic sinus and the *siphonium*. The later connects with the articular recess of the mandible. The siphonial tube is not observed in *A. hulki*, but the place where it was supposed to be is partially occupied by the enlarged quadratic sinus. Thus, we hypothesise that it could be relatively short, extending from the caudal end of the quadratic sinus and the *foramen aëreum* placed near the posterior edge of the quadratic hemicondyle.

The unique cranial pneumaticity configuration observed in *A. hulki*, especially with regard to the paratympanic system (e.g., an anterodorsal tympanic recess and enlarged caudal tympanic recesses) and the enlargement quadratic sinus, suggests some degree of otic specialisation. Although being just a hypothesis, the paratympanic configuration of *A. hulki* could result in a more efficient pressure difference receiver mechanism, which is related to directional hearing (*Bierman et al., 2014*). We hope that future studies could shed light on this question.

Forelimb myology and functional morphology

Three types of limb posture are traditionally identified in quadrupedal tetrapods during terrestrial locomotion: sprawling, semi-erected, and erected. Extant crocodilians locomotion ranges from sprawling, in which the limbs are positioned laterally, to a semi-erected high walk, in which limbs are strongly adducted (*Briknam, 1980*; *Parish, 1986*; *Parish, 1987*; *Gatesy, 1991*; *Allen et al., 2014*), whereas some extinct crocodylomorphs, such as notosuchians, could exhibit the erect posture (*Sertch & Groenke, 2011*; *Chamero, Buscalioni & Marugán-Lobón, 2013*; and references therein). However, most of these postures and locomotion inferences are based on anatomical features of the pelvic girdle and hind limbs rather than the pectoral girdle and forelimbs. In addition, the reconstruction of appendicular musculature is also regarded as being increasingly important in understanding locomotion behaviour in fossil vertebrates. Thus, recognising the morphological features in anterior limbs that characterise each type of limb posture is a clue to infer not only locomotion but also the lifestyle of *Allodaposuchus hulki*.

From a morphological point of view, the scapula of *A. hulki* exhibits a robust appearance. It is primarily characterised by having a well-developed anterior process with a wide deltoid crest, a marked scapular buttress, and scapular blade margins flared dorsally. Although no quantitative analyses can be conducted because of the fragmentary nature of the element, the combination of those features is consistent with the general scapular configuration of extant alligatorids and gavialids according to *Brochu (1997)* and *Chamero, Buscalioni & Marugán-Lobón (2013)*, whereas crocodiles tend to show more slender scapulae with narrow blades. The presence of a prominent scapular buttress has been considered characteristic of upright posture in several terrestrial crocodilomorph taxa, whereas the absence of this treat is characteristic of primarily aquatic ones (*Sertch & Groenke, 2011*; *Chamero, Buscalioni & Marugán-Lobón, 2013*). Although this feature is present in *Allodaposuchus hulki*, it is not as developed as in terrestrial mesoeucrocodylian (e.g., *Simosuchus* or *Araripesuchus*). Thus, it may indicate some degree of upright posture, but not fully erect, or additional bracing of the forelimb. The angular morphology of the glenoid fossa suggests a moderate range of rotation of the humeral head within the glenoid cavity, which also agrees with a non-fully erect posture. Accordingly, sprawling or the semi-erected postures are the most likely terrestrial locomotion model to be inferred in *A. hulki*.

Another important trait of the scapula of *A. hulki* is the presence of several rough surfaces related to muscular attachment. Especially noteworthy are those located in the anterior process of the scapula, such as *M. supracoracoideus intemedius*, *M. supracoracoideus longus*, and *M. coracobrachialis brevis dorsalis*, which occupy relatively more of the surface than in extant crocodilomorph (Figs. 5A–5C; see *Meers, 2003*). These muscles are primarily involved in stabilising the shoulder joint, but they are also powerful protractors and adductors of the humerus, and may assist in extension of the forelimb. The *M. deltoideus clavicularis*, another powerful protractor of the humerus, is not specially developed in *A. hulki*, but muscle insertions are strongly marked. As a result, the morphology and myology configuration of the scapula of *A. hulki* seems to point at a powerful shoulder, with strong protractor/adduction capacities capable of supporting a robust body, keeping it off the ground.

Like the scapula, the humerus has an overall robust aspect, and it could be relatively short (Figs. 5D–5G). Because it lacks both epiphyseal ends, few assessments in regards to the torsion of the shaft or development of the articular parts can be performed. Furthermore, the preserved humerus does not exhibit any distinctive feature in its diaphysis if compared with extant crocodilians. Apart of the wide rough areas related to the *M. scapulohumeralis caudalis*, and the *triceps brachii* muscle complex, the humerus is a nearly smooth (Figs. 5D–5G). The *M. scapulohumeralis caudalis* assists in the elevation of the humerus and its stabilisation within the glenohumeral joint, but also plays an important role in protraction of the humerus. The main function of *triceps brachii* complex is to assist in the flexion of the brachium on the shoulder while extending the antebrachium on the brachium, thus supporting the body off the ground against gravity (*Meers, 2003*). These muscular features are in line with previous ideas suggesting that *A. hulki* could have robust forelimbs capable of performing powerful protractor movements during terrestrial locomotion.

The ulna is the most distinctive element of the forelimb of *Allodaposuchus hulki*. It is featured by an expanded proximal epiphysis with prominent processes, a shaft compressed mediolaterally with wide grooves located in both medial and lateral sites, and a marked twist of the distal end of the shaft. Overall, the ulna of *A. hulki* resembles those of extant crocodile taxa, but its expanded proximal epiphysis and twisted distal part resemble that of *Simosuchus* and *Sebecus* (*Sertch & Groenke, 2011*). As previously stated, the most prominent rugosity of the ulna is located in the olecranon process, corresponding to the insertion of *M. triceps brachii* (Figs. 5H and 5I; *Meers, 2003*; *Allen et al., 2014*). Less marked are those areas related with the insertion of *M. flexor ulnaris* and *M. pronator quadratus*, although they occupy relatively more surface than in current crocodile taxa (see *Meers, 2003*). This would mean that *A. hulki* could exhibit powerful muscles related to the flexion and pronation of the antebrachium. The crest placed at the origin of the *M. flexor digitorium longus* also suggests that a complex mechanism is involved in flexion of the wrist. Although characteristics of the appendicular skeleton suggest that *A. hulki* was not suited to a fully erect posture, several features indicate a powerful forelimb capable of performing sprawling and semi-erect postures. Furthermore, the robust configuration of the forelimbs seems to be consistent with a terrestrial lifestyle, or semi-terrestrial, rather than a semi-aquatic one.

The semi-terrestrial lifestyle hypothesis for *Allodaposuchus hulki* is also supported by the high degree of pneumaticity observed in its skull. Although large cranial cavities of *A. hulki*, such as the caudal tympanic recesses and quadrate sinuses, seem to be primarily related to a specialised otic system, they could also play an important role in lightening the weight of the skull like in large non-avian theropods (see *Witmer et al., 2008*; *Witmer & Ridgely, 2009*; *Witmer & Ridgely, 2010*), or other terrestrial vertebrates.

Ecological implications

According to both cranial and postcranial features displayed in *Allodaposuchus hulki*, it could exhibit some kind of terrestrial or semi-terrestrial lifestyle rather than semi-aquatic ones. This interpretation is also supported by paleoenvironmental evidence.

Charophyte fructifications at the Casa Fabà outcrop were found in the grey claystones above the pedogenised channelised sandstone bed belonging to the lower part of the fluviatile 'lower red unit' (*Riera et al., 2009*). The charophyte assemblage is formed by extremely small gyrogonites of *Microchara cristata* Grambast, *Microchara nana* Vicente & Martín-Closas, *Microchara punctata* Feist & Colombo and *Microchara aff. laevigata* Grambast & Gutiérrez. Most of the samples show well-preserved gyrogonites, suggesting that they belong to an autochthonous assemblage. Charophytes were also found along with gastropod shells and operculi, fragmentary vertebrate remains and slightly eroded eggshells and planktonic foraminifera.

Assemblages formed exclusively by species bearing small gyrogonites (e.g., *M. nana)* have been related to turbid and warm ephemeral ponds usually found in terrigenic floodplains (*Vicente et al., 2015*). Despite also being common in lacustrine and palustrine environments, the absence of typically lacustrine species in the assemblages suggests that this highly fluctuant and stressed continental environment favours the thriving of these adapted species bearing small gyrogonites.

In addition, no channel or lake deposits have been found near the Casa Fabà site, or at least no closer than 2.5 km away. These evidences, along with anatomical characteristics, may suggest that *Allodaposuchus hulki* could perform relatively large incursions on the earth, moving from place to place, only stopping in ephemeral water bodies looking for food or other resources.

Institutional Abbreviations

MCD	Museu de la Conca Dellà, Lleida, Spain.
MZB	Museu Zoològic de Barcelona, Barcelona, Spain.

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The authors declare there are no competing interests.

Author Contributions

- Alejandro Blanco and Albert G. Sellés conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Josep Fortuny performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Alba Vicente analyzed the data, wrote the paper.
- Àngel H. Luján prepared figures and/or tables, reviewed drafts of the paper.
- Jordi Alexis García-Marçà wrote the paper.

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The following information was supplied regarding the registration of a newly described species:

Allodaposuchus hulki urn:lsid:zoobank.org:act:267AADFA-AD84-45F4-B195-D08E174559CC.

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A first attempt to explain the crocodylomorph diversity in the Maastrichtian of northeastern Iberia based on tooth qualitative traits

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Abstract

During the last years the knowledge about the crocodylomorph diversity of the uppermost Cretaceous from Europe has been substantially improved. Palaeontological efforts have been also focused on the microvertebrate diversity and its palaeoecological implications. Isolated crocodylomorph teeth are, by far, one of the most frequently recovered elements from the microvertebrate samples. In the present paper, morphological features of crocodylomorph teeth collected throughout the complete Maastrichtian section of the Tremp Formation (northeastern Spain) are described and analysed. Teeth were grouped in morphotypes and their taxonomic significance is discussed. The results point to a diverse crocodylomorph assemblage in this area throughout the Maastrichtian. In addition, evidence for food habits and habitat preferences for the identified taxa are explained according to dental features and taphonomy.

Introduction

During the last years the knowledge about the crocodylomorph diversity of the uppermost Cretaceous from Spain and southern France has been substantially improved. During the Maastrichtian, these landmasses formed a large island, the so-called Ibero-Armorican domain, in the westernmost edge of the southern European archipelago (Dercourt et al., 2000). Recent studies suggest that the crocodylomorph faunas inhabiting marine, transitional and continental settings within this island were dominated by eusuchians, mostly belonging to the clade Allodaposuchidae (e.g., Puértolas-Pascual et al., 2016).

Four species of allodaposuchid crocodiles from the Maastrichtian beds of the Tremp Formation (southern Pyrenees; Mey et al., 1968; Rosell et al., 2001; Oms et al., 2007) have been described: *Allodaposuchus subjuniperus* Puertolas-Pascual, Canudo & Moreno-Azanza 2014 (recently relocated within the genus *Agaresuchus*; Narváez et al., 2016a); *A. palustris* Blanco, Puértolas-Pascual, Marmi, Vila & Sellés 2014; *A. hulki* Blanco, Fortuny, Vicente, Luján, García-Marçà & Sellès 2015 and *Arenysuchus gascabadiolorum* Puértolas, Canudo & Cruzado-Caballero 2011—initially considered a basal crocodyloid (Puértolas et al., 2011), but included within the clade Allodaposuchidae in further analyses (Blanco et al., 2014, 2015a; Narváez et al., 2015). Additionally, in the upper Campanian-lower Maastrichtian beds from Lo Hueco, which deposited in the Iberian Basin, other two allodaposuchid species were erected: *Lohuecosuchus megadontos* Narváez, Brochu, Escaso, Pérez-García & Ortega 2015 and *Agaresuchus fontesi* Narváez, Brochu, Escaso, Pérez-García & Ortega 2016. Undescribed allodaposuchid bone remains collected from Armuña (Segovia, Spain) might correspond to another additional taxon (Pérez-García et al., 2016). Moreover, up to three other allodaposuchid taxa or related forms have been reported in coeval localities from the Basque-Cantabrian Region and southern France: *Musturzabalsuchus buffetauti* Buscalioni, Ortega & Vasse 1997, *Lohuecosuchus mechinorum* Narváez, Brochu, Escaso, Pérez-García & Ortega 2015 and three skulls from Velaux-La Bastide Neuve site, referred to an indeterminate allodaposuchid (Blanco & Brochu, in press). Similarly, several partial specimens originally referred to *Allodaposuchus precedens* by Buscalioni et al. (1986, 2001) are regarded as indeterminate allodaposuchids after recent revisions (Blanco & Brochu, in press; Narváez et al., 2016b).

Besides Allodaposuchidae, other eusuchian taxa composed the Ibero-Armorican faunas, as evidenced by fossil remains of the basal gavialoid *Thoracosaurus*, the indeterminate eusuchian *Massaliasuchus* as well as the Hylaeochampsid *Acynodon iberoccitanus* Buscalioni, Ortega & Vasse 1997 from southern France and the Iberian Peninsula (Puértolas-Pascual et al., 2016). The fossil record of non-eusuchian taxa seems, however, less diverse, being represented by *Ischyrochampsa meridionalis* Vasse 1995 and the Sebecosuchian *Doratodon ibericus* Company, Pereda-Suberbiola, Ruiz-Omeñaca & Buscalioni 2005.

All of these crocodylomorph species were described on the basis of fragmentary or complete skulls and partial skeletons. However, teeth are the most abundant crocodylomorph remains recovered from vertebrate fossil accumulations in the uppermost Campanian and Maastrichtian beds from Spain and southern France, providing evidence for non-eusuchians atoposaurids (*i.e.*, *Theriosuchus*) and perhaps for trematochampsids in addition to most of the aforementioned taxa (Marmi et al., 2016; Puértolas-Pascual et al., 2016). These latter authors pointed out that the taxonomic value of isolated crocodylomorph teeth is limited and classification of specimens should be taken with caution. Although it is difficult to distinguish among generalist taxa (e.g., genera and species within Allodaposuchidae), isolated teeth have revealed the presence of members of Atoposauridae (*Theriosuchus*), Paralligatoridae (*Sabresuchus*), Hylaeochampsidae (*Acynodon*), Notosuchia (*Doratodon*), Gavialoidea (*Thoracosaurus*) and ?Trematochampsidae in many localities lacking bone remains (see Puértolas-Pascual et al., 2016 and references therein). Furthermore, the species *Acynodon lopezi* Buscalioni, Ortega & Vasse 1997 was erected on the basis of tribodont teeth collected in the Quintanilla del Coco locality (Burgos, Spain; Buscalioni et al., 1997).

In the present paper, morphological features of crocodylomorph teeth collected throughout the complete Maastrichtian section of the Tremp Formation (northeastern Spain) are described and analysed in order to distinguish morphotypes and explore their taxonomic significance. One of the main goals of the work is to obtain a more complete picture of the crocodylomorph assemblage in the area during the last six millions of years before the Cretaceous-Paleogene (K/Pg) event and compare this diversity with other coeval European localities. In addition, evidence for food habits and habitat preferences for the identified taxa are discussed according to dental features and taphonomy.

Geological setting

During most of the Late Cretaceous, the Pyrenean area (northeastern Iberia) was submerged under shallow marine waters. Near the Campanian-Maastrichtian boundary, a marine regression began in this region, being recorded in the sediments deposited in an east-to-west elongated foreland trough connected to the Atlantic, the so-called southern Pyrenean basin. Campanian-Maastrichtian marine deposits consist of barrier island and beach sandstones of the Arén Sandstone Formation (Mey et al., 1968) and lateral equivalents such as the near shore calcarenites of the Terradets Formation (Pons, 1977). These marine sediments are overlaid by the transitional to continental beds of the Tremp Formation, which deposited between the Maastrichtian and the Thanetian (Mey et al., 1968). The south Pyrenean foreland basin was active from the Late Cretaceous until the Oligocene due to the uplift of the Pyrenean range. During this period, a series of thrust sheets developed and moved southwards several tens of kilometres splitting up the southern Pyrenean basin (Puigdefàbregas et al., 1986). As a result, nowadays, the Tremp Formation materials crop out in different synclines, which are, from east to west, Vallcebre, Coll de Nargó, Tremp and Àger (Fig. 1).

By means of basin analysis, Rosell et al. (2001) divided the Tremp Formation into four lithological units, which are from the base to the top:

I) 'Grey unit', which is composed of marls, lignite, limestones, and sandstones. It is interpreted as lagoon settings including mudflats and coastal wetlands of variable salinity, overlying or laterally connected to the barrier island systems that made up the Arén Sandstone Formation.

II) 'Lower red unit', which consists of ochre to red mudstones with paleosols, sandstones, conglomerate. These materials deposited in floodplain alluvial and fluvial settings with braided and meandering channels as well as ephemeral lakes.

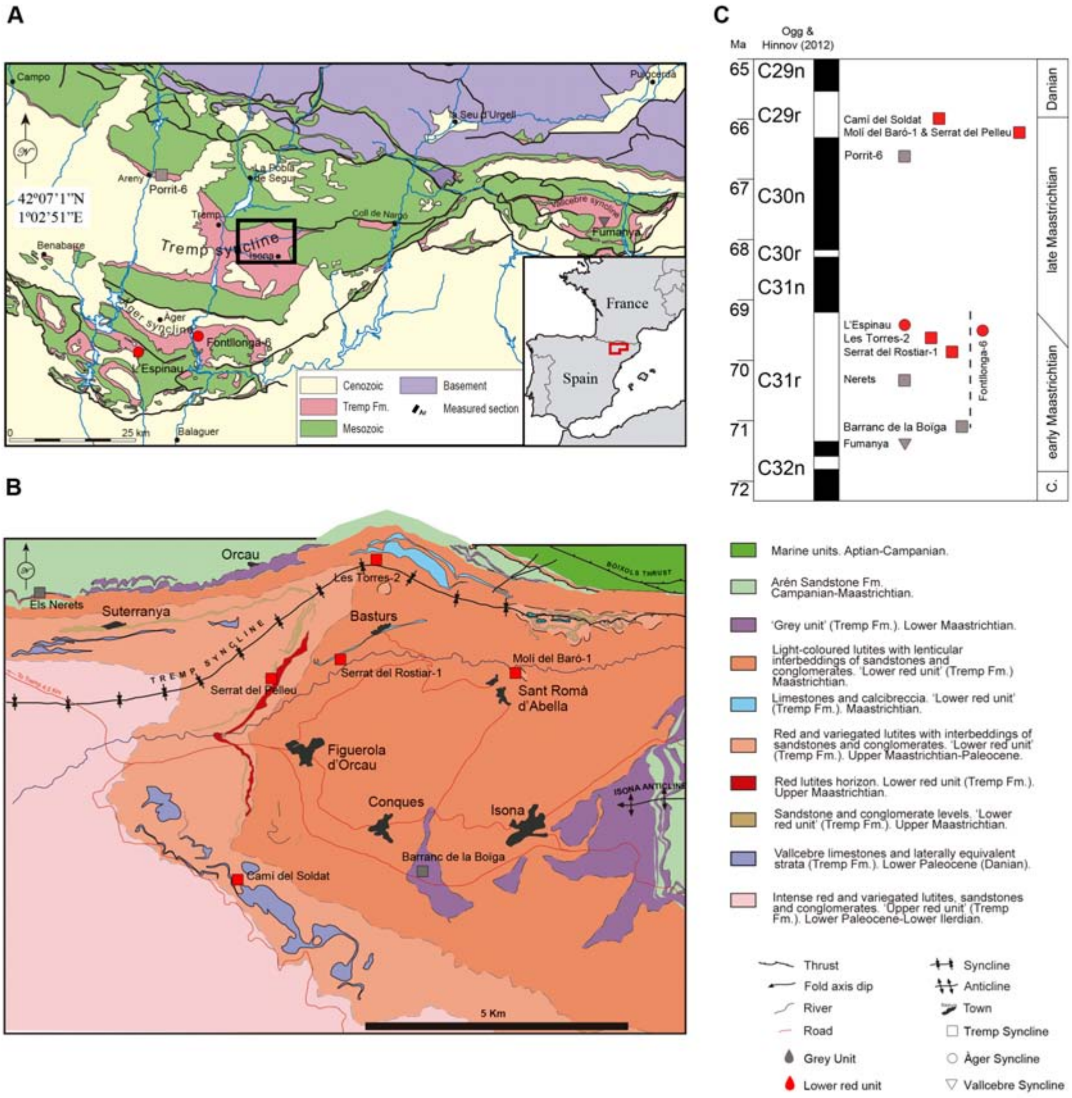

Figure 1. Geographic and geological context of the studied sites. **(A)** Geological map of the south-central Pyrenean unit (enlarged from the western Europe map), showing the outcrops of the Cretaceous-Paleocene Tremp Fm. and the location of Fumanya, Porrit-6, L'Espinau and Fontllonga sites (modified from Blanco et al., 2016, 2017). **(B)** Geological map of the Isona area (enlarged from A) with the position of the Camí del Soldat, Serrat del Pelleu, Serrat del Rostiar-1, Molí del Baró-1, Les Torres-2, Barranc de la Boïga and Els Nerets sites (modified from Blanco et al., 2016, 2017). **(C)** Temporal distribution of the aforementioned sites based on magnetostratigraphic data (modified from Blanco et al., 2017).

III) Vallcebre limestone and laterally equivalent deposits. Micritic limestones interpreted as lacustrine environments.

IV) 'Upper red unit', which is composed of mudstones, sandstones, conglomerates and limestones, deposited in fluvial and alluvial systems.

Based on biostratigraphy (Feist & Colombo, 1983; Díez-Canseco et al., 2014; Vicente et al., 2015) and magnetostratigraphy (Oms et al., 2007), the 'grey unit' and the 'lower red unit' are Maastrichtian in age whereas the Vallcebre limestone and the 'upper red unit' fall within the Paleocene.

The crocodilian material herein studied was collected from the following localities: Fumanya in the Vallcebre syncline; Molí del Baró-1 (most of this material was previously reported by Marmi et al., 2016), Serrat del Rostiar-1, Serrat del Pelleu, Camí del Soldat, Les Torres-2, Els Nerets, Pont d'Orrit-6 and Barranc de la Boiga in the Tremp syncline; L'Espinau and Fontllonga-6 in the Àger syncline (Fig. 1).

Materials and methods

The fieldwork was carried out between 2010 and 2011. Samples of about 200 kg of rock from Pont d'Orrit-6, 375 kg from Els Nerets, Les Torres-2 and Barranc de la Boiga, 525 kg from Serrat del Pelleu and Fontllonga-6, 575 kg from Camí del Soldat, 625 kg from Serrat del Rostiar-1 and 1250 kg from L'Espinau were collected for processing. Samples were then macerated employing successive water immersions and sun drying in order to shred the rock matrix. Screenwashing was carried out using running water and a sieve series of 1.4, 0.8 and 0.5 mm. The fossils from Fumanya and Molí del Baró-1 were recovered by picking them from rock matrices, instead of by screenwashing techniques; this took place during the digging work carried out in 2007, 2010 and 2011. The samples were then sorted under a Leica M60 binocular microscope. Photographs were taken under a Zeiss Evo MA10 environmental scanning electron microscope (ESEM) at the Servei de Microscopia de la Universitat Autònoma de Barcelona. The specimens described in this paper are housed in the collection of the Museu de la Conca Dellà (Isona, Lleida, Spain) and Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain).

Isolated teeth were grouped and described in morphotypes following the methodology of previous studies (*i.e.*, Prasad & de Lapparent de Broin, 2002; Puértolas-Pascual et al., 2015; Marmi et al., 2016). These morphotypes were subsequently compared with similar material from geographically close and chronologically coeval sites, available in the literature. Additionally, the tooth sample is complemented with some dentaries collected during prospections and digging works in the sampled sites. These dentaries were described and their taxonomic affinities were discussed in order to support the inferred taxa for the morphotypes.

Results

Tooth morphotypes

A total of 107 teeth were recovered and grouped in 14 morphotypes (Fig. 2), which are described below. Morphotypes 1–10 match with the ten morphotypes described by Marmi et al. (2016) from the Molí del Baró-1 site.

CROCODYLOMORPHA Walker 1970 (*sensu* Clark, 1986)
CROCODYLIFORMES Hay 1930
MESOEUCROCODYLIA Whestone & Whybrow 1983 (*sensu* Benton & Clark, 1988)
NOTOSUCHIA Gasparini 1971 (*sensu* Pol et al., 2014)
ZIPHOSUCHIA Ortega et al. 2000

Morphotype 6

Ziphosuchia indet. form 1
Localities: Molí del Baró-1, Serrat del Rostiar-1, L'Espinau.
Material: MCD5560-63, MB11-80, IPS-96636, IPS-96646 .
(Fig. 2A-C)

Description: Conical and pointed teeth, resembling the generalist morphotype 1 in shape. They are 8.8-9.2 mm basiapically high and 3.3-4.0 mm mesiodistally wide. The enamel lacks ornamentation in both lingual and labial sides. MCD-5560 and MCD-5561 are subcircular in cross-section, curved posteriorly and bear only a distal carina. MCD-5562 is also subcircular in cross-section, but shows mesial and distal carinae. The other studied teeth are slightly compressed labio-lingually, thus the cross-section is elliptical. Carinae, if present, show small crenulations but do not develop true denticles. This feature, however, could be also considered true ziphodonty since crenulations are not consequence of the ornamentation of the enamel overhanging the carinae.

Remarks: Differences in shape between MCD-5560, MCD-5561, MCD-5562 and the other teeth could be related to the position in the dental series. According to the shape of the cross-section and the presence of a mesial carina, MCD-5560 and MCD-5561 would be more anterior tooth than MCD-5562, and the latter could be more anterior than the remaining teeth. Isolated ziphodont teeth are usually referred to *Doratodon* sp. (e.g., Martin et al., 2006), which teeth are subtriangular in shape, compressed labio-lingually, and present well-defined denticles in both anterior and posterior carinae (Grigorescu et al., 1999; Company et al., 2005; Rabi & Sebők, 2015). However, these latter features are not present in the studied material. Thus, this morphotype is regarded to belong to an indeterminate ziphodont crocodile, likely included within Ziphosuchia.

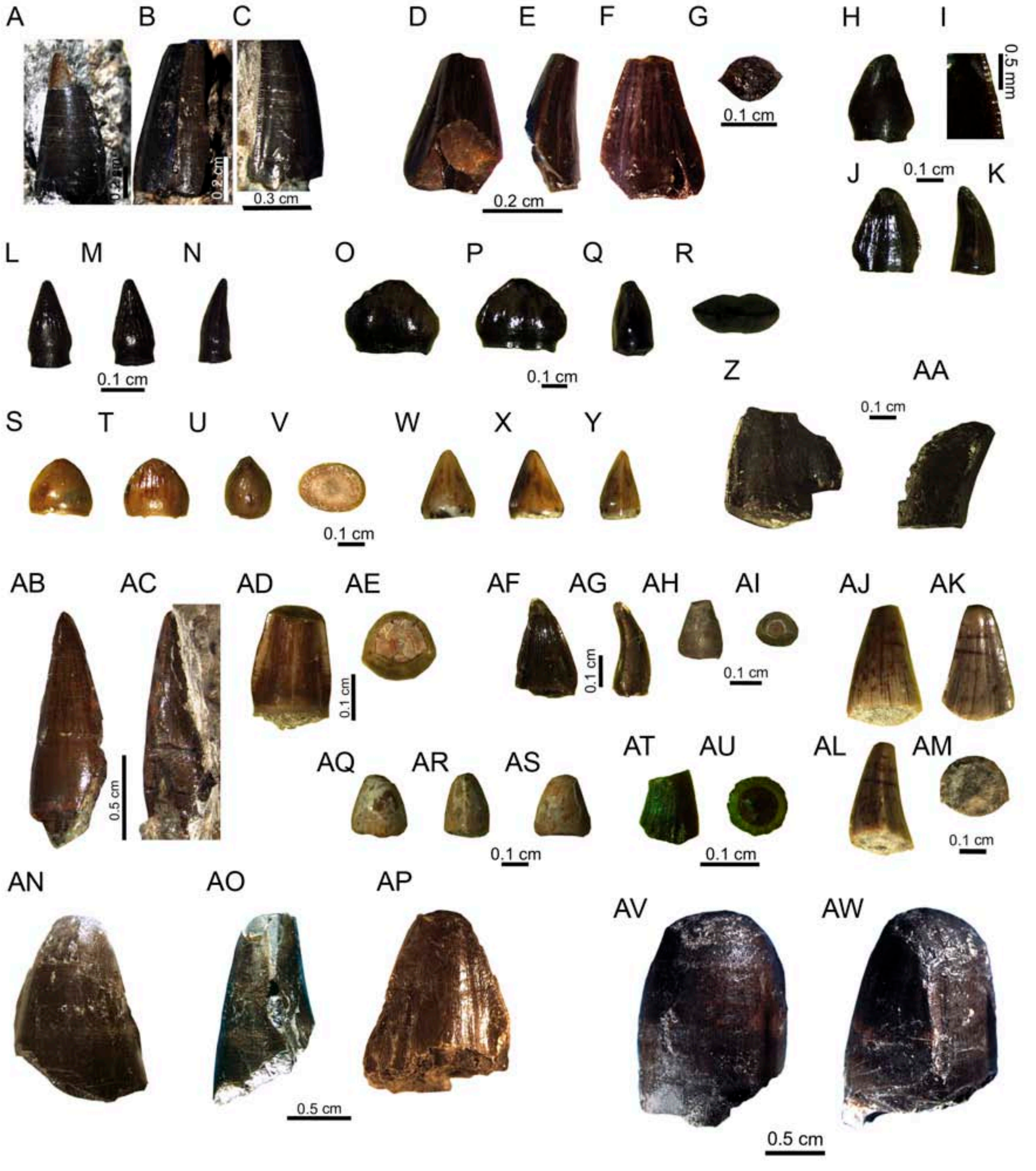

Figure 2. Tooth-morphotypes: **(A-C)** Morphotype 6, Ziphosuchia indet. (MCD-5562). **(D-G)** Morphotype 7, Ziphosuchia indet. (MCD-5564). **(H-K)** Morphotype 14, cf. *Doratodon* sp. (IPS-96661). **(L-N)** Morphotype 8, cf. *Theriosuchus* sp. (IPS-96680). **(O-R)** Morphotype 10, cf. *Theriosuchus* sp. (IPS-85796). **(S-V)** Morphotype 13, ? *Acynodon* sp. (IPS-85800). **(W-Y)** Morphotype 13, ? *Acynodon* sp. (IPS-96692). **(Z-AA)** Morphotype 4, *A. palustris* (MCD-5557). **(AB-AC)** Morphotype 1, Allodaposuchidae sp. 1 (MCD-5548). **(AD-AE)** Morphotype 1, Allodaposuchidae sp. 1 (IPS-96689). **(AF-AG)** Morphotype 2, Allodaposuchidae sp. 2 (MB10-162). **(AH-AI)** Morphotype 2, Allodaposuchidae sp. 2 (IPS-96697). **(AJ-AM)** Morphotype 5, Allodaposuchidae indet. (IPS-96696). **(AN-AP)** Morphotype 5, Allodaposuchidae indet. (MCD-5556). **(AQ-AS)** Morphotype 12, ?Allodaposuchidae indet. (IPS-96688). **(AT-AU)** Morphotype 11, cf. *Thoracosaurus* sp. (IPS-96662). **(AV-AW)** Morphotype 9, Crocodylomorph form 1 (MCD-5567).

Morphotype 7

Ziphosuchia indet.
Localities: Molí del Baró-1, L'Espinau.
Material: MCD5564, IPS-96647.
(Fig. 2D-G)

Description: Triangular and near blunt teeth, labio-lingually compressed and lingually curved. The complete specimen is 3.3 mm basiapically high and 2.2 mm mesiodistally wide, based on. The cross-section is elliptic. They bear mesial and distal carinae, both bearing small crenulations as in morphotype 6. The enamel presents faint basiapical ridges in both lingual and labial surfaces.

Remarks: The shape is similar to teeth described from *Doratodon ibericus* (Company et al., 2005). However, *Doratodon* shows well-defined denticles and smooth enamel surfaces. On the basis of overall shape and ornamentation, these teeth probably represent a posterior position in the same series that could also include the former morphotype 6.

SEBECOSUCHIA Colbert 1946
DORATODON Seeley 1881

Morphotype 14

cf. *Doratodon* sp.
Localities: L'Espinau.
Material: IPS-96631, IPS-96638, IPS-96661.
(Fig. 2H-K)

Description: The best preserved tooth is 3.1 mm basiapically high and 2.2 mm mesiodistally wide. The crown is high and triangular shaped, with a well-marked basal constriction. The apex is lingually inclined. The tooth is labio-lingually compressed, although in a lesser degree than theropod dinosaurs. The cross-section is elliptical. The enamel is nearly smooth, but both mesial and distal carinae show true denticles.

Remarks: Isolated ziphodont teeth are usually referred to *Doratodon* sp. (e.g., Grigorescu et al., 1999; Martin et al., 2006; Rabi & Sebők, 2015). *Doratodon* teeth are subtriangular in shape, compressed labio-lingually, and present well-defined denticles in both anterior and posterior carinae. *Doratodon ibericus* was described from the late Campanian of Sierra Perenchiza Fm. (Valencia, Spain; Company et al., 2005). However, teeth preserved in the holotype show no constriction between the crowns and the root. In addition, unlike the morphotypes regarded as an indeterminate ziphosuchian, the tooth-morphotype 14 shows true denticles.

NEOSUCHIA Benton & Clark 1988
ATOPOSAURIDAE Gervais 1871
THERIOSUCHUS Owen 1879

Morphotype 8

cf. *Theriosuchus* sp. 1
Localities: Molí del Baró-1, Serrat del Rostiar-1, Camí del Soldat, L'Espinau.
Material: MCD-5565-66, MB11-133, IPS-96630, IPS-96637, IPS-96644, IPS-96648, IPS-96654, IPS-96655, IPS-96659, IPS-96663, IPS-96665, IPS-96671, IPS-85797, IPS-96680, IPS-96683, IPS-85799, IPS-96699-702.
(Fig. 2L-N)

Description: Wide and lineolate teeth bearing a well-marked basal constriction. They are 1.6-2.7 mm basiapically high and 0.9-2.1 mm mesiodistally wide. The teeth are labio-lingually compressed, being the lingual surface flatter than the labial side. Mesial and distal carinae converge up to the apex. Carinae lack denticles. The enamel is ornamented with longitudinal ridges, well-marked in lingual side but faint in the labial face. Ridges are not parallel: medial ridges converge towards the apex whereas lateral ones diverge towards the carinae forming false ziphodonty.

Remarks: This morphotype differs from morphotype 2 in bearing ornamented keels and labial surface with ridges. These features have been commonly described in fossil remains referred to *Theriosuchus*, in which heterodonty have been well assessed (Tennant et al., 2016). Specifically, the shape of the tooth-morphotype 8 matches well with teeth of anterior dental positions preserved *in situ*.

However, after the revision of this clade carried out by Tennant and collaborators, most of the taxa included within *Theriosuchus* split into *Theriosuchus* (*sensu* Tennant et al., 2016) and *Sabresuchus*. According to these authors, *Theriosuchus* is restricted to the Jurassic and Early Cretaceous, whereas the Late Cretaceous species (e.g., Martin et al., 2014) were relocated in the genus *Sabresuchus*. Although the studied material from the Tremp Formation falls within the chronological range of *Sabresuchus*, it differs from the dental morphology of this taxon (Martin et al., 2014), and resembles that of *Theriosuchus* (Tennant et al., 2016).

Morphotype 10

cf. *Theriosuchus* sp.
Localities: Molí del Baró-1, L'Espinau.
Material: MCD-5569–70, MB10-148, MB10-165, IPS-96649, IPS-96660, IPS-85795, IPS-96669, IPS-96679, IPS-85796.
(Fig. 2O-R)

Description: Leaf-shaped teeth, wider than longer, showing a well-marked apex. They are 2.9-4.3 mm basiapically high and 2.9-3.3 mm mesiodistally wide. Teeth are laterally compressed but not lingually inclined. The crowns show a basal well-marked constriction. Mesial and posterior carinae are present. The enamel bears very-faint basiapical ridges in both sides, but they are more marked in the lingual surface. As in morphotype 8, medial ridges converge to the apex, whereas lateral ridges diverge to the carinae. Ridges reaching the carina develop false-ziphodont crenulations. These teeth also present a medial basiapical depression in the basal-most part of both lingual and labial surfaces that divides the crown into two bulbous halves. Thus, the cross-section is 8-shaped.

Remarks: This morphology resembles the spatulated teeth of the Atoposauridae. Similar teeth reported from Cruzy (Hérault, France; Martin et al., 2014) and La Cantalera (Teruel, Spain; Puértolas-Pascual et al., 2015) were referred to ?*Theriosuchus* sp. Part of the studied sample coming from Molí del Baró-1, was previously referred to *Theriosuchus* (Marmi et al., 2016). The taxonomic assignment of these teeth was also corroborated by Tennant et al. (2016) according to the ornamentation pattern, although these authors also remarked that these teeth fall in the chronological range of *Sabresuchus sympiestodon* (Martin, Rabi & Csiki 2010). Morphotype 10 includes some teeth in the studied sample which tend to the morphotype 8 in shape. This could reinforce the hypothesis that both morphotypes belongs to the same dental series of *Theriosuchus*. Heterodonty in the tooth-row of atoposaurids is well known (Tennant et al., 2016): morphotype 10 would represent posterior (molariform) teeth¸ whereas morphotype 8 would be located in the anterior part of the series.

EUSUCHIA Huxley 1875
?HYLAEOCHAMPSIDAE Williston 1925
?*ACYNODON* Buscalioni et al. 1997

Morphotype 13

?*Acynodon* sp.
Localities: Barranc de la Boiga, Serrat del Rostiar-1, Serrat del Pelleu, L'Espinau.
Material: IPS-85800, IPS-85802, IPS-96691, IPS-96692, IPS-96633, IPS-96653, IPS-96657, IPS-96667, IPS-96674, IPS-96676, IPS-96704.
(Fig. 2S-Y)

Description: These teeth show bulky, low and rounded crowns. The enamel is ornamented with well-marked basiapical ridges parallel to the others. Crowns are 0.7-2.9 mm basiapically high and 0.9-2.0 mm mesiodistally wide. Teeth recovered from Serrat del Pelleu site (IPS-85800, IPS-85802, IPS-96691, IPS-96692) probably conform a single dental series. IPS-96692 bears high crown with straight lateral margins forming an isosceles triangle. The basal constriction is stronger than in the others. IPS-85800 and IPS-85802 show bulky low crowns with curved lateral margins. The basal constriction is less marked than IPS-96692. IPS-96691 is of intermediate morphology between IPS-96692 and the other two teeth. All of them show ornamented enamel with very-faint longitudinal and parallel ridges (less marked than teeth from other sites). Mesial and distal carinae are not serrated. Almost all teeth show a worn apical facet. Teeth from Serrat del Pelleu are not compressed labio-lingually and show a subcircular cross-section. In turn, teeth from the other localities are slightly labiolingually compressed regardless their size and overall shape (*i.e.*, the tooth position).

Remarks: Teeth from Serrat del Pelleu and those from the other sites were tentatively grouped together despite showing intriguing differences. However, it should not be rejected that both groups belong to different taxa. The increase of the sample size might change our viewpoint. This morphotype differs from the similar morphotype 10, in the presence of an apical surface, the orientation of the ridges and the absence of serrated carinae. The shape and morphological features of this morphotype match well with teeth referred to Bernisartiidae (e.g., Puértolas-Pascual et al., 2015). However, bernisartiids are mainly restricted to the Early Cretaceous and lack European fossil record from the lower Cenomanian on (Puértolas-Pascual et al., 2016). Furthermore, this type of teeth may be present in other durophagous crocodyliforms. The most likely candidate, due to chronological and geographical range, is *Acynodon* (Buscalioni et al., 1997; Martin, 2007; Delfino et al., 2008b). Nevertheless, *Acynodon* lacks lateral carinae and bears a central apical crest, unlike morphotype 13.

ALLODAPOSUCHIDAE Narváez et al. 2015
ALLODAPOSUCHUS Nopcsa 1928

Morphotype 4

Allodaposuchus palustris
Localities: Fumanya, Molí del Baró-1, Les Torres-2, L'Espinau.
Material: MCD5557-58; IPS-96650, IPS-96708-10, IPS-90162, IPS-90182.
(Fig. 2Z-AA)

Description: Relatively wide and blunt teeth, with the labial surface more convex than the flatter lingual surface. The complete tooth is 4.9 mm basiapically high and 4.6 mm mesiodistally wide. The cross-section is D-shaped. The anterior and posterior carinae are well developed, with two well-marked longitudinal grooves in the lingual side. The enamel has numerous, short and fine ridges in both labial and lingual faces. The ridges are not parallel and develop false-ziphodont crenulations at the contact with the carinae.

Remarks: Allodaposuchus palustris is the only allodaposuchid with similar ornamentation and false-ziphodont dentition (Blanco et al., 2014; Blanco & Brochu, in press). No other crocodyliform with similar ornamentation has been described in the Tremp Formation.

Morphotype 1

Allodaposuchidae sp.1
Localities: Molí del Baró-1, Serrat del Rostiar-1, Serrat del Pelleu, Els Nerets, L'Espinau.
Material: MCD5547-50, MCD-6850, MCD6853, IPS-96634, IPS-96678, IPS-96689, IPS-96693.
(Fig. 2AB-AE)

Description: Conical and pointed teeth with high crowns showing a faint basal constriction. They are 0.9-14 mm basiapically high and 0.5-5 mm mesiodistally wide. The crowns are subcircular in cross-section, more convex labially than lingually; slightly labio-lingually compressed and lingually bended. The enamel is smooth. Faint anterior and posterior carinae are present, but lack denticles.

Remarks: This morphology is typical of crocodiles with generalist habits. Thus, it is difficult to assign confidently to any a particular taxon. However, the most reliable candidates would be members of Allodaposuchidae due to the presence of several species in this area during the Maastrichtian (Puértolas-Pascual et al., 2011, 2014; Blanco et al., 2014, 2015). For instance, these features have been observed in teeth belonging to *Allodaposuchus hulki* and *A. subjuniperus*. Teeth of this latter species, however, are less acute and have two longitudinal lingual grooves next to the carinae, but variation related to the tooth-row position cannot be discarded. On the other hand, tooth-morphotype 1 are clearly different from those of *A. precedens*, which bear enamel ornamented with basiapical ridges, and from the false-ziphodont teeth of *A. palustris* (Delfino et al., 2008a; Blanco et al., 2014; Blanco & Brochu, in press).

Morphotype 2

Allodaposuchidae sp. 2
Localities: Molí del Baró-1, Serrat del Pelleu, L'Espinau.
Material: MCD5551-54; IPS-96643, IPS-96652, IPS-96656, IPS-96664, IPS-96666, IPS-96668, IPS-96685-87, IPS-96695, IPS-96697.
(Fig. 2AF-AI)

Description: Conical and pointed teeth with high crowns showing faint basal constriction. They are 1.4-6.1 mm basiapically high and 0.9-2.8 mm mesiodistally wide. The teeth are slightly labio-lingually compressed and lingually inclined. The cross-section is subcircular. They bear well-developed mesio-distal keels, without denticles. The lingual surface delimited by both keels bears longitudinal, basiapical ridges, whereas the labial surface is nearly smooth. The ridges of the labial surface are parallel, oriented towards the apex and do not overhang the keels.

Remarks: Similar teeth are present in most neosuchians with generalist dentition. For example, tooth-morphotype 2 resembles those of Goniopholididae from La Cantalera site

(Puértolas-Pascual et al., 2015). However, goniopholidid teeth also show ornamented labial surface and the transition between the crown and the root is unconstricted. Furthermore, goniopholidids are mainly restricted to the Early Cretaceous and lack reliable European fossil record from the middle Albian on (Puértolas-Pascual et al., 2015, 2016). This morphotype is also reminiscent of teeth belonging to *Allodaposuchus precedens* (Grigorescu et al., 1999; Delfino et al., 2008a). However, in *A. precedens*, teeth bear ridges in the labial surface. On the other hand, teeth of other allodaposuchid species, such as *A. hulki*, *A. subjuniperus*, *A. fontesi* or *Lohuecosuchus*, lack ornamented enamel. *Allodaposuchus palustris* wore developed false-ziphodont teeth (Puértolas-Pascual et al., 2014; Blanco et al., 2014, 2015a; Narváez et al., 2015, 2016a; Blanco & Brochu, in press), a feature that is not present in the studied material. Furthermore, morphotype 2 also differs from other teeth from the studied sample (e.g., morphotype 8) in the ornamental pattern. Because its similarity to teeth of some allodaposuchian taxa (e.g., *A. precedens*), this morphotype is tentatively assigned to an indeterminate allodaposuchid.

Morphotype 5

Allodaposuchidae indet.

Localities: Molí del Baró-1, Serrat del Pelleu, Barranc de la Boiga, Pont d'Orrit-6, Les Torres-2, L'Espinau.

Material: MCD5559, IPS-85801, IPS-96640-42, IPS-96645, IPS-96682, IPS-96694, IPS-96696, IPS-96703, IPS-96705, IPS-96707.

(Fig. 2AJ-AM)

Description: Similar to the morphotype 1, these teeth are conical and show a basal constriction. However, they are wider and blunt with relative low crowns. They are 2.8-13.2 mm basiapically high and 1.1-8.1 mm mesiodistally wide. The enamel is smooth bearing well-developed mesial and posterior carinae lacking denticles. Unlike the morphotype 1, they show mesial and distal basiapical grooves on the lingual side, near to the carinae.

Remarks: These features are usually described in allodaposuchid teeth (Puértolas-Pascual et al., 2014; Blanco et al., 2015a; Narváez et al., 2015, 2016a; Blanco & Brochu, in press). A crocodile tooth reported from the Reptile Sandstone level by Blanco et al. (2015b), resembles this morphotype. However, the presence of faint ridges directed to the carinae prevents to include confidently this tooth in the morphotype 5. Marmi et al. (2016) pointed that the shape of these specimens is identical to that of the teeth belonging to the holotype of *A. subjuniperus* (MPZ 2012/288, Puértolas-Pascual et al., 2014). In spite of we still agree with this assertion, the larger sample studied in the present work includes some specimens of intermediate shape between morphotypes 1 and 5. Therefore, these morphotypes might consist of teeth belonging to different positions within the same tooth-row. Thus they could belong to the same species.

Morphotype 3

Allodaposuchidae indet.
Localities: Molí del Baró-1.
Material: MCD5555-56.
(Fig. 2AN-AP)

Description: Wide, elongated and blunt teeth. They are approx. 17.4 mm basiapically high and approx. 11.8 mm mesiodistally wide. They show a convex labial surface, whereas the lingual side is flattened. The cross-section is D-shaped. Anterior and posterior carinae are faint and lack serration. The enamel is smooth, but there are two basiapical grooves, lingually to the carinae. Several basiapical ridges are present between the grooves.

Remarks: This morphology resembles the caniniform (4th dentary tooth) of *Allodaposuchus hulki* (Blanco et al., 2015a), although caniniform teeth are unknown in other Maastrichtian Iberian allodaposuchids. Following the same hypothesis as in morphotype 1 we tentatively refer these specimens to Allodaposuchidae. In this sense, they might represent caniniform teeth of the same dental series of morphotypes 1 or 5 (see below). Thus it is not possible to discern if they belong to a single or several species of allodaposuchids.

Morphotype 12

?Allodaposuchidae indet.
Localities: Serrat del Rostiar-1, Serrat del Pelleu.
Material: IPS-96635, IPS-96639, IPS-96688.
(Fig. 2AQ-AS)

Description: Small molariform teeth with wide, low and blunt crowns. They are 0.9-2.2 mm basiapically high, 1.3-1.8 mm mesiodistally wide and subcircular or subtriangular in cross-section. The crown tends to be wider than high. They are not compressed labio-lingually. Enamel is smooth and unornamented. Carinae are absent.

Remarks: The studied specimens resemble typical posterior-most teeth of a generalist dentition. They likely belong to the same tooth series of morphotypes 1 and 5, but the pairing with the other morphotypes cannot be refuted.

GAVIALOIDEA Brochu 1997
THORACOSAURUS Leidy 1852

Morphotype 11

cf. *Thoracosaurus* sp.
Localities: L'Espinau.
Material: IPS-96662.
(Fig. 2AT-AU)

Description: This morphotype includes a partial, single tooth. The whole tooth was probably conical and mostly straight. The cross-section is circular. The enamel is ornamented with abundant, short basiapical ridges. No carina is present.

Remarks: After morphological comparisons, the tooth is similar to others reported from Blasi-1 and Barranco de Extremadura sites (Huesca, Spain) within the Arén Sandstone Formation. Straight conical teeth with striated ornamentation were referred to *Thoracosaurus* sp. (Puértolas-Pascual et al., 2016). The presence of this marine gavialoid in the L'Espinau site is in concordance with the microvertebrate assemblage reported from this site, with includes some marine fishes (Blanco et al., 2016, 2017).

CROCODYLOMORPHA INDET.

Morphotype 9

Crocodylomorph form 1
Localities: Molí del Baró-1, Pont d'Orrit-6.
Material: MCD5567-68, IPS-96706.
(Fig. 2AV-AW)

Description: Rounded and blunt teeth, circular in cross-section. They are 2.4-19.9 mm basiapically high and 2.4-13.9 mm mesiodistally wide. The crown is mostly straight, and the "apex" is slightly lingually oriented. In lateral view, crowns are not caudally curved. The enamel is smooth and they bear mesial and posterior carinae. Both carinae are tenuous and lack ornamentation.

Remarks: The overall morphology prevents to refer these specimens to neither allodaposuchid nor atoposaurid taxa since the diagnostic features of these clades are absent. This morphotype resembles grinding dentition of specialized durophagous habits. Durophagous crocodyliforms such as *Acynodon* and *Iharkutosuchus* are known from the Late Cretaceous of Europe. However, teeth assigned to *Acynodon* are tribodont with an apical crest and lack lateral carinae (Buscalioni et al., 1997; Martin, 2007; Delfino et al., 2008b); whereas those of *Iharkutosuchus* show striking mammalian-like molariform teeth (Ősi et al., 2007). Thus, this morphotype is regarded as an enigmatic durophagous crocodile.

Dentaries

EUSUCHIA Huxley 1875
HYLAEOCHAMPSIDAE Williston 1925
ACYNODON Buscalioni et al. 1997
Acynodon sp.

Localities: Els Nerets.
Material: IPS-13360.
(Fig. 3A-C)

Description: The specimen IPS-13360 preserves the anterior branch of the left dentary, the splenial and sixteen dental alveoli without teeth. The lateral surface of the mandible is heavily ornamented with pits and grooves. The first fourteen dental alveoli are perfectly distinguishable. However, towards the posterior region, the alveolar area is partially eroded, although the presence of two larger alveoli is likely present, being a total of sixteen teeth. The posterior region is not preserved so the presence of more alveoli cannot be safely determined. All the alveoli are circular and with similar size, being the first three and the last two alveoli slightly larger. The interalveolar space is minimal pointing to all teeth were almost confluent. The occlusal contour of the dentary is totally smooth and flat, without festooned profile. In lingual view the anterior region of the splenial is well preserved. In its anterior margin, the splenial is limited by a large *foramen intermandibularis oralis* for the mandibular branch of the nerve V. No more perforations in the splenial are observed, although it could be due to a preservation factor. The splenial does not participate in the mandibular symphysis and its anterior margin surpasses the *foramen intermandibularis oralis* and the Meckelian groove dorsally. The mandibular symphysis extends posteriorly up to the sixth dentary alveolus.

Remarks: Teeth with similar size (isodonty) along the tooth-row; absence of 4th enlarged dentary tooth (caniniform); and non-festooned occlusal margin are characteristic of *Acynodon* (Buscalioni et al., 1997; Martin, 2007; Delfino et al., 2008b).

ALLODAPOSUCHIDAE Narváez et al. 2015
Allodaposuchidae sp. 2

Localities: Fontllonga-6.
Material: MCD-6868.
(Fig. 4)

Description: The specimen MCD-6868 preserves the anterior branch of the right mandible that includes the first nine dental alveoli. The lateral surface of the jaw is heavily ornamented with pits and grooves. The fourth, sixth, seventh and ninth teeth have been preserved and are dorsally projected. The dorsal margin of the tooth-row is festooned, with its

Figure 3. Dentaries from Els Nerets. **(A-C)** *Acynodon* sp. in A) lateral, B) occlusal and C) lingual views. **(D-F)** Allodaposuchidae indet. in D) lateral, E) occlusal and F) lingual views.

maximum convexity at the height of the fourth tooth, which is the largest. Posteriorly to the fourth tooth, the size of the alveoli decreases and the dorsal margin of the tooth-row becomes concave. The point of maximum concavity is placed between the seventh and eighth teeth, where there is a large interalveolar diastema, probably for the reception of the fourth tooth of the maxilla. From the eighth tooth onwards, the dorsal margin of the tooth-row begins to rise again acquiring a convex contour in lateral view accompanied by a new dental growth. The region of the mandibular symphysis is not well preserved, but seems to reach the third dentary tooth posteriorly. Although the lingual surface is not well preserved, it seems that the splenial is lost, allowing to observe a channel that may correspond with the Meckelian groove.

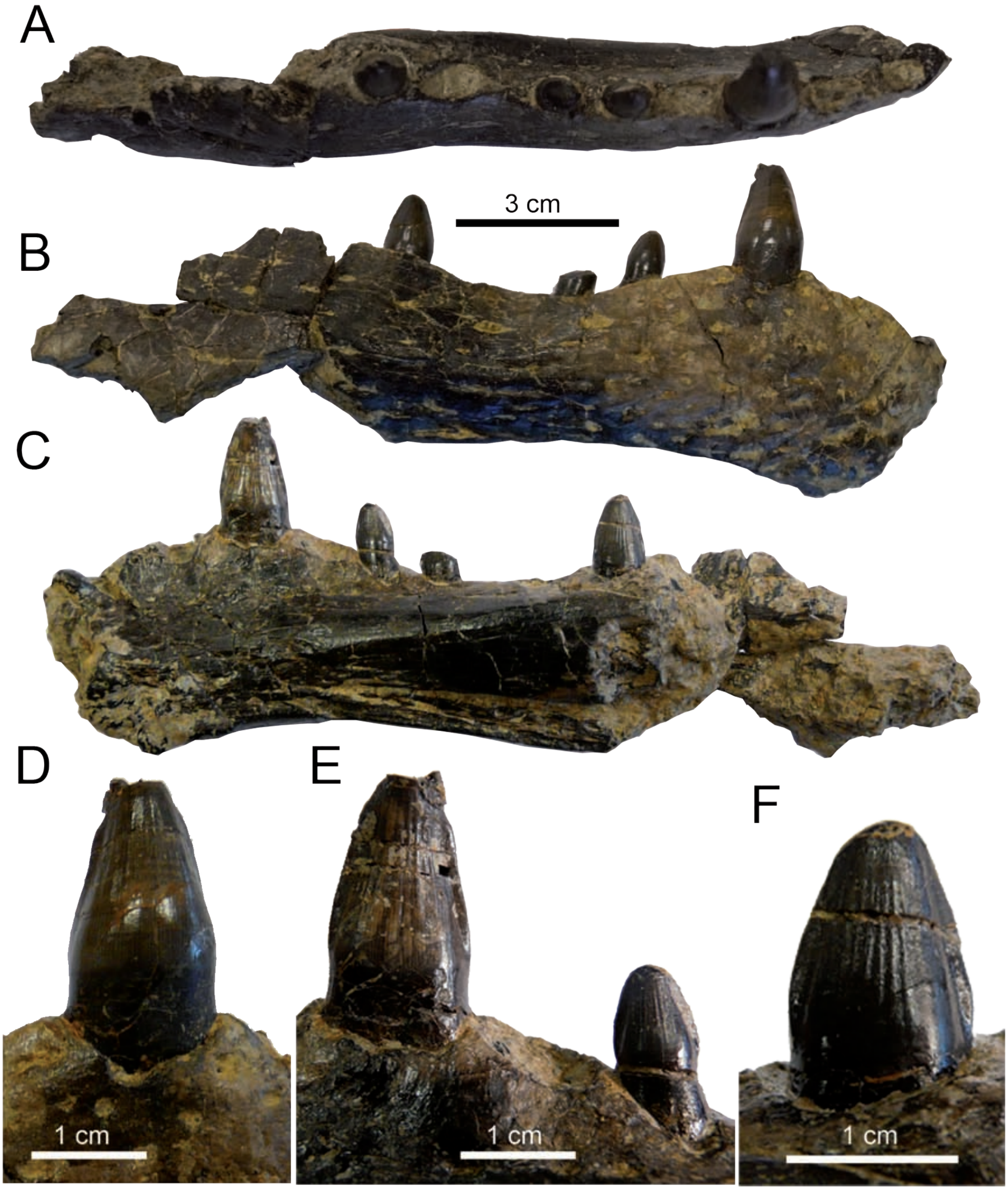

Figure 4. Dentary from Fontllonga-6. **(A-C)** Allodaposuchidae indet. in A) occlusal B) lateral and C) lingual views. **(D-F)** Preserved teeth in D) labial and E, F) lingual views.

Therefore the presence of foramina, the anterior extension of the splenial and its relation to the mandibular symphysis cannot be determined.

The preserved teeth are conical, with a slight constriction at the base and somewhat lingually curved. The labial surface of the enamel is convex with the presence of marginal ridges near the apex, being the base quite smooth. The lingual surface is flatter, with well-marked longitudinal ridges extending from the base to the apex. There are two well-developed and smooth carinae in the mesial and distal margins. On the lingual surface two grooves adjacent to the carinae are present. This morphological features match with teeth grouped in the morphotype 2.

Remarks: MCD-6868 preserves few diagnostic remains. Features present match well with published dentaries referred to allodaposuchids (Blanco et al., 2014; Narváez et al., 2015, 2016a). Moreover, tooth morphology argues against the belonging to any atoposaurid, ziphosuchian and hylaeochampsid taxon.

Allodaposuchidae indet

Localities: Els Nerets.
Material: NE12-z.
(Fig. 3D-F)

Description: The specimen NE-12z is a nearly complete left mandible. The articular and the posteriormost region, including the tip of the retroarticular process, have not been preserved. The lateral surface of the mandible is heavily ornamented with pits and grooves.
Only a small replacement tooth within the 4th alveolus has been preserved. The dental alveoli are circular and have a similar size, with the exception of the 4th alveolus which is the largest. In the anterior dental positions, there are a series of small foramina placed lingually to the alveoli. There is a diastema between the seventh and the eighth alveoli. Posteriorly to the tenth alveolus the tooth-row is not well preserved making difficult to determine the exact number of teeth, but there are between 13 and 16. In lateral view, the dorsal margin of the tooth-row is quite linear and very little festooned, with only a slight concavity between the fourth and the ninth alveoli. The dentary symphysis extends up to the 4th alveolus posteriorly. There is no external mandibular fenestra.

The splenial covers the medial surface of the mandibular ramus. Although the surface of the splenial is not very well preserved throughout its length, no perforations for the mandibular ramus of cranial nerve V are observed. In its anterior margin, the splenial is wedged and reaches the 4th alveolus, passing ventrally to the Meckelian groove with a longer ventral process but without reaching the mandibular symphysis. The Meckelian canal surpasses the anterior end of the splenial. The splenial contacts the tooth-row from the ninth dental position onwards, surpassing the end of the row; and also contacts the dentary in the ventral margin.

The coronoid is boomerang-shaped and covers the anterior margin of the mandibular adductor fossa or Meckelian fossa. The medial surface of the coronoid is not well preserved and it is pushed inward due to deformation, therefore the presence of perforations or its relationships with the *foramen intermandibularis medius* cannot be determined. The superior edge of coronoid is sloping anteriorly rather than horizontal. The inferior process of the coronoid contacts the angular and the splenial. The joint of the ventral posterior ramus of the splenial with the dorsal branch of the angular prevents the coronoid to contact the *foramen intermandibularis caudalis*.

The angular forms the posteroventral portion of the mandible. In medial view, the *foramen intermandibularis caudalis* is surrounded posteriorly, and dorsally by the angular. The angular does not reach the anterior edge of the *foramen intermandibularis caudalis* at its dorsal margin, and this edge appears to be blunt rather than acute. The dentary sends a posterior process within the angular forming the ventral margin of the foramen.

The surangular forms the posterodorsal length of the mandible. In lateral view, the suture with the angular is linear and slopes anteriorly. However, the suture with the dentary goes almost vertically towards the occlusal margin, passing posteriorly to the last alveolus. In medial view, the suture crosses the mandibular adductor fossa diagonally at half height. The articular and the posterior tip of the retroarticular process are not preserved, thus the sutural relationships cannot be assessed.

Remarks: Morphological features mostly match with published dentaries referred to allodaposuchids (Blanco et al., 2014; Narváez et al., 2015). However, classification at specific level is not possible. This dentary shows some peculiar features. For instance, the lineal (non-festooned) occlusal margin is reminiscent of *A. palustris*; whereas the inclusion of the dentary in the *foramen intermandibularis caudalis* differs from the condition observed in some allodaposuchids (*Lohuecosuchus*, *Agaresuchus*) but it is unknown in other taxa.

Discussion

Usefulness of qualitative traits of crocodylomorph teeth in taxonomy

Because of the great homoplasy shown in the tooth morphology between many crocodylomorph taxa with generalist dentition, it is difficult to assign isolated teeth to low taxonomic categories with confidence (Prasad & de Lapparent de Broin, 2002). We have, thus, decided to emphasize the differentiation in morphotypes, providing a tentative taxonomic assignment for each morphotype based on geographical- and chronological-close species previously reported. On the contrary, some morphotypes show a few diagnostic characters (*i.e.*, ornamentation, denticles and crenulations) that allowed to better discuss their taxonomic implications.

Teeth were grouped in 14 morphotypes, which might represent, at least, 9 different taxa: two indeterminate allodaposuchids (dental features shared with *A. subjuniperus*, *A. hulki* and/or *Arenysuchus*, as well as other enigmatic form with ridged enamel; also evidenced by dentaries), *A. palustris*, ?*Acynodon* sp., cf. *Theriosuchus* sp., cf. *Thoracosaurus*, ?*Doratodon* sp., other indeterminate ziphosuchian, and other indeterminate crocodylomorph. All of these taxa are expected to be found in the Late Cretaceous of the Ibero-Armorican Island: allodaposuchids were diverse in the Campanian and Maastrichtian of Spain and France (Buscalioni et al., 2001; Puértolas-Pascual et al., 2011, 2014; Blanco et al., 2014, 2015a; Narváez et al., 2015, 2016a; Blanco & Brochu, in press) from where they dispersed to other regions of the European archipelago, such as Haţeg Island (Blanco et al., 2014); *Acynodon* is known from the Campanian and Maastrichtian of Spain, France and Italy (Buscalioni et al., 1997; Martin, 2007; Delfino et al., 2008b); *Doratodon* reached a wide distribution in Europe ranging from the Santonian to the Maastrichtian (Rabi & Sebők, 2015); *Theriosuchus* is known from the Middle or Late Jurassic to the Maastrichtian (Tennant et al., 2016); whereas *Thoracosaurus* was dispersed between Europe and North America (Puértolas-Pascual et al., 2016).

All of these morphotypes show some intragroup morphological variation, likely related to the position in the tooth-row. Regardless of taxa, this type of variation consists in a general trend to decrease in height and increase in width towards the posterior positions. This change in shape can assessed comparing with tooth-series preserved *in situ* (Delfino et al., 2008b; Rabi & Sebők, 2015; Narváez et al., 2016a; Tennant et al., 2016). Except for *Theriosuchus* and ziphosuchians, there is no evidence that ornamentation changes through the dental series of the other taxa. In the case of *Theriosuchus*, ridges and serrations are more evident in the anterior positions (morphotype 8) than in posterior teeth (morphotype 10), although the same type of ornamentation is present along the series. Regarding ziphosuchians, anterior teeth are more rounded in cross section with the apex curved posteriorly, and the mesial carinae could be absent (Rabi & Sebők, 2015), as in MCD-5560 and MCD-5561. Following positions progressively become more compressed, less curved and show mesial carina (Rabi & Sebők, 2015).

Palaeoecology of crocodylomorph faunas from the Maastrichtian of northeastern Iberia

Of these taxa, at least seven species are present in both L'Espinau and Molí del Baró-1 sites, which hold the richest diversity of the sample. The other sites yielded four species or less. Compared to other Campanian and Maastricthian crocodilian assemblages, four taxa (*Musturzabalsuchus*, *Acynodon*, one allodaposuchid and one ?trematochampsid) have been reported from Laño (Basque-Cantabrian region, Spain; Pereda-Suberbiola et al., 2015). *Acynodon*, *Allodaposuchus*, *Doratodon*, *Sabresuchus*, and other durophagous and ziphodont crocodiles have also been reported from southern France, Romania and Hungary (Csiki-Sava et al., 2015). However, L'Espinau and Molí del Baró-1 localities have yielded two of the most diverse crocodilian assemblages in Europe (Csiki-Sava et al., 2015; Puértolas-Pascual et al., 2016). Such crocodilian diversity could be explained in terms of different ecological niches:

Concerning allodaposuchids, different species were related with diverse palaeoenvironments (Blanco & Brochu, in press). Based on the studied sample, the allodaposuchid sp. 1 (morphotypes 1 and 5) is more abundant in fluvial settings (68% of the teeth), whereas the teeth recovered from coastal wetland settings are significantly broken and eroded. The allodaposuchid sp. 2 (morphotype 2) is similarly abundant in coastal wetlands (53%) or fluvial settings, but teeth from coastal settings are better preserved as evidenced by the dentary MCD-6868. Some teeth (morphotype 4) testify to the presence of *A. palustris* in fluvial settings, but all of them are very broken and show evidence for transporting. On the contrary, those recovered from coastal wetland settings are better preserved.

Acynodon specimens were found in fluvial ecosystems (Buscalioni et al., 1997; Delfino et al., 2008b). Teeth confidently referred to *Acynodon* (morphotype 13) were only found at freshwater settings (Serrat del Pelleu site), whereas some other well-preserved teeth attributed with doubts to the same taxon might testify its presence in coastal environments. The dentary IPS-13360 also was collected in freshwater settings. The other indeterminate crocodylomorph (morphotype 9) were recovered from both fluvial and coastal wetland settings, without evidence for transport in any specific environment.

Atoposaurids are considered terrestrial crocodiles (Buscalioni & Sanz, 1988; Tennant et al., 2016). Teeth referred to cf. *Theriosuchus* (morphotypes 8 and 10) are recovered from both freshwater and coastal settings in a similar way, although the taphonomic study of the sample suggest that transporting processes were stronger in the coastal wetland environments.

Most of the ziphosuchians (including sebecosuchians) are also terrestrial crocodiles (Rabi & Sebők, 2015). The teeth referred to the indeterminate ziphosuchian and cf. *Doratodon* are more abundant in freshwater settings (67%). They are also better preserved in fluvial than in coastal settings, but preservation suggests parauthocthony regardless the palaeoenvironment. This fact agrees with the terrestrial habits inferred for these taxa, which lived far from water and their remains were transported to aquatic deposition environments.

Thoracosaurus is a fully marine gavialoid (Brochu, 2004; Delfino et al., 2005). Their presence in the Tremp basin is related to the marine-influenced localities such as Barranco de Extremadura and Blasi-1 (Arén Sandstone Fm) (Puértolas-Pascual et al., 2016). Its presence in the Tremp Fm is restricted to L'Espinau site, based on the studied sample. This site is interpreted as an estuary or a coastal swamp, where both freshwater and marine microvertebrates cohabited (Blanco et al., 2016, 2017). *Thoracosaurus* is absent in other freshwater settings.

The different taxa recognized from the sample can be also distinguished into different trophic guilds: Allodaposuchids are supposed to have had generalist predatory habits (e.g., Delfino et al., 2008a; Puértolas-Pascual et al., 2011, 2014; Blanco et al., 2014), although they likely reduced the interspecific competition through environmental selection, as mentioned above; *Acynodon* probably had a durophagous diet (Martin, 2007; Delfino et al., 2008b), and by comparison, also the indeterminate crocodylomorph with rounded blunt teeth; insectivorous habits were inferred to *Theriosuchus* (Buscalioni & Sanz, 1988); *Doratodon* was associated with carnivorous and predatory habits (Company et al., 2005; Rabi & Sebők, 2015); in contrast, *Thoracosaurus* likely had piscivorous diets, as compared with living gavials.

Temporal distribution of crocodylomorph taxa in the Maastrichtian of northeastern Iberia

All the crocodilian taxa show a continuous fossil record from the early Maastrichtian to the end of the late Maastrichtian in the southern Pyrenean basin. Early Maastrichtian crocodilian assemblages are dominated by allodaposuchids. Allodaposuchids almost compose the sample collected in the 'grey unit', except one tooth and one dentary referred to *Acynodon* and another tooth referred to the indeterminate durophagous crocodylomorph. Furthermore, cf. *Theriosuchus*, ?*Doratodon* and the other indeterminate ziphosuchian occur in the early Maastrichtian Serrat del Rostiar-1 site ('lower red unit').

Late Maastrichtian assemblages, however, contain higher abundances of cursorial forms (atoposaurids, ziphosuchians) than in the early Maastrichtian. This fact could be related to an environmental change underwent in the Pyrenean basin due to a marine regression since the Campanian-Maastrichtian transition (e.g., Puértolas-Pascual et al., 2015; Tennant et al., 2016). This environmental change would have promoted the adequate habitats for some terrestrial crocodiles. On the other hand, the few occurrences of *Thoracosaurus* in the southern Pyrenean basin are late Maastrichtian in age (Barranco de Extremadura, Blasi-1 and L'Espinau). These three localities belong to different geological units (Arén Sandstone, and 'lower red' unit, respectively), sharing strong marine influence during the late Maastrichtian. It is remarkable, however, the absence of *Thoracosaurus* remains in the marine settings of the 'grey' unit during the early Maastrichtian.

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Chapter 8. THE YOUNGEST MAASTRICHTIAN RECORD FROM NORTHEASTERN IBERIA

Art by Aina & Agnès Amblàs (ICRA)

THE MOLÍ DEL BARÓ-1 SITE, A DIVERSE FOSSIL ASSEMBLAGE FROM THE UPPERMOST MAASTRICHTIAN OF THE SOUTHERN PYRENEES (NORTH-EASTERN IBERIA)

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Mi contribución en este trabajo consistió en la ordenación y clasificación preliminar del material recogido en el yacimiento (767 restos), elaborando una base de datos completa. Posteriormente este material fue repartido entre diversos especialistas. Llevé a cabo la clasificación taxonómica y descripción del material perteneciente a peces, anfibios, cocodrilos, terópodos y un dentario de hadrosauroideo, así como la redacción de su correspondiente parte en las secciones de Paleontología Sistemática, Tafonomía, Discusión y Conclusiones. Colaboré también en la creación de las Figs. 7, 8, 9 y 11 y de las Tablas 1 y 2.

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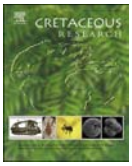

The Molí del Baró-1 site, a diverse fossil assemblage from the uppermost Maastrichtian of the southern Pyrenees (north-eastern Iberia)

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ABSTRACT

The Molí del Baró-1 site (north-eastern Iberia) has yielded one of the richest fossil assemblages of the continental upper Maastrichtian from western Europe. It includes abundant plant (charophytes, sporomorphs, angiosperm leaves, seeds and logs), invertebrate (mollusc shells, partial insect exoskeletons and eggs) and vertebrate (teeth, bones, eggshells) fossils. The fossil assemblage is composed of both parautochthonous and allochthonous remains that mostly deposited in a pool formed at the edge of a meandering river. Plant megafossil evidence suggest that at least three angiosperm species (a willow-like dicot, palms and a likely typhacean monocot) formed the plant community growing in this fluvial environment. Tooth remains indicate that crocodylomorphs were diverse (including atoposaurids, ziphosuchians and eusuchians) which together with small theropod dinosaurs likely consumed prey carcasses or scavenged near the depositional setting. Prismatoolithid eggshells also suggest the presence of nearby nesting area of theropods. On the other hand, hadrosauroids apparently dominated phytophagous faunas including lambeosaurines as well as more basal forms. The taxonomic composition of the Molí del Baró-1 site matches the expected for the timespan and environment and represents a relevant locality to know the diversity of the latest Cretaceous terrestrial ecosystems in south western Europe.

1. Introduction

In the southern Pyrenees (north-eastern Iberian Peninsula), dinosaur fossils are known since the early 20th century. From then on, the number of fossil sites containing Late Cretaceous vertebrates has hugely increased in this area, which is one of the few places in Europe recording the last six million years of the terrestrial ecosystems before the Cretaceous–Palaeogene (K–Pg) mass extinction. Excavation works carried out in the last two decades yielded an extensive dinosaur fossil record including titanosaurian sauropods, dromaeosaurid theropods, hadrosauroid ornithopods and nodosaurid ankylosaurs (Riera et al., 2009). Remains of other vertebrates, such as fish (Kriwet et al., 2007), amphibians and squamates (Blain et al., 2010; Blanco et al., this volume), turtles (Marmi et al., 2012a), crocodylomorphs (Blanco et al., 2014, in press; Puértolas Pascual et al., 2014, this volume) and pterosaurs (Dalla Vecchia et al., 2013) are also found in the same beds. Foraminifera, molluscs and ostracods (Liebau, 1973) as well as charophytes and vascular plants (Feist and Colombo, 1983; Vicente i Castells, 2002) have provided interesting palaeoecological and biostratigraphical data (Villalba-Breva and Martín-Closas, 2013; Díez-Canseco et al., 2014; Vicente et al., 2015; Villalba-Breva et al., 2015).

The fossil and geological records from the Pyrenees are relevant to understand the palaeoecology and palaeobiogeography of the end-Cretaceous faunas in southern Europe and allow discussing on

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differential adaptation to habitats, faunal turnovers and faunal exchanges among landmasses. During the Maastrichtian, exposed areas in the southern Pyrenees region evolved from transitional (brackish to freshwater) coastal wetlands to inner fluvial settings (Rosell et al., 2001). Evidence from several localities suggest that bothremydid turtles, crocodylomorphs and titanosaurian sauropods inhabited both coastal and fluvial environments (Marmi et al., 2012b; Vila et al., 2012), while nodosaurid ankylosaurs seem restricted to the early Maastrichtian coastal settings (Riera et al., 2009). Hadrosauroid ornithopods dominated the late Maastrichtian fluvial environments (Vila et al., 2013). From a palaeogeographical point of view, most of vertebrate taxa were of Laurasian origins (e.g. hadrosaurid and nodosaurid dinosaurs, solemydid turtles, eusuchian crocodylomorphs) (Pereda-Suberbiola, 2009). However, the presence of some Gondwanan taxa (e.g. bothremydid turtles) suggests connections also with southern landmasses (Lapparent de Broin and Murelaga, 1999).

Regarding to plants, taphonomy and palaeobotanical evidence suggest that the vegetated areas of the coastal wetlands were freshwater lakes and surrounding swamps. These environments were inhabited by cheirolepidiacean conifers, palms and, locally, ferns, which formed low diversity plant communities (Villalba-Breva et al., 2012). On the contrary, vegetation from inland fluvial settings appears to be more diverse and was dominated by angiosperms, being the ferns abundant in the understory (Villalba-Breva et al., 2015). According to these data, plant communities from the uppermost Cretaceous of north-eastern Iberia likely formed mosaics in which angiosperms were still competing with conifers and ferns in some habitats (Villalba-Breva et al., 2012; Marmi et al., 2014).

In the present study, the new upper Maastrichtian locality of Molí del Baró-1 is reported. It consists of an extensive and diverse fossil assemblage including plants (mostly angiosperms), invertebrates (gastropods and arthropods) and vertebrates (dinosaurs, crocodylomorphs, amphibians, and fish). The presence of such diversity of fossils in a single locality is exceptional in the fossil record from the Pyrenees. The aims of the study are: i) to describe the depositional setting of Molí del Baró-1; ii) to report the taxonomic composition of the fossil assemblage; iii) to reconstruct its taphonomical history; iv) to discuss on the palaeoecology of fluvial settings from the late Maastrichtian of southern Europe.

2. Materials and methods

The Molí del Baró-1 site was discovered by palaeontologists Rodrigo Gaete and Anna Maria Bravo in 2001. During summers 2002, 2007, 2010 and 2011, the site was excavated by a team composed by members of the Museu de la Conca Dellà and the Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Palentologia de Sabadell), as well as a number of local and foreign volunteers. The 2002 and 2007 fieldworks were focused on the search for dinosaur bones, although several plant fossils, small teeth and bones belonging to other clades were also collected. A total surface between 8 and 10 square metres of a greyish muddy bed (the so called 'level 2', see Section 4 for details) was excavated. The outcrop was divided into two spots, spaced from each other by about six metres, which corresponded to the 'Tibia Hill' and 'Tendal' sections (see Section 4 for details). The 2010–2011 fieldwork consisted of a careful collection of every fossil remain present in the same sections including sandy horizons above 'level 2'. Most of the specimens were collected in situ, breaking the rock containing them. In addition, 500 kg of sediment from 'level 2' were processed by means of sieving-washing techniques in order to search for microfossils. Most of the eggshell fragments considered in this study were collected from the screenwashing portion, although several fragments were also found in situ. Some fossils were collected during prospecting works, but they were not considered in this study. Detailed data on lithology, stratigraphy and sedimentology were collected in the 2010 and 2011 campaigns (see Section 4 for details). Thin sections of rock samples were examined under polarised light with a Nikon Eclipse e400 pol microscope to study their composition. A total of 767 fossils were recovered including plants (mostly monocot and dicot angiosperms), invertebrates (gastropods and arthropods), vertebrates (fish, amphibians, crocodylomorphs, theropods, hadrosauroid ornithopods) and eggshells. They are housed in the Museu de la Conca Dellà (MCD) collection (Isona, Lleida province, Catalonia).

The fossil specimens were compared with published material from the Maastrichtian of Pyrenees as well as other localities from the Upper Cretaceous of Europe. Some of them are going to be described more specifically elsewhere (e.g. plants in Marmi et al., 2015). Specimens were photographed with a Panasonic DMC-FZ18 digital camera. Details were examined under a Leica M60 stereomicroscope with integrated digital camera or a Zeiss Evo MA10 electronic microscope at the Servei de Microscopia of the Universitat Autònoma de Barcelona. Measurements were taken from digital pictures using the freeware ImageJ v.1.40 (Rasband, 2008). The following variables were considered for taphonomic descriptions: taxonomic composition, type of body element, size and shape as well as evidence for breakage, abrasion and weathering.

3. Geological setting

During the Late Cretaceous, an east to west elongated foreland trough, which was opened to the Atlantic ocean, developed in the north-eastern Iberian Peninsula. Between the late Santonian and the Campanian, sediments accumulated in marine settings (continental slope basinal turbidites of the Vallcarca Formation to near shore calcarenites of the Terradets Formation) (Mey et al., 1968; Pons, 1977). From the late Campanian to the Thanetian, the basin underwent a marine regression and sedimentation evolved from the coastal to the transitional-continental environments of the Arén and Tremp Formations, respectively (Fig. 1A) (Mey et al., 1968; Rosell et al., 2001). The Tremp Formation was divided into four informal units by Rosell et al. (2001), described from the base to the top as follows: (1) a marine to continental transitional 'grey unit' mainly composed of grey marls, lignite, limestones and sandstones; (2) a 'lower red unit' with red lutites, sandstones and paleosols; (3) the lacustrine 'Vallcebre Limestone' and laterally equivalent strata; and (4) the fluvial 'upper red unit' consisting of red lutites, sandstones and conglomerates. Palaeontological and biostratigraphic data indicate a Maastrichtian age for the Cretaceous portion of the Tremp Formation ('grey' and 'lower red' units) in the Tremp Syncline (Riera et al., 2009 and references therein, Villalba-Breva and Martín-Closas, 2013; Díez-Canseco et al., 2014).

The Molí del Baró-1 site was first reported in Riera et al. (2009) and was located by the same authors in the upper part of the 'lower red unit' of the Tremp Formation (Fig. 1B and C). In the eastern part of the Tremp Syncline, this unit is built up by sandstones (interpreted as meandering rivers) interbedded within thick mudstone lithosomes (representing floodplain deposition). Palaeomagnetic data after Vila et al. (2012) indicate that the Molí del Baró section (MB) belongs to a reverse polarity interval correlated with the C29r magnetochron (Fig. 1C). The site occurs 70 m below the Tossal de la Doba limestones, and approximately 100 m below the Sant Salvador de Toló and Suterranya limestones (Riera, 2010; Vila et al., 2012); the latter are dated as Paleocene (Feist and Colombo, 1983; Díez-Canseco et al., 2014).

During the prospecting works carried out in the 2002 campaign, another fossiliferous horizon was discovered about 50 m below the Molí del Baró-1 site. It was named Molí del Baró-2 and also consists of a marl bed interbedded with sandstones that is eroded by the Abella stream. Only a partial femur of a small titanosaur was reported from this site (Vila et al., 2012).

4. Sedimentology

The Molí del Baró-1 site is located within a 10–15 m thick sandstone body interbedded with reddish mudstones (Figs. 1C and 2A–D). The sandstone lithosome is divided into two main sandstone-dominated bodies (lower and upper in Fig. 2B–E), which are separated by a reactivation surface (i.e. an erosive surface that is laterally conformable). Both bodies exhibit fining-upward trends, ranging from coarse to very fine sandstone and even, to siltstone. In the lowermost part, thin gravelly lags with bone fragments and natural casts of hadrosauroid footprints occur (Fig. 2F and G). The lower parts of the sandstone bodies present cross to parallel lamination, whereas their upper parts have current ripples (Fig. 2E–G). Plant and invertebrate bioturbation is extensively developed as burrowing and root mottling, respectively, and often obliterate most of the sedimentary structures.

These sandstone bodies display an arrangement consisting of lateral accretion surfaces exhibiting inclined heterolithic stratification (IHS, see Thomas et al., 1987). These features were described in detail by Díez-Canseco et al. (2014) for the meandering channels of the Tremp Formation a few kilometres west of the site under examination.

The fossil content is mostly found in a greyish muddy layer, which represent the finest elements of the IHS, interbedded with fine sandstone lateral accretions including mottling. This layer is located at the top of the lower sandstone body (see Fig. 2B–D) and has the composition of a marl since the amount of $CaCO_3$ in the rock is around 45% and the amount of quartz grains is around 5–10% (Fig. 3A). Its thickness ranges from 0.3 to 1 m (Fig. 2B–E). Arenite lenses of 15 cm in maximum thickness, exhibiting limited continuity and no erosive bases, occur within these fine sediments. They pass gradually to the adjacent marls. The granulometry of the lenses varies from fine sand to microconglomerate, including higher amounts of grains, such as quartz, than the marl. However, grains exceeding 3–4 mm are rare (Fig. 3B). The major coarse components of these lenses are intraclasts. Among them, paedogenic carbonate nodules of submillimetric to millimetric diameter represent the main component (about 90% of the intraclasts). Very few of these nodules are oxydized. Moreover, there are groups of nodules that appear pyritised. Oncolites, coated grains, rizoliths, planktonic foraminifera, bones, eggshells, coal fragments, seeds, plant remains, and amber drops are also present in much smaller amount. Finally, limestone, calcite and bigger quartz fragments were also identified as extraclasts (Fig. 3) but they are very scarce.

At least three local sections could be measured and studied in detail during the excavation (Fig. 2C–E). Two of these sections contained the two fossil-bearing outcrops studied herein: 'Tibia Hill' and 'Tendal 1' (Fig. 2C and D, respectively). In addition, two other sections ('Southwest' and 'Basal', see Fig. 2F and G) were measured at the base of the sandstone unit to improve the whole sedimentological interpretation. During the fieldwork, each of the

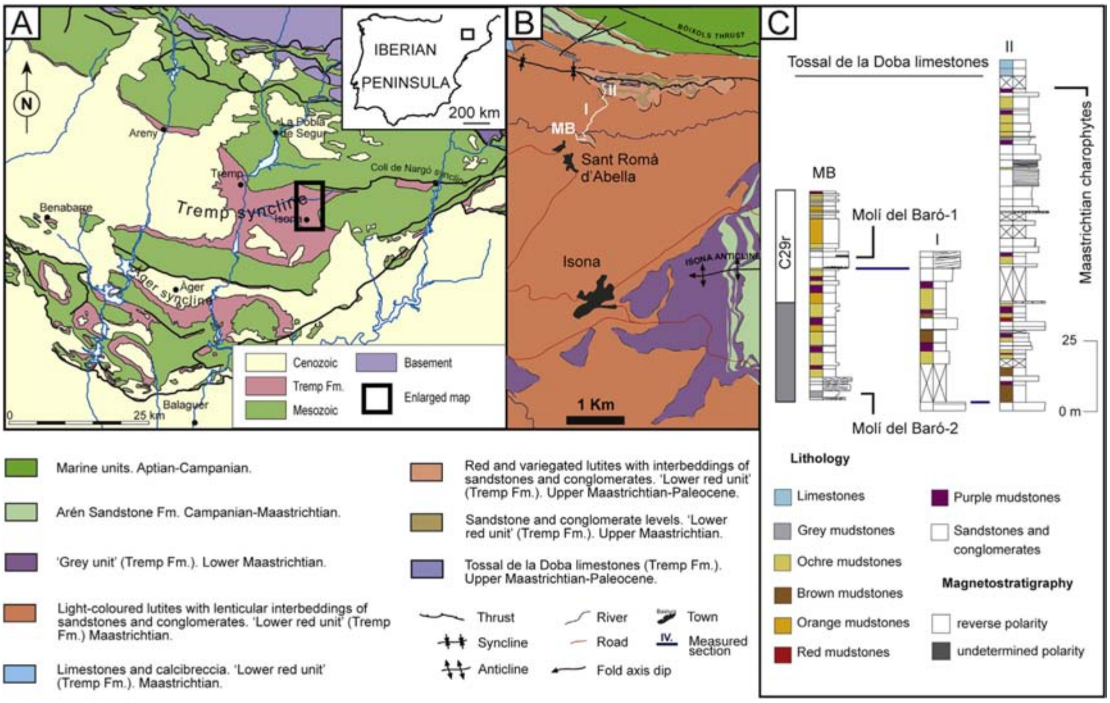

Fig. 1. Geological context of the Molí del Baró-1 site. A, Geological map of the south-central Pyrenees, showing the outcrops of the Cretaceous–Paleocene Tremp Formation, modified from López-Martínez and Vicens (2012). B, Geological map of the Isona area (enlarged from A) with the position of the Molí del Baró section (MB) and other correlated sections, modified from Riera et al. (2009). C, Stratigraphic framework of the Molí del Baró-1 site. Charophyte data and magnetostratigraphy are taken from Feist and Colombo (1983) and Vila et al. (2012), respectively. Sections MB, I and II correspond to Sections XXIII, XXIV and XXV in Riera et al. (2009).

excavated facies was quoted numerically (i.e. levels ‘1’ to ‘5’) and this nomenclature is used here again to locate more precisely the fossil remains (Fig. 2C and D).

The ‘Tendal 1’ section displays the marly layer overlying the mottled sandstones of a former accretion surface. Four lenses of the above mentioned arenites are placed within the marl. The lens

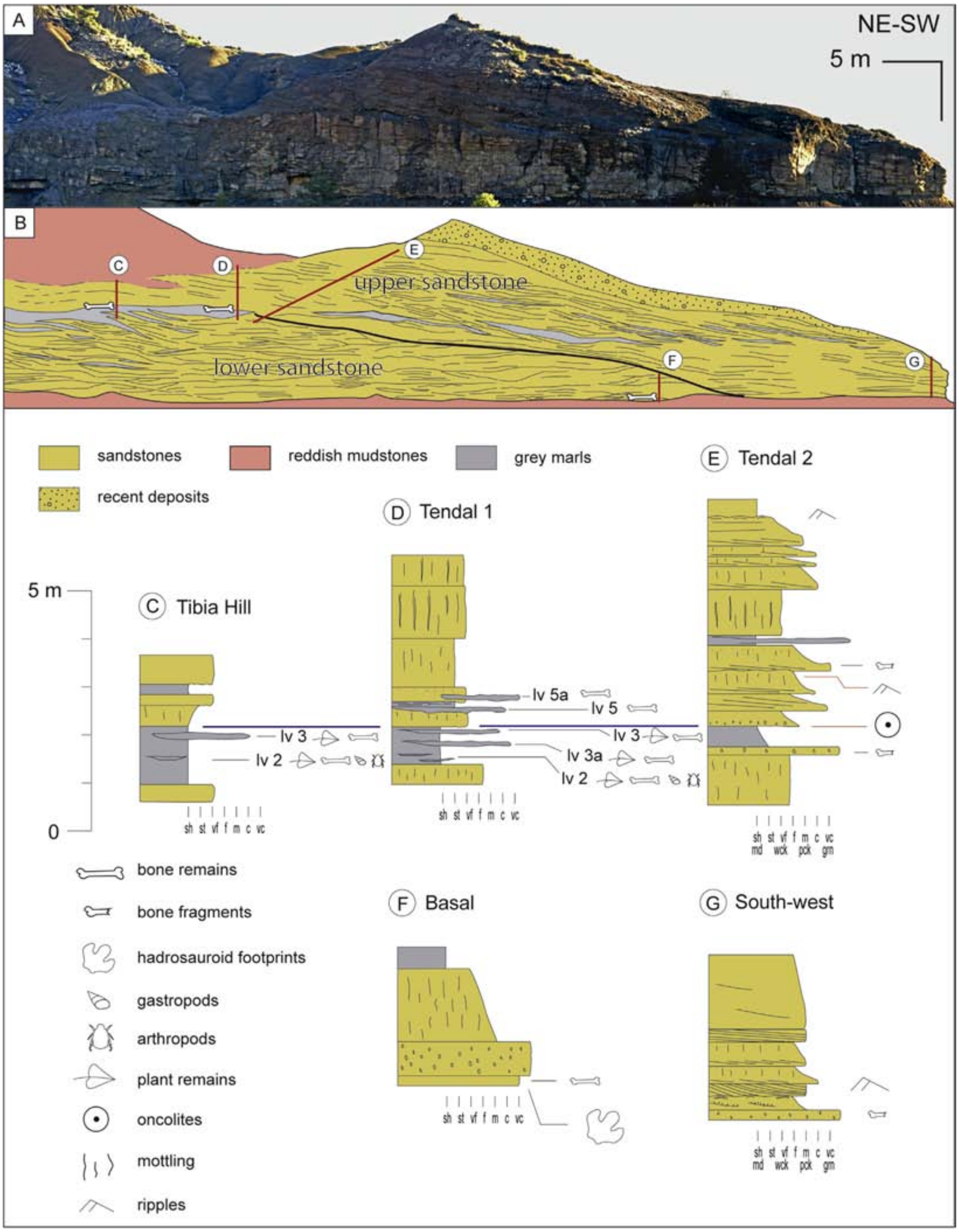

Fig. 2. Fluvial architecture and sedimentology of the Molí del Baró-1 locality. A, Picture of the Molí del Baró-1 outcrop. B, Interpretative scheme of the major structures. C–E, Detailed sections and fossiliferous levels of the Molí de Baró-1 site. F and G, Basal sections of the sandstone lithosome.

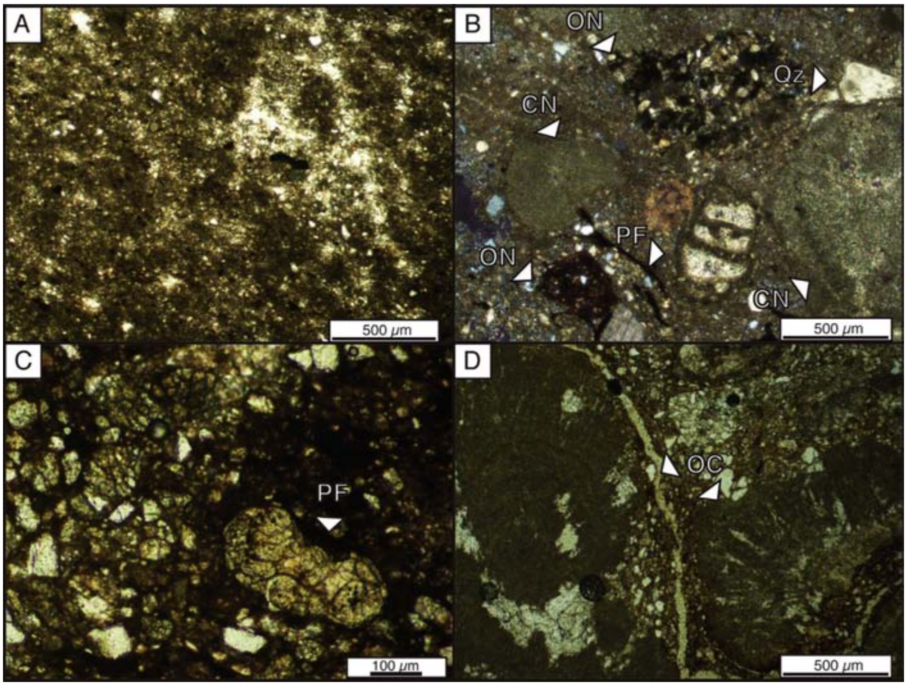

Fig. 3. Photomicrographs of thin sections under polarised light from the fossiliferous levels of the Molí del Baró-1 site. A, Grey marl. Clays and micrite are the main components, but about 5–10% of detritic quartz grains are present. B, Intraclasts, such as carbonate nodules (CN), oxide (ON, in black, with detritic grains inside) nodules and planktonic foraminifera (PF) within a sandy-marly matrix from the arenite lenses inside the grey marl (see Fig. 2B–C). C, Detail of a planktonic foraminifer in the matrix of an arenite lens. Quartz grains are abundant in the matrix of this facies. D, Oncolites (OC) from an arenite lens.

located at the top of the marl is locally coarser than the others. The marly and sandy facies within the greyish layer are reported as levels ‘2’ and ‘3’, respectively. Overlying it, the section is represented by successive mottled accretion surfaces of the upper sandstone lithosome. Some lenses of microconglomerate with a similar composition than the arenite lenses occur within this sandstone above the main fossiliferous layer. The ‘level 5’ refers to this facies. The ‘Tibia Hill’ has a similar succession than Tendal ‘1’, but it is truncated above the first overlying lateral accretion (Fig. 2B–D).

5. Palaeontological content

5.1. Plant remains

The plant fossil assemblage from Molí del Baró-1 has been studied by Marmi et al. (2015). It is composed of sporomorphs, seeds, leaves and stems (Fig. 4). Little drops of amber are present within some rock samples and coal fragments are common in ‘level 2’. A sample for sporomorph analysis from ‘level 2’ was studied by Marmi et al. (2015). Up to 110 grains were identified; most of them (83%) belonged to angiosperms including monocots (Arecaceae and Typhaceae) and eudicots (Juglandaceae, Altingiaceae and Ulmaceae). The remaining portion consisted of zygnematacean zygospores (1%), fern spores (8%) and conifer pollen (8%). Seeds are relatively abundant in levels ‘2’ and ‘3’ (49% and 83% of the plant sample, respectively). Seven types were distinguished and most were assigned to indeterminate angiosperms (Fig. 4A–E), except seed type 7, which resembled those of extant palms (Fig. 4F) (Marmi et al., 2015).

Leaves are very abundant and represent the 69% of the total plant portion (n = 317). The leaf sample includes ferns (n = 3), conifers (n = 2), monocots (n = 72) and eudicots (n = 144) (Fig. 4). Most monocot foliage consist of fragments of ribbon shaped leaves with parallelodromous venation (attributed to Typhaceae) and costapalmate leaves of the palm *Sabalites longirhachis* (Unger, 1850) Kvaček and Herman 2004 (Fig. 4I–K). Ninety-three percent of specimens from the eudicot portion consists of nanophyllous to microphyllous, linear leaves bearing pinnate eucamptodromous to brochidodromous venation, which probably belonged to the same taxon (Fig. 4L–N). They were assigned to a new eudicot form species with uncertain botanical affinities: *Saliciphyllum gaetei* Marmi et al. (2015). Other eudicot forms (e.g. Fig. 4O) are represented by very few specimens and were grouped into six form-taxa by Marmi et al. (2015). Stems and logs are only the 5% of the total plant sample. Most stems lack details and their botanical affinity is uncertain. However, two specimens (MCD5424 and 5517) are attributed to palm axes. The best preserved specimen, MCD5424 (Fig. 4P and Q), is 5.1 cm long and 2.9 cm wide and is composed of densely packed, long, parallel fibrovascular bundles with rounded or elliptical sections (Fig. 4Q). It has been interpreted by Marmi et al. (2015) as the subdermal or central zone of a palm stem.

Charophytes are rare in the Molí del Baró-1 site and are only represented by a few utricles of *Clavator brachycerus* (Grambast, 1962) Martín-Closas 1996 and gyrogonites of *Peckichara cancellata* Grambast 1971 in ‘level 2’. This assemblage contrasts with the charophyte assemblages found in the underlying red beds (floodplain facies) which are exclusively formed by *Microchara nana* Vicente and Martín-Closas in Vicente et al. (2015).

5.2. *Molluscs*

At least three different taxa within Gastropoda are distinguished. Two specimens are assigned to the genus *Lychnus* Matheron 1832, which is a typical fossil snail from the uppermost Cretaceous of northern Iberia and southern France. It belongs to the clade Stylommatophora (air-breathing land snails and slugs) (Babinot et al., 1983; Kiel, 2001). The shells are large, 5.9–8.5 cm long and 4.6–6.5 cm wide, elliptic in apical view, with the bodywhorl wrapping most of the spire (Fig. 5A). One specimen has the three apical whorls lying down, perpendicular to the columellar axis, and the bodywhorl ornamented with spiral lines (Fig. 5A), like *L. repelinii* Vidal in Repelin and Parent 1920 and *L. vidalii* Repelin and Parent 1920 from the Maastrichtian of the neighbouring Vallcebre Syncline (Repelin and Parent, 1920: pl. 4, Figs. 1–4; pl. 5, Figs. 1–6).

Other specimens were also preserved as internal casts, but in these cases a precise taxonomic identification was avoided due to the lack of diagnostic characters. However, some heliciform shells (0.8–3.6 cm long and 0.5–2.1 cm wide, Fig. 5B), and a single specimen with an elongate conical shell (0.7 cm long and 1.8 cm height, Fig. 5C) could represent at least two additional taxa.

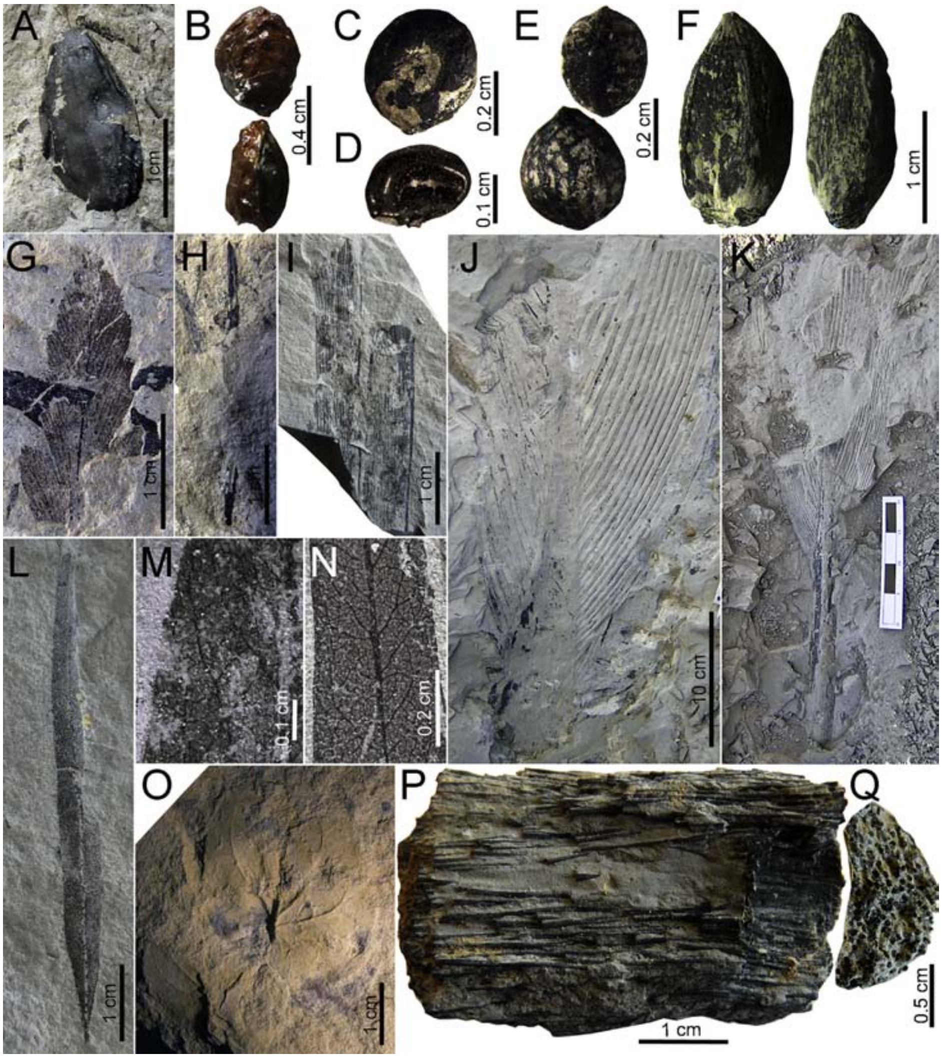

Fig. 4. Plant fossils collected from the Molí del Baró-1 locality. A, Oval seed covered with a coaly envelope, MCD5252. B, Elliptic seed covered with a brownish cuticle, MCD5494. C, Basal view of a semispherical seed showing the hilum and vascular bundle, MCD5482. D, Small, auriform seed with smooth surface, MCD5350a. E, Spherical seed with rough surface. A wide crest divides the seed into two hemispheres, MCD5350b. F, A likely palm seed with longitudinal grooves in its surface, MCD5516. G, Fragment of a fern leaf with once or twice dichotomously ramified secondary veins, MCD5467. H, Needle shaped leaf of a conifer, MCD5502. I, Fragment of a ribbon-shaped monocot leaf with parallelodromous venation, MCD5453. J, Costapalmate lamina of *Sabalites longirhachis*. K, Lamina of *S. longirhachis* with petiole attached (scale bar equals 20 cm), MCD5263. L, Complete leaf of *Saliciphyllum gaetei*, MCD5433. M, Detail of a *S. gaetei* leaf with eucamptodromous secondary veins, MCD5244. N, Detail of a *S. gaetei* leaf with brochidodromous secondary veins, MCD5256. O, Eudicot-like leaf, MCD5417. P, Fragment of the subdermal or central zone of a palm stem composed of parallel fibrovascular bundles, MCD5424. Q, Cross section of MCD5424.

5.3. Arthropods

Crustaceans and insects were identified among the few arthropod remains recovered from the Molí del Baró-1 site. A partial cheliped (probably a dactyl) is attributed to an indeterminate member of Decapoda (Fig. 5D–F). It is 1.1 cm long and its height decreases forwards. The lateral surface has tubercles, while the medial surface is smooth and contains small foramina aligned near the dorsal edge. Denticles of the dorsal edge are rounded and variable in size (1–2 mm long).

A pronotum of a coleopteran insect was found in the 'level 2' (Fig. 5G). It is pentagonal, 1 cm long and 1.1 cm wide. A prominent medial groove divides the structure into two equal halves. The anterior edge is straight with two lateral tips. The posterior end is rounded. Two small protuberances are located medially, close to the anterior edge. The surface is smooth. It resembles the pronotum of some species within the extant genera *Melambia* (Trogossitidae) — e.g. *M. crenicollis* Guérin and *M. striata* Olivier (Kolibáč, 2013: Fig. 7b, c) — and *Phanodesta* (Kolibáč, 2013: Fig. 5i). However, the fossil pronotum from Molí del Baró-1 is anteriorly narrower and, in extant species, the pronota are ornamented with pits and lack the medial groove and anterior protuberances.

Another specimen (MCD5423) is interpreted as a left elytron of a coleopteran insect (Fig. 5H and I). It is sickle-shaped, 7.1 mm long and 2.2 mm wide and covered by a black cuticle. The ornamentation consists of 11 or 12 parallel rows, composed of small, circular pits, 0.1 mm in diameter (Fig. 5I). Parallel to the convex edge, there is a thin longitudinal groove that could be a longitudinal vein (Fig. 5H and I). Elytra with similar dotted ornamentation arranged in rows have been observed in different taxa within Coleoptera such as the Early Permian *Permocoleus wellingtonensis* (Lubkin and Engel, 2005: Figs. 1 and 2; Beckemeyer and Engel, 2008: Fig. 1), Early Cretaceous cupedids (Soriano and Delclòs, 2006), and extant chrysomelids (e.g. *Donacia vulgaris* Zchach; *Chaetocnema ussuriensis* Heikertinger, J.M. personal observation).

An insect egg was found at the boundary between levels '2' and '3'. It is ovoid, 1.9 mm long and 1.1 mm wide (Figs. 5J and 6). The visible surface is ornamented with up to nine longitudinal ridges, which are triangular in cross-section and converge in both apices (Fig. 5J). The ridges are 50–85 μm wide. The base has a small central projection surrounded by the ends of longitudinal ridges. The specimen preserves a partial cuticle showing details of the inner ornamentation (Figs. 5J and 6). It consists of rectangular cell-like structures, 100–110 μm long and 30–38 μm wide, arranged in

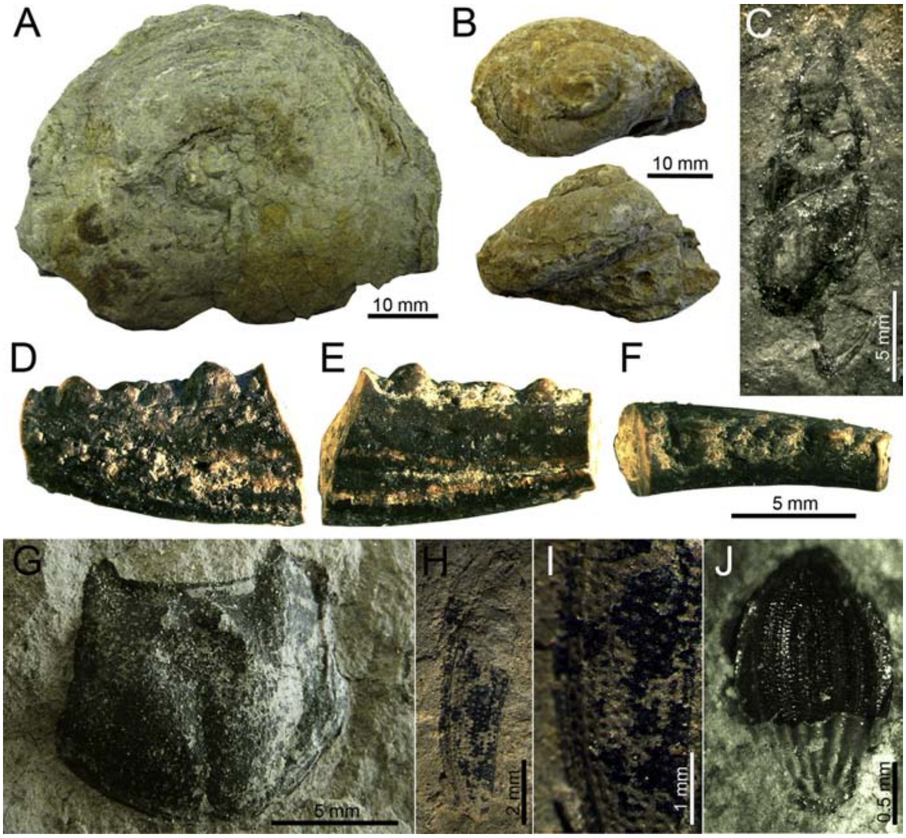

Fig. 5. Invertebrates collected from Molí del Baró-1 site. A, Internal cast of a *Lychnus* gastropod, MCD5536. B, Internal cast of an indeterminate gastropod in apical and apertural views, MCD5271. C, Compression of a turriculate gastropod, MCD5537. D–F, Fragment of a possible dactyl of an indeterminate decapod in lateral, medial and occlusal views, respectively, MCD5538. G, Pronotum of an indeterminate coleopteran, MCD5539. H, I, Elytron of an indeterminate coleopteran showing details of ornamentation (I), MCD5423. J, Insect egg, MCD5491.

nine parallel rows. Each cell has a circular pore in the middle that is 20–27 μm in diameter. Cell rows are separated from each other by longitudinal columns, 37–62 μm wide. In cross-section, the cuticle is 119 μm thick and composed of a single row of prismatic cells, 32–43 μm wide. The specimen resembles *Knoblochia cretacea* Heřmanová et al. 2013 from the Campanian–Danian of the Czech Republic, Austria and Poland (Heřmanová et al., 2013) in size, shape, inner ornamentation and shape of wall cells. However, structures of the apical end (projection, coronal rim), as well as other diagnostic features (e.g. the micropapillae) of this egg-species are not visible in the MCD5491. Moreover, the wall of the Molí del Baró-1 egg is three times thicker than that of *K. cretacea*. In this species, the pores are up to five times smaller and not located in the middle of rectangular cells. Longitudinal columns between cell rows are also lacking in the inner surface of *K. cretacea*. Eggs resembling *K. cretacea* are laid by different taxa within orders Lepidoptera and Phasmatodea (Heřmanová et al., 2013).

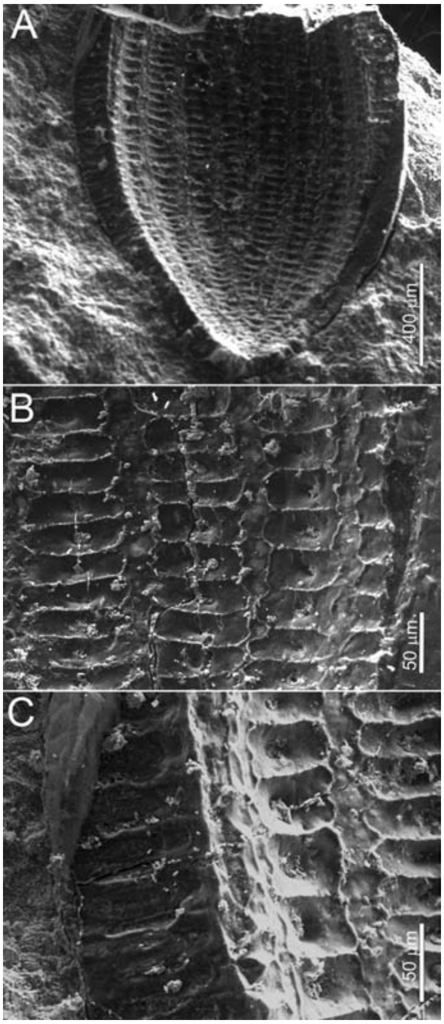

Fig. 6. SEM microphotographs of the insect egg MCD5491. A, General view of the inner surface of the egg cuticle. B, Detail of the rectangular cells arranged in longitudinal rows. Each cell bears a circular pore in the middle. C, Detail of the cross section of the cuticle showing a single row of prismatic cells.

5.4. *Fish*

Osteichthyes are only represented by two scales (Fig. 7A–C) and a single isolated vertebra (Fig. 7D). The scales are of the crenated ctenoid type (Fig. 7A). They are nearly circular and 2.5–4.4 mm long and 3.0–4.2 mm wide. Their posterior edge is rounded and serrated (Fig. 7C). The anterior half is ornamented with radial striae (Fig. 7A). Growth rings are visible around the focus (Fig. 7A and B). The scales resemble those of extant Percoidea and are tentatively assigned to indeterminate Percomorpha. Remains of the ginglymodian genera *Lepisosteus* and *Lepidotes* are commonly recovered from the uppermost Cretaceous localities around the Tethys Ocean (Grigorescu et al., 1999; Laurent et al., 2002; Cuny et al., 2010a, b; Blanco and Bolet, 2014). These genera bear ganoid scales (Grigorescu et al., 1999; Fanti et al., 2012), unlike Teleostomi, which are not found in the sample under description. Thus, ginglymodians are not reported in the Molí del Baró-1 site.

The vertebra consists of a centrum lacking neural and hemal arches. It is circular in cross section and measures 1.7 mm in diameter (Fig. 7D). The articular surface is convex. The notochord canal is circular and located in the centre of the centrum. It measures 0.4 mm in diameter. The specimen is assigned to an indeterminate Osteichthyes.

5.5. *Amphibians*

The presence of anurans is testified by an almost complete and two partial tibiofibulae (Fig. 7E) and a fragmentary urostyle (Fig. 7F). The best preserved tibiofibula is straight, elongated and gracile (Fig. 7E). It is 13.6 mm long and 0.8–1.7 mm wide. The tibiofibulae show longitudinal sulci on the ventral and dorsal sides of the proximal and distal ends of their diaphyses (e.g. Fig. 7E). The urostyle fragment corresponds to the anterior end of the bone (Fig. 7F). It has two anterior cotyles, which are dorsoventrally compressed, and show a nearly straight articular surface. Both cotyles meet in the longitudinal plane of the bone. The upper part of the dorsal crest is not preserved, revealing the floor of the neural canal. The ventral surface of the bone is nearly flat.

Amphibians are frequently recovered from micropalaeontological samples collected in Upper Cretaceous localities from Spain (Duffaud and Rage, 1999; Blain et al., 2010; Company and Szentesi, 2012; Blanco et al., this volume), France (Garcia et al., 2000), Romania (Grigorescu et al., 1999; Venczel and Csiki, 2003; Folie and Codrea, 2005) and Hungary (Szentesi and Venczel, 2010, 2012). However, the specimens from Molí del Baró-1 are classified as indeterminate Anurans because of the lack of diagnostic characters.

5.6. *Crocodylomorphs*

The crocodylomorph fossil assemblage is composed of teeth and bones (Fig. 7G–M); teeth representing 89.7% of the crocodylomorph sample (Fig. 8).

5.6.1. *Crocodylomorph teeth*

Thirty-five isolated crocodylomorph teeth were recovered from all levels, but most of them come from the ‘level 3’ (n = 18). Twenty-four teeth were assigned to the following ten morphotypes (Fig. 8; Table 1), but eleven teeth remained as indeterminate.

Cf. *Allodaposuchus* sp. morphotype 1 (MCD5547–50; Fig. 8A–C). It consists of conical and pointed teeth with high crowns showing

Fig. 7. Fish, amphibian and crocodylomorph remains collected from Molí del Baró-1 site. A–C, Ctenoid fish scale showing details of the circuli (B) and ctenii (C), MCD5540. D, Centrum of a fish vertebra showing the circular notochord canal, MCD5542. E, Tibiofibula of an indeterminate anuran, MCD5543. F, Partial urostyle of an indeterminate anuran, MdB28. G–K, Femur of an indeterminate crocodylomorph in lateral, medial, dorsal, ventral and distal views, respectively, MCD5544. L and M, Osteoderm of an undetermined crocodylomorph in dorsal and ventral views, MCD5545.

faint basal constriction. They are 6–14 mm apicobasally high and 3–5 mm mesiocaudally wide. The crowns are subcircular in cross section, more convex labially than lingually (Fig. 8C). The enamel is smooth. Faint carinae lacking denticles are present in the mesial and posterior edges. These features have been observed in *Allodaposuchus subjuniperus* Puértolas-Pascual et al. (2014) and in an eusuchian crocodylomorph recovered from the close Maastrichtian locality of Casa Fabà, which is assigned to the genus *Allodaposuchus* Nopcsa 1928 (Puértolas-Pascual et al., 2014; Blanco et al., in press). However, the teeth from Molí del Baró-1 are more acute than those of the *A. subjuniperus* holotype (MPZ 2012/288, Puértolas-Pascual et al., 2014), and also lack the lingual grooves present in this species.

Cf. *Allodaposuchus* sp. morphotype 2 (MCD5551–54; Fig. 8D–F). Conical and pointed teeth with relative high lanceolate crowns showing faint basal constriction. The most complete tooth is 6.1 mm apicobasally high and 2.8 mm mesiocaudally wide. The teeth are labiolingually compressed and lingually inclined. They bear well-developed mesiocaudal carinae without denticles. The lingual surface delimited by both keels bears apicobasal ridges, whereas the labial surface is smooth. This morphotype is similar to the teeth of *Allodaposuchus precedens* Nopcsa 1928 (see Grigorescu et al., 1999; Delfino et al., 2008). However, in *A. precedens*, teeth bear ridges in the labial surface.

Cf. *Allodaposuchus* sp. morphotype 3 (MCD5555–56, Fig. 8G and H). The teeth are wide (11.8 mm), elongate (17.4 mm) and blunt. They show a convex labial surface, whereas the lingual is flattened. Anterior and posterior carinae are unserrated. The enamel is smooth, but there are two apicobasal grooves lingually to the carinae, and several apicobasal ridges are present between the grooves. The specimen resembles the caniniform (4th dentary tooth) of *Allodaposuchus* sp. from Casa Fabà (Blanco et al., in press).

Allodaposuchus palustris type (MCD5557–58; Fig. 8I and J). These teeth are relatively wide (4.6 mm) and low (4.9 mm

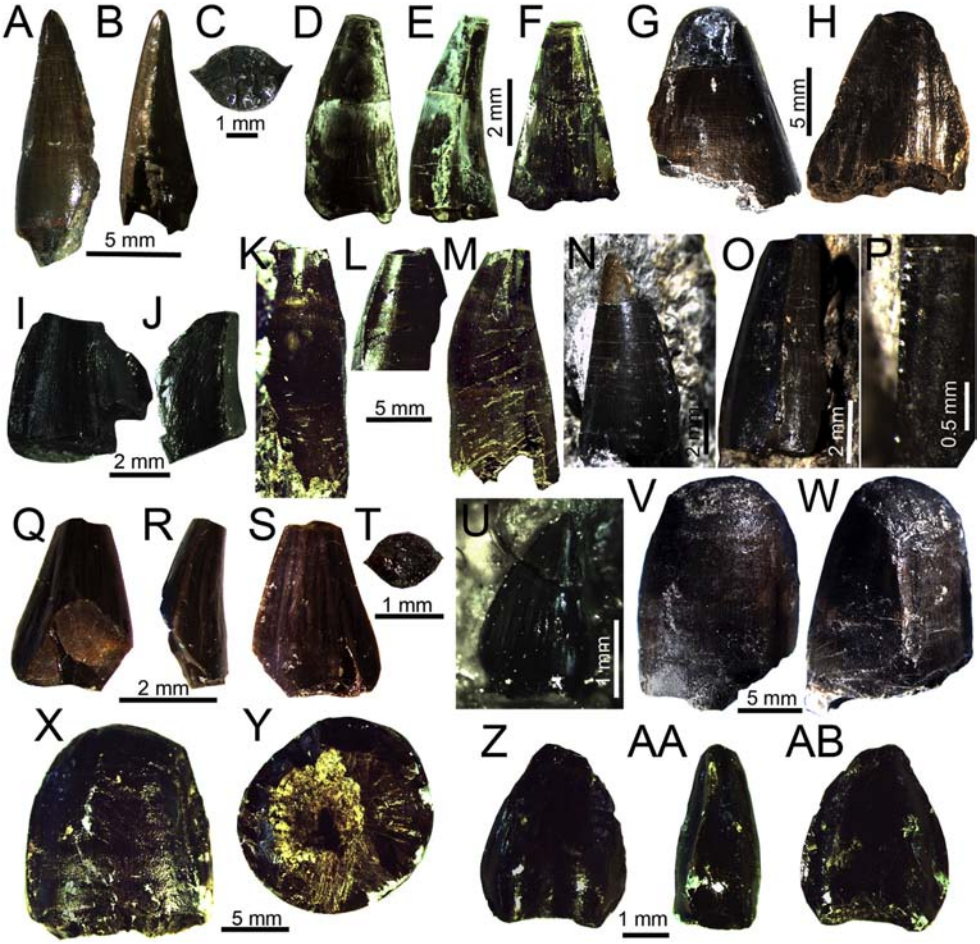

Fig. 8. Morphotypes of crocodylomorph teeth collected from Molí del Baró site. A–C, cf. *Allodaposuchus* sp. morphotype 1 in labial (A), caudal (B) views (MCD5547) and cross section (C) MCD5548. D–F, cf. *Allodaposuchus* sp. morphotype 2 in labial (D), mesio-caudal (E) and lingual (F) views, MCD5551. G and H, cf. *Allodaposuchus* sp. morphotype 3 in labial (G) and lingual (H) views, MCD5556. I and J, *Allodaposuchus palustris* type in lingual (I) and mesio-caudal (J) views, MCD5557. K–M, *Allodaposuchus subjuniperus* type in labial (K), lingual (L) and mesio-caudal (M) views, MCD5559. N–P, Indeterminate Crocodylomorpha morphotype 1 in labial (N), mesial (O) views and detail of the denticulated carina (P), MCD5562. Q–T, Indeterminate Crocodylomorpha morphotype 2 in labial (Q), caudal (R), lingual (S) views and cross section (T), MCD5564. U, Indeterminate Crocodylomorpha morphotype 3 in lingual view, MCD5565. V–Y, Indeterminate Crocodylomorpha morphotype 4 in labial (V), mesio-caudal (W), lingual (X) views and cross section (Y), MCD5567. Z–AB, Indeterminate Atoposauridae in labial (Z), mesio-caudal (AA), lingual (AB) views, MCD5570.

apicobasally high). They are apically blunt, and their labial surface more convex than the lingual surface. The anterior and posterior carinae are well developed, with two relatively deep apicobasal grooves lingually to the carinae (Fig. 8I). The enamel is ornamented with numerous and fine longitudinal ridges, developing false-ziphodont crenulations where they contact the carinae. This feature is present in the teeth of the early Maastrichtian *A. palustris* described by Blanco et al. (2014).

A. subjuniperus type (MCD5559; Fig. 8K–M). Like the cf. *Allodaposuchus* sp. type 1, this tooth is conical with smooth enamel, but it is wider and blunt. It is 19.4 mm apicobasally high and 8.1 mm mesiocaudally wide. The MCD5559 has a relative low crown (13.2 mm high). Both mesial and posterior carinae are scarcely developed and lack denticles. Unlike the cf. *Allodaposuchus* sp. type 1, the MCD5559 shows mesial and posterior grooves on the lingual side near and parallel to the carinae. The shape of the studied specimen is identical to that of the teeth belonging to the holotype of *A. subjuniperus* (MPZ 2012/288, Puértolas-Pascual et al., 2014).

Indeterminate Crocodylomorpha morphotype 1 (MCD5560–63; Fig. 8N–P). The teeth (8.8–9.2 mm apicobasally high and 3.3–4 mm anteroposteriorly wide) are conical and pointed, resembling those of cf. *Allodaposuchus* sp. type 1, but they are elliptical in cross-section and slightly bended caudally. The enamel lacks ornamentation in both lingual and labial sides. The mesial carina is low-developed, or absent. The posterior carina shows small crenulations, forming a true ziphodont tooth (Fig. 8P). The shape of the crown is different to that of *Doratodon* Seeley 1881 teeth (Grigorescu et al., 1999; Company et al., 2005). Teeth assigned to *Doratodon* are triangular, labiolingually compressed and they present well-defined denticles in mesial and posterior

Table 1
Tooth morphotypes represented in the Molí del Baró-1 site.

	Taxa	Material	Sample (n)
Crocodylomorpha			**24**
Morphotype 1	cf. *Allodaposuchus* sp.	MCD5547–50	4
Morphotype 2	cf. *Allodaposuchus* sp.	MCD5551–54	4
Morphotype 3	cf. *Allodaposuchus* sp.	MCD5555–56	2
Morphotype 4	*Allodaposuchus palustris*	MCD5557–58	2
Morphotype 5	*Allodaposuchus subjuniperus*	MCD5559	1
Morphotype 6	'Ziphodont' crocodylomorph	MCD5560–63	4
Morphotype 7	'Ziphodont' crocodylomorph	MCD5564	1
Morphotype 8	Crocodylomorpha indet.	MCD5565–66	2
Morphotype 9	Crocodylomorpha indet.	MCD5567–68	2
Morphotype 10	Atoposauridae	MCD5569–5570	2
Theropoda			**7**
Morphotype 1	Dromaeosauridae	MCD5579	1
Morphotype 2	cf. ?*Richardoestesia*	MCD5032, MCD5580	2
Morphotype 3	aff. *Paronychodon*	MCD5581	1
	?*Euronychodon*	MCD5582	1
Morphotype 4	Theropoda indet.	MCD5033	1
Morphotype 5	Theropoda indet.	MCD5583	1

The entire samples for Crocodylomorpha and Theropoda are marked in bold.

carinae. In contrast, specimens from Molí del Baró-1 show denticles only in the posterior carina (MCD5561, 5562, 5562), except MCD5560 that presents a poorly-developed anterior carina in the rounded mesial end, bearing faint crenulations in its apical-most edge. The MCD5562 also has a low-developed, but unserrated, mesial carina.

Indeterminate Crocodylomorpha morphotype 2 (MCD5564; Fig. 8Q–T). It only comprises a single tooth recovered from 'level 4'. It is a triangular (3.3 mm apicobasally high and 2.2 mm mesiocaudally wide) and blunt tooth, which is labiolingually compressed and lingually curved. It bears mesial and posterior carinae, both bearing small denticles as in the former tooth morphotype. Enamel presents well-developed apicobasal ridges in the lingual and labial surfaces. The MCD5564 is similar in shape to *Doratodon ibericus* Company et al. (2005). However, *Doratodon* teeth have well-developed denticles and smooth enamel surfaces, in contrast to MCD5564.

Indeterminate Crocodylomorpha morphotype 3 (MCD5565–66; Fig. 8U). The teeth assigned to this morphotype are mesiocaudally wide (1.1 mm) and lanceolate (2.1 mm apicobasally high). Mesial and posterior carinae are unserrated. Enamel is ornamented with seven apicobasal ridges. A marked constriction is present at the base of the crown.

Indeterminate Crocodylomorpha morphotype 4 (MCD5567–68, Fig. 8V–Y). These specimens are significantly larger than the others (19.9 mm apicobasally high, 13.9 mm mesiocaudally wide), and could represent caniniform teeth. They are cylindrical, blunt and circular in cross-section. The crown is slightly curved lingually, and it is not posteriorly curved in lateral view. The specimens present both mesial and posterior tenuous and unserrated carinae (Fig. 8W and X). The enamel is smooth.

Indeterminate Atoposauridae morphotype (MCD5569–5570; Fig. 8Z–AB). These teeth are triangular and apically blunt (2.9–4.3 mm apicobasally high and 2.9–3.3 mm mesiocaudally wide), labiolingually compressed and not lingually recurved. The crowns are basally constricted. Mesial and posterior carinae are present. The enamel bears faint apicobasal ridges, which are more tenuous in the labial surface. In lingual view, the ridges reaching the carina develop false-ziphodont crenulations. These teeth also present a medial apicobasal groove in the lingual surface that divides the crown into two bulbous halves. This morphology resembles the spatulate teeth of the Atoposauridae. Martin et al. (2014) reported similar teeth referred to ?*Theriosuchus* sp. from Cruzy (Hérault, France).

5.6.2. Crocodylomorph bones

MCD5544 is a nearly complete left femur of an indeterminate crocodylomorph (Fig. 7G–K). The bone is 18.8 cm long. The proximal epiphysis is partially eroded, but the shaft and the distal condyles are well preserved. Scars for muscle or ligament attachments are conspicuous in the lateral and medial surfaces of the proximal epiphysis. In lateral view, the shaft is sigmoidal-shaped (Fig. 7G), being the fourth trochanter the point of maximum curvature. This trochanter is clearly visible in medial (Fig. 7H) and ventral (Fig. 7J) views. The distal condyles are largely different in size: the lateral condyle is 1.9 cm wide and the medial is thinner (1.1 cm wide) and shorter (Fig. 7J and K).

Three osteoderms (MCD5571–73) were also found. They are flattened bones, subcircular in outline, 3.6 × 2.8 cm (Fig. 7L and M). Each osteoderm is keeled and ornamented with irregular pits that completely occupy its dorsal surface.

5.7. Dinosaurs

The dinosaur sample recovered from Molí del Baró-1 comprises isolated teeth, bones and eggshells of ornithopod, sauropod and theropod dinosaurs.

5.7.1. Dinosaur teeth

Six rhomboid teeth (MCD5542, 5574–78) are assigned to hadrosauroid ornithopods. They are diamond-shaped with carinae in the mesial and posterior edges as well as in the lingual surface, all of them lacking denticles. The teeth do not show secondary carinae.

Theropod teeth are more abundant and have been assigned to five morphotypes (Table 1):

Cf. Dromaeosauridae morphotype (MCD5579; Fig. 9A and B). The crown is caudally recurved, labiolingually compressed and has a serrated posterior carina but not mesial carina. It is 5.2 mm apicobasally high and 4.2 mm mesiocaudally wide. Its cross-section is teardrop-shaped, with the wider and blunt part occurring mesially. The denticles are asymmetrical, apically pointed, caudodorsally oriented and constricted at the base (Fig. 9B). The general morphology and the shape of the denticles suggest affinity to teeth assigned to Velociraptorinae and previously reported in the Cretaceous of Spain (e.g. López-Martínez et al., 2001; Canudo and Ruíz-Omeñaca, 2003; Barroso-Barcenilla et al., 2009; Ortega et al., 2015). Also, MCD5579 resembles velociraptorine teeth reported from the Maastrichtian of Romania (Grigorescu et al., 1999). However, because its fragmentary nature and the lack of unequivocal diagnostic characters, the specimen is allocated to cf. Dromaeosauridae.

Cf. ?*Richardoestesia* morphotype (MCD5032, 5580; Fig. 9C and D). The crowns are posteriorly recurved, labiolingually flattened and bear a serrated posterior carina. There is no mesial carina. Its cross-section is teardrop-shaped, with the wider and blunt part occurring mesially. The incomplete crowns are 8.4–10.5 mm apicobasally high and 5.4–6.2 mm mesiocaudally wide. Denticles are similar and only partly preserved in both specimens. However, those of MCD5580 are proportionally smaller. Denticles are rectangular, perpendicular to the cutting margin and show the asymmetrical apical part pointing toward the apex of the crown (Fig. 9D). The interdenticular slits are deep and narrow ending in well-developed cellae; from the latter, long blood grooves start, which are directed toward the base of the crown. These two specimens are very similar in the overall morphology, teardrop-shaped cross-section and absence of a mesial carina to the dromaeosaurid

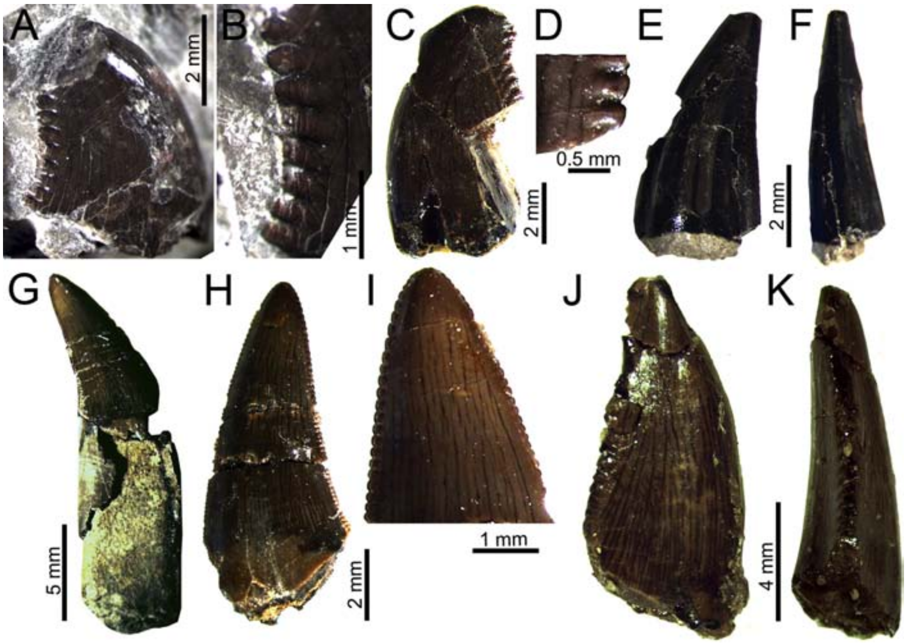

Fig. 9. Morphotypes of dinosaur teeth collected from Molí del Baró site. A and B, Indeterminate cf. Dromaeosauridae morphotype in labial view (A) and detail of denticles (B), MCD5579. C and D, cf. *Richardoestesia* morphotype in labial view (C) and detail of denticles (D), MCD5032. E and F, aff. *Paronychodon* morphotype in labial (E) and caudal (F) views, MCD5582. G–I, Indeterminate Theropod morphotype 1, complete specimen (G), detail of the crown (H), detail of denticles (I), MCD5033. J and K, Indeterminate Theropod morphotype 2 in labial (J) and caudal (K) views, MCD5583.

morphotype reported above. However, these two morphotypes clearly differ on denticle morphology, which could just be due to a different position in the jaw. Additionally, MCD5032 and 5580 were compared to teeth assigned to the genus *Richardoestesia* Currie et al. (1990) from the Maastrichtian of the southern Pyrenees (Prieto-Márquez et al., 2000; Torices et al., in press, Fig. 3i–l). According to Torices et al. (in press), the genus *Richardoestesia* is featured by having posterior denticles rectangular and slightly tilted toward the tooth apex. Moreover, these authors estimated that nearly the 25% of the teeth from Iberian localities showed anterior denticles. However, the studied specimens differ from the tooth described by Prieto-Márquez et al. (2000) in having the posterior carina placed in the medial plane of the crown and totally denticulated. The multivariate analysis carried out by Torices et al. (in press) revealed clear differences among the specimen studied by Prieto-Márquez and collaborators and the remaining Iberian sample. Accordingly, the assignment of this tooth to *Richardoestesia* seems rather doubtful. On the other hand, the presence of blood grooves (found only in MCD5032) is an uncommon feature in teeth of this size and shape, being common in tyrannosauroid teeth (Currie et al., 1990; Abler, 1992).

Aff. *Paronychodon* morphotype (MCD5581–82; Fig. 9E and F). These crowns are small; 5.6–6.53 mm apicobasally high and 2.23–3.1 mm mesiocaudally wide; pointed and almost straight or slightly curved caudally. The MCD5581 lacks its apical portion. It is unusually slender and labiolingually compressed. Its basal cross-section is sub-rectangular, while the apical section is elliptical. The labial and lingual surfaces have a central apicobasal depression, extended toward the apical part of the crown. The surface presents small, irregular wrinkles of the enamel. There are thin, unserrated carinae in both mesial and caudal margins; the mesial carina does not reach the base of the crown and is slightly asymmetrically displaced on the lingual side; the caudal carina is symmetricaly placed on the caudal margin. The labiolingual flatness supports its identification as a theropod tooth. Although it is not common, theropod teeth can have unserrated carinae. The displacement of the mesial carina would suggest a mesial position for this tooth, which is also supported by the shape of the crown. MCD5582 is also a crown (Fig. 9E and F). In labial view, the mesial carina is concave and the posterior carina is straight. Both carinae are unserrated. Several apicobasal ridges are present in the lingual and labial surfaces of MCD5582, forming two lateral grooves. Based on the lack of denticles and general shape of the crowns, these two teeth are tentatively assigned to aff. *Paronychodon*. The MCD5581 resembles *Paronychodon* Cope 1876 teeth described by Torices et al. (in press) in having sub-rectangular cross-section, the flat lingual surface, the apex caudally recurved and the presence of the central apicobasal depression. The teeth belonging to *Paronychodon* have been reported in several Maastrichtian localities of the southern Pyrenees (Torices et al., in press). In addition, a new species of paronychodontid theropod, *Euronychodon portucalensis* Antunes and Sigogneau-Russell 1991, was erected based on several isolated teeth recovered from Portugal (Antunes and Sigogneau-Russell, 1991). Unlike *Paronychodon* teeth reported by Torices et al. (in press), MCD5582 has a straight posterior carina, and lateral ridges are more conspicuous. Like *Euronychodon* Antunes and Sigogneau-Russell 1991, MCD5582 shows two well-developed lateral grooves in the crown (Antunes and Mateus, 2003). However, *Euronychodon* has been regarded as junior synonym of *Paronychodon* by several authors (Rauhut, 2002; Torices et al., in press).

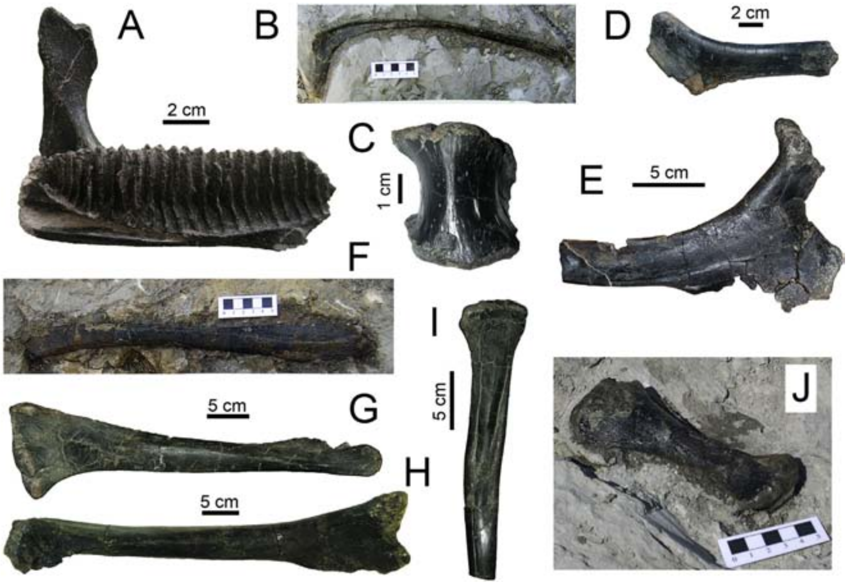

Fig. 10. Hadrosauroid dinosaur bones from Molí del Baró-1 site. A, Left dentary in lingual view, MCD5281. B, Dorsal rib, MCD5588. C, Isolated sacral vertebra in ventral view, MCD5589. D, Sternal plate, MCD5592. E, The proximal part of a right ischium, MCD5089. F, Left ulna, MCD5594. G, Right tibia, MCD4733. H, Left tibia, MCD5595. I, Right fibula lacking the distal third, MCD4734. J, Left metatarsal II, MCD5597. In B, F, and J the scale bar is in centimetres.

Indeterminate Theropod morphotype 1 (MCD5033; Fig. 9G–I). It is a complete tooth with the crown and root. The total apicobasal height of the whole tooth is 18.4 mm and the maximum mesiocaudal length is 5.1 mm. The crown is apicobasally elongated, 8 mm high and the apex is slightly oriented caudally. In cross section, it is highly compressed labiolingually and 8-shaped because of central apicobasal depressions on both the labial and lingual sides. Denticles are present in both mesial and caudal carinae, being slightly larger in the caudal carina (Fig. 9I). As a whole, they are comparatively small, giving a caudal denticular density of ~7 denticles per mm. Denticles are generally rounded but become rectangular toward the apex of the crown (Fig. 9I). The root is long and rectangular in lateral view and is labiolingually flattened (Fig. 9G). It shows a central, apicobasal depression that extends on the basal part of the crown. This morphotype resembles the Morphotype 1 described by Torices et al. (in press), but the specimen from Molí del Baró-1 is smaller and has a different cross section. These differences could be attributed to ontogeny or a distinct position within the jaw. These authors suggested that Morphotype 1 could belong to a neoceratosaur, but it was finally referred to Theropoda indet. because of the absence of diagnostic material. The relatively small size of the denticles suggests affinity to *Richardoestesia* (Currie et al., 1990; Sankey et al., 2002; Llorens, 2010). MCD5033 resembles the *Richardoestesia* specimen from the lower Maastrichtian of the L'Abeller locality in the Eastern Tremp Syncline (Prieto-Márquez et al., 2000). However, unlike the tooth described by Prieto-Márquez et al. (2000), the studied specimen has the caudal carina symmetrically placed in the crown and totally denticulated. As mentioned above, it is important to note that the specimen described by Prieto-Márquez et al. (2000) probably belongs to a different taxon to *Richardoestesia* (Torices et al., in press). Taking into account all these evidence, MCD5033 is assigned to an indeterminate theropod morphotype.

Indeterminate Theropod morphotype 2 (MCD5583; Fig. 9J and K). The tooth crown is pointed and recurved posteriorly. It is 10.8 mm apicobasally high and 4.7 mm mesiocaudally wide. The enamel is smooth. The posterior carina bears well-defined denticles that are rounded and slightly oriented toward the apex. The interdenticular slits are scarcely marked. The mesial edge of the crown is smooth and rounded, without a carina. The crown is teardrop-shaped in cross section. In caudal view, the tooth crown is sinuous and lingually recurved. The posterior carina is also sinuous and located in the middle of the crown.

5.7.2. *Dinosaur bones*

All identifiable dinosaur bones belong to the Ornithopoda Hadrosauroidea and were mostly collected in the ‘sandstone’ lenses inside the grey marl interval. They were all found disarticulated and scattered; no associate skeletal remains have been found. They consist of skull and mandible elements — a fragment of a maxilla, MCD5584; a small left dentary, MCD5281 (Fig. 10A); a portion of a larger, toothless dentary, MCD5585– axial elements — a cervical vertebra, MCD5586; a dorsal vertebra, MCD5587; a complete dorsal rib, MCD5588 (Fig. 10B); an isolated sacral vertebra, MCD5589 (Fig. 10C); an isolated sacral centrum, MCD5590; a mid-caudal vertebral centrum, MCD5591; and 15 small segments of tiny ossified tendons, –girdle elements — a small sternal plate, MCD5592 (Fig. 10D); the proximal part of a right ischium with portions of the shaft, MCD5089 (Fig. 10E); and the fragment of an another ischial shaft, MCD5593,– and limb bones — a left ulna, MCD5594 (Fig. 10F); a right and a left tibiae, MCD4733 and MCD5595 (Fig. 10G and H, respectively); a right fibula lacking the distal third, MCD4734 (Fig. 10I); the distal end of a right metatarsal III, MCD5596, and a left metatarsal II, MCD5597 (Fig. 10J). All those bones belong to comparatively small-sized individuals (Dalla Vecchia et al., 2014).

The hadrosauroid dentary MCD5281 was studied by Blanco et al. (2015). This specimen was described and figured also in Dalla Vecchia et al. (2014, p. 304, Fig. 16.5E, Appendix 16.2). The specimen is small and almost complete, slightly broken in the rostral end, lacking the edentulous region. The dental battery is over 11.76 cm long and 3.04 cm high. It shows 26 alveoli, but no teeth were preserved in situ. The coronoid process is straight and slender. This process is 5.38 cm high and its minimum ramus width is 1.49 cm. Despite the fact that an ischium from this site is assigned to a lambeosaurine hadrosaur (see below), Blanco et al. (2015) suggest that this dentary belongs to a more basal hadrosauroid taxon.

The two small sacral vertebrae were clearly unfused to the other sacrals and, at least in one case (MCD5590), to the neural arch, suggesting they belonged to immature individuals. The sternal plate is only 8 cm long. The two tibiae are 47 and 54 cm long, and the estimated length of the fibula is 37 cm, so they belong to different individuals. According to Prieto-Márquez et al. (2013), the right ischium MCD5089 is assigned to the Lambeosaurinae, because of the well-developed curvature in the caudodorsal corner of the distal margin of the iliac process of the ischium. All the other postcranial elements are taxonomically uninformative.

5.8. *Eggshells*

Most of the oological remains from Molí del Baró-1 site were recovered by screen-washing sediment, though some specimens were obtained in situ. At least, four types of eggshells were distinguished, and some of them were studied in detail by Sellés et al. (2014) and Sellés and Vila (2015).

The first type is represented by 26 eggshells characterised by having a relatively great shell-thickness (1.2–1.7 mm including ornamentation). Its outer surface is covered with coalescent rounded nodes (0.4–0.6 mm in diameter) forming short chains. In radial thin-section, the shell is composed of fan-shaped shell units, sometimes fused one each other. Thus, the boundaries between these units are somewhat difficult to assess. Growth lines are arched at the base of the shell units but they turn undulating in its upper part, following the topography of the outer surface and crossing neighbour-fussed units. The pore channels are simple, narrow and straight like the tubocanaliculate morphotype (Mikhailov, 1997). The combination of these features allows classifying this eggshell type as belonging to the oofamily Megaloolithidae and more precisely to *Fusioolithus baghensis* (Khosla and Sahni, 1995) Fernández and Khosla 2015 (*sensu* Fernández and Khosla, 2015). Based on several evidence, megaloolithid eggs and eggshells can be taxonomically assigned to titanosaurian sauropods (Chiappe et al., 1998; Wilson et al., 2010; Grellet-Tinner et al., 2011 and references therein).

The second type is represented by 150 eggshells and diagnosed by showing a thin cross-section (0.25–0.50 mm in thickness), and a mainly smooth outer surface sometimes covered by small-scattered flat nodes. In radial view, the eggshell exhibits column-shaped shell units composed by two distinct structural layers: the lower mammillary layer and the upper columnar one. The former is built up of blade-shape crystals that radially grow from the base of the shell unit, and they gradually merge into the non-squamatic columnar layer. Growth lines are arched in the mammillary layer but become horizontal in the columnar layer. The ratio between these two structural parts is established at 1:4–1:5. Only few pore channels were observed in the specimens from the site, which are very narrow and straight, such as in the angustocanaliculate pore types (Mikhailov, 1997). The characters described herein are typical of the oofamily Prismatoolithidae, and the specimens from Molí del Baró-1 have been assigned to *Prismatoolithus trempii* Sellés et al. 2014. From a taxonomic point of view, prismatoolithid eggs have been largely related to theropod dinosaurs, and more probably to maniraptorans (see Sellés et al., 2014, and references within for a review).

The third type is represented by only eight eggshells. It is easily identifiable by the following features: very thin eggshell (0.21–0.34 mm including ornamentation, 0.15–0.22 mm without it); the outer surface covered by small irregular and scattered knobs of 50–200 μm in diameter; circular pore channel apertures (30 μm–50 μm in diameter) located at the top of the ornamental nodes. In radial section, the eggshell exhibits a single structural-layer of not well-distinguished prismatic-shape shell units. Under SEM, shell units exhibit irregular prismatic crystals showing squamatic texture. Horizontal to undulating growth lines appear in the middle part of the shell. Really narrow and straight pore channels are visible, ranging from 30 to 50 μm in width, corresponding to the angusticanaliculate pore system. The most diagnostic feature of this eggshell type is the ornamental pattern and the location of pore apertures on the top of the nodes. The combination of these features is characteristic of the oogenus *Pseudogeckoolithus* defined by Vianey-Liaud and López-Martínez (1997). Its certain taxonomic adscription is unknown, but because it is included within the Prismatoolitidae oofamily (Vianey-Liaud and López-Martínez, 1997) it might be produced by some group of theropod dinosaur.

The forth eggshell morphotype is the scarcest in the site (only four eggshells). It is 0.3–0.5 mm in thickness, and its outer surface is smooth or slightly undulate. In radial thin section, the eggshell is apparently composed of a single calcareous structural layer of wide wedge-like shell units. However, when specimens are examined more closely, they show three distinct layers. The lower layer (inner layer *sensu* Moreno-Azanza et al., 2013) is formed of large trapezoidal-shaped crystals of calcite radiating from the base of shell units, which form the basal plate group. The middle layer shows incipient tabular ultrastructure. The uppermost layer is not well-preserved, but given that undulating growth lines are more pronounced in the outer layer than in the middle one, it suggests a tabular ultrastructure for the external layer. The described features are consistent with the crocodylomorph eggshell morphotype (Moreno-Azanza et al., 2013; Marzola et al., 2014).

6. Taphonomy

A total of 767 fossils were collected from the 2002 to 2011 campaigns. Leaves and eggshells represent the 60% of the whole sample while bones and teeth are less than 20% (Fig. 11A). Excluding eggshells, plants are the 60% of the fossil assemblage and, in the remaining sample, crocodylomorphs and dinosaurs represent only the 8% and 7%, respectively. Mollusc, arthropod, fish and amphibian remains are scarcer (<10% all together). Based on data of 2010 and 2011 fieldwork, the levels ‘2’ and ‘3’ yielded 87.7% of fossil specimens (eggshells excluded). Plant remains mostly accumulated in ‘level 2’ (Fig. 11B), while vertebrate remains (teeth, bones and ossified tendons) were six times more abundant in ‘level 3’ than in ‘level 2’. Eggshells were also more frequent in ‘level 3’ than in ‘level 2’ (19% and 3%, respectively) (Fig. 11B and C). The few remains recovered from levels ‘4’, ‘5’ and ‘6’ mostly consist of fragments of mollusc shells, indeterminate bones, isolated teeth and eggshells (Fig. 11D–F). In ‘level 5’, eggshells are significantly abundant (56% of the sample).

Level ‘2’ and ‘3’ facies are multitaxon accumulations of disarticulated remains of plants, insects and vertebrates. This accumulation is represented by a high diversity of organs or structures including leaves, stems, seeds, sporomorphs, gyrogonites and utricles of charophytes, partial insect exoskeletons, insect eggs,

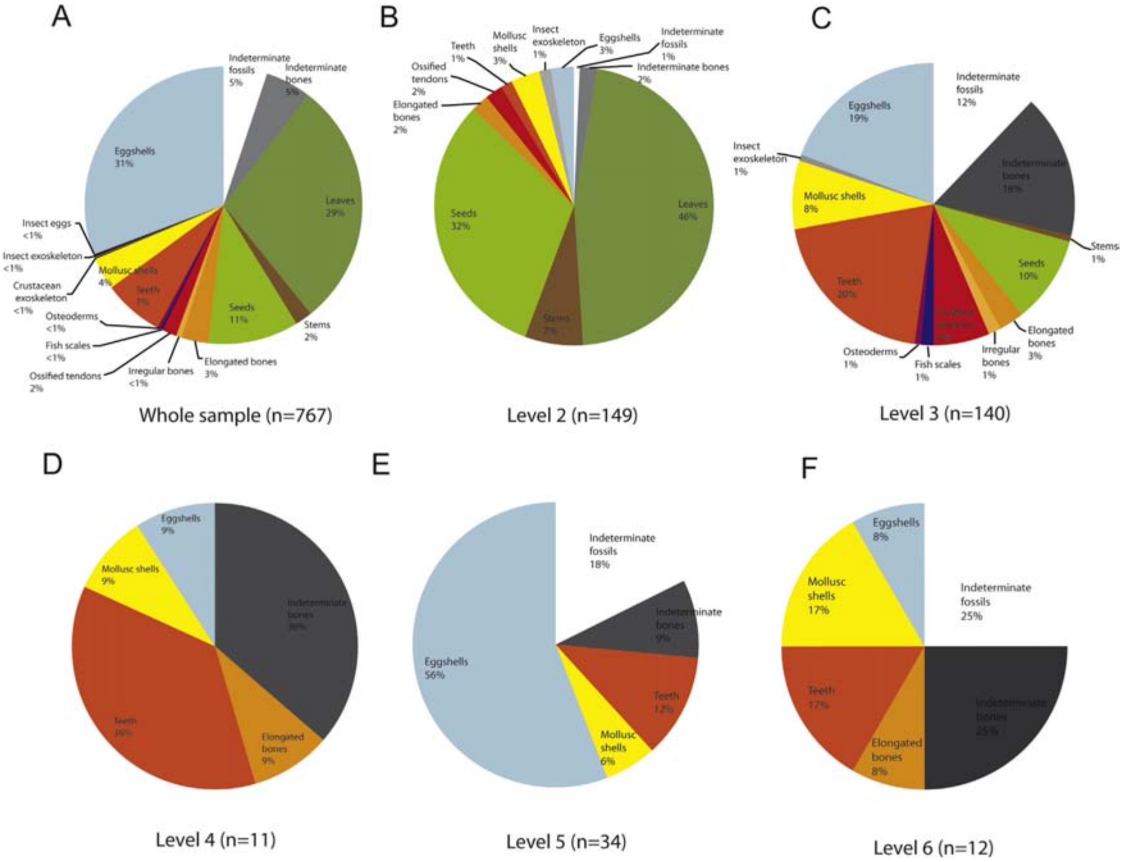

Fig. 11. Relative abundance of types of fossil remains from the Molí del Baró-1 locality. A, The whole sample including all campaigns (2002, 2007, 2010 and 2011). B, Sample collected in 'level 2' during 2010 and 2011. C, Sample collected in 'level 3' during 2010 and 2011. D, Sample collected in 'level 4' during 2010 and 2011. E, Sample collected in 'level 5' during 2010 and 2011. F, Sample collected in 'level 6' during 2010 and 2011.

teeth and bones as well as eggshell fragments, coal and amber (Fig. 11B and C). The sizes range from some hundreds micrometers (charophyte fructifications) or a few millimeters (insect egg, eggshell fragments, some seeds) to large hadrosauroid tibiae, up to 54 cm long, or a large log nearly two meters long. Shapes are also heterogeneous (e.g. spherical to obovoid seeds; small, linear or large, palmate leaves; elongated stems; conical teeth; long and narrow ossified tendons; irregular osteoderms or large, elongated appendicular bones of dinosaurs). Small and linear leaves of *S. gaetei* form massive accumulations in 'level 2' and represent the 62% of the leaf litter (Marmi et al., 2015). Large leaves of the palm *S. longirhachis* are also abundant (17%) in the same horizon. Frequently, the laminae of *Saliciphyllum* and *S. longirhachis* are well-preserved showing fine venation details and, in some cases, bear the petiole attached. The third more abundant leaf type was attributed to a reed-like monocot by Marmi et al. (2015) and form the 11% of the leaf litter. In all cases, the leaves are randomly orientated. Stems are also found in levels '2' and '3'. Among them, there is a large log (180 cm long) that was excavated in the 2002 campaign (A.G. personal observation). Seeds were also found in both levels, yet they are the most abundant plant remain in 'level 3' (Fig. 11C). Charophyte fructifications show contrasting preservations. *P. cancellata* gyrogonites display erosion and fragmentation whilst the delicate superficial characters of *C. brachycerus* utricles are very well-preserved. Large shells of *Lychnus* were recovered from level '2' as well as a delicate elythron and a pronotum of indeterminate Coleopterans (Fig. 5G and H). Fish remains and an anuran tibiofibula (Fig. 7) came from 'level 3'. Crocodylomorph and theropod teeth were collected from 'level 2' and, especially, 'level 3', representing the 25% of the sample. In this latter facies, a complete hadrosauroid tibia was recovered in the 2010 campaign (Fig. 10G and H). Other well preserved crocodylomorph and hadrosauroid bones (Fig. 7F–L, Fig. 10A–B, J) were also excavated in levels '2' or '3' during the 2002 and 2007 campaigns (A.G. personal observations). None of these bones show strong evidence for abrasion or weathering. Hadrosauroid jaws were likely fragmentary when deposited; the small dentary was missing the rostral and caudal ends (Fig. 10A). Some of the vertebrae lack neural arch that it was probably broken before burial. Unidentified, small bone fragments represent the 50–75% of the bone sample from levels '2' and '3' collected during the 2010 and 2011 campaigns. Eggshell fragments from these horizons were collected by in situ picking up and screen-washing. Megaloolithid eggshells recovered from 'level 2' are very small, weathered or coated with calcite. On the other hand, very small fragments of the fragile eggshells of *Prismatoolithus* Zhao and Li 1993, *Pseudogeckoolithus*, and crocodiloids were exclusively recovered from 'level 2'. They have no evidence for erosion.

In the remaining levels, plant remains are lacking. Teeth are locally abundant and bones are strongly fragmented in all cases (Fig. 11D–F). Most megaloolithid eggshells come from 'level 5'. They are relatively large and, in general, well-preserved, showing details of ornamentation and lacking evidence for weathering.

7. Discussion

7.1. Sedimentology and interpretation of the Molí del Baró-1 taphofacies

The sedimentological features described for the entire sandstone lithosome permit to state that the Molí del Baró-1 site, included in both 'Tibia Hill' and 'Tendal 1' sections (Fig. 2), occurs at the uppermost, inner part of a meander loop. Hence, the grey marl would record periods of low energy, when mud accumulated in the meander margins. This situation allowed the formation of small pools in that part of the meander, where the plant and animal remains deposited. The IHS arrangement of the marly and sandy strata observed in the whole sandstone lithosome records an alternation of relatively low and high energy periods of deposition, respectively. Hence, the heterolithic stratification excludes the possibility that Molí del Baró-1 formed within an oxbow lake, as previously thought (Riera, 2010). This last setting would have fine sediment deposition under a static water regime when the meander loop was abandoned (Miall, 1996). The minor non-erosive arenite lenses would represent sporadic arrivals of debris derived from the surrounding floodplains or from the river margin collapse and washout. Carbonate nodules are present in high amounts in the paleosols of the Tremp Formation (Riera et al., 2013), which are broadly developed in the floodplains that surround the channel facies. Hence, the paleosols represent the main source for this component and explain their predominance against the rest of intraclasts in the arenite lenses. These debris supplies could include vertebrate remains and might be generated by processes not linked to the main channel dynamics (e.g. transport and deposition by increasing water discharge). The occurrence of well-preserved planktonic foraminifera in these debris, but also in the floodplain rocks of the Tremp Formation, suggests marine influence in the fluvial settings of the Tremp Formation, according to Díez-Canseco et al. (2014). This is also supported by the presence of celestite into fossil bones from Molí del Baró-1 (Piga et al., 2014). Altogether, the Molí del Baró-1 locality can be envisaged as a result of plant and other organic material accumulation in small meandering rivers during the periods of relative low activity, or cessation of it.

Taphonomical analysis of plant remains from Molí del Baró-1 was carried out by Marmi et al. (2015). Massive accumulation of linear leaves of the willow-like dicot *S. gaetei* suggested that the parent plants grew near the depositional setting and might be important elements of a riparian plant community. This is supported by limited fragmentation of laminae, some of them bearing the petiole attached. *S. longirhachis* leaves also suggest limited transport (Marmi et al., 2015). In addition to leaves, palms were represented by some fragmented stems and possible fruits, suggesting that palm trees also grew up at the edges of the meandering river. The riparian plant community would be also composed of a reed-like monocot. Seeds are diverse in the Molí del Baró-1 site and were likely transported by floatation, from longer distances. Finally, the sporomorph assemblage was mostly allochthonous, since it was mainly composted of wind-pollinated taxa, being representative of regional vegetation (Marmi et al., 2015). The contrasting preservation of charophyte fructifications found in Molí del Baró-1 suggests that *P. cancellata* gyrogonites were reworked from older rocks and transported as a bioclast to the depositional site whilst *C. brachycerus* was an autochthonous element of the assemblage.

Invertebrate and vertebrate portions of the fossil assemblage of levels '2' and '3' included both parautochthonous and allochthonous remains. Gastropods were represented from shell fragments to internal casts of complete shells of the large snail *Lychnus*, these latter suggesting short transport. Delicate exoskeleton elements (pronotum and elythron) of indeterminate coleopterans also suggest some parautochthony. On the contrary, the isolated decapod remains (an incomplete dactyl and a small fragment of carapace) would indicate allochthony because their very low abundance and fragmentary nature. Well-preserved crocodylomorph and hadrosauroid bones (Fig. 7F–L, Fig. 10) suggest that their respective carcasses decayed nearby the depositional setting and some bones suffered only a brief transport to the pond formed at the inner edge of the meander loop (i.e. level '2' and '3'). The absence of deep longitudinal and transverse cracks rules out the possibility of long subaerial exposure before burial in these bones. Based on tooth remains, different crocodylomorph and theropod species would dwell around this fluvial setting. All these teeth but two only preserve just the crown, suggesting that they are shed teeth, so they were detached when the animals were still alive. Crocodylomorphs and theropods likely laid their eggs near the river, as indicated by the presence of small eggshells lacking evidence for neither abrasion nor erosion in 'level 2'. Megaloolithid eggshells were transported far away from possible nesting areas of sauropods. Allochthonous bone fragments and eggshells represented an important portion of fossils collected in 'level 3' and composed most of the assemblage in levels '4', '5' and '6'. This is consistent with the coarser nature of these sediments, especially in the latter levels, indicating more energy flow.

7.2. The plant fossil assemblage from Molí del Baró-1 compared with other localities from the Mastrichtian Iberoarmorican Domain

The plant community from Molí del Baró-1 was reconstructed by Marmi et al. (2015). It consisted of a riparian community mostly composed of a willow-like eudicot (represented by *S. gaetei* leaves), the palm *S. longirhachis* and a likely member of Typhaceae. The plant megafossil assemblage from Molí del Baró-1 differs from that of the lower Maastrichtian of South Isona, which includes conifer twigs, *Sabalites*, likely pandanaceans and at least fifteen dicot form leaves (Marmi et al., 2014). In this neighbouring locality, plant remains deposited in a distal floodplain and revealed some information about plant communities that grew up in the early Maastrichtian fluvial environments of the area. Based on plant megafossils and sporomorphs, Villalba-Breva et al. (2015) suggested that a portion of leaves from South Isona were transported from a source riparian community composed of a likely member of Betulaceae with a diversity of ferns growing up in the understory. According to Marmi et al. (2015) these differences may be due to the true composition of plant communities or taphonomic biases. Plant remains from South Isona were mostly allochthonous (Villalba-Breva et al., 2015).

The sporomorph sample from Molí del Baró-1 is different to those from South Isona in taxonomic composition and taphonomy. In the South Isona locality, spores dominated most of the samples and, in some cases, conifer pollen was more abundant than angiosperm pollen in the remaining sample (Villalba-Breva et al., 2015). On the contrary, angiosperm pollen represents the 83% of the sample collected in Molí del Baró-1 (Marmi et al., 2015). Spore-dominated samples were interpreted as autochthonous by Villalba-

Breva et al. (2015) while bissacate conifer pollen as well as pollen of members of Juglandaceae, Altingiaceae and Ulmaceae (these latter being relatively abundant in the Molí del Baró-1 assemblage, Marmi et al., 2015) are easily transported by wind and would represent regional vegetation.

Charophytes growing in the ponds of the meandering loop of Molí del Baró-1 were exclusively formed by the clavatoracean *C. brachycerus*, which is a very common species in the Maastrichtian of the Iberoarmorican Island, from where it appears to be endemic (Provence, Languedoc, Pyrenees). The palaeoecology of this species is well-known from a study of the lower grey unit by Villalba-Breva and Martín-Closas (2013), showing that this species occurs always in facies representing the lake margins. In the lower red unit of the Vallcebre Basin, Vicente el al. (2015) also reported this species in shallow lakes occurring in the fluvial floodplain. These results fit well with the depositional setting of Molí del Baró-1.

7.3. The vertebrate fossil assemblage of Molí del Baró-1 compared with other localities from the Campanian–Maastrichtian Iberoarmorican Domain

Some rich and diverse fossil assemblages have been reported in fluvial settings from other uppermost Cretaceous localities in Europe. Among them, the upper Campanian–lower Maastrichtian locality of Laño (Basque-Cantabrian Region to the North of the Iberian Peninsula) is one of the best studied to date (Pereda-Suberbiola et al., 2000). Its depositional setting was interpreted as a braided-river system with channels, interchannel pools and sandflats and included a broad diversity of vertebrate taxa with bony fish, amphibians, lizards, snakes, turtles, crocodylomorphs, dinosaurs, pterosaurs and mammals (Astibia et al., 1990; Pereda-Suberbiola et al., 2000). As a whole, some taphonomical features (e.g. wide range of size, dominance of small elements, multispecies vertebrate accumulation, occurrence of both autochthonous and allochthonous elements mixed together) resemble those from the Molí del Baró-1. However, unlike the Molí del Baró-1, the Laño locality included some specimens articulated (e.g. a partially articulated skeleton of an ankylosaur as well as articulated partial turtle shells) (Pereda-Suberbiola et al., 2000). These authors suggested that this fossil assemblage was compatible with a fluvial attritional model (Behrensmeyer, 1991) of sorted remains of both small and large vertebrates, deposited within fluvial channels with a minor influence of moving waters. Although some taphonomical features reported in the Molí del Baró-1 site are compatible with this model, it should be noted that most of the fossil remains come from the marly and arenite facies, that are interpreted as a pool located at the edge of a meander. This would also explain the abundance of plant remains in these facies from Molí del Baró-1 unlike the Laño locality.

Fish and herpetofauna are very poorly represented in the Molí del Baró-1 sample and consist of a few scales assigned to Percomorpha and some appendicular and axial bones of indeterminate anurans. On the contrary, Laño has a variety of bonny fish (lepisosteids, phyllodontids and likely palaeolabrids), amphibians (albanerpetontids, discoglossines, palaeobatrachids) and squamates (scincomorphs, iguanids, anguids or amphisbaenians, mastsoid snakes) (Cavin, 1999; Duffaud and Rage, 1999; Rage, 1999). Herpetofauna remains were also collected from other Maastrichtian sites in the Tremp Formation (L'Espinau, Serrat del Rostiar-1, Serrat del Pelleu, Camí del Soldat and Blasi-2), yielding albanerpetontids (*Albanerpeton* aff. *nexuosum*), four different anurans (palaeobatrachids, pelobatids or gobiatids, discoglossines and alytines), and 7–9 types of squamates (including scincomorphs, iguanids, anguids, snakes and probably gekkotans) (Blain et al., 2010; Blanco et al., this volume). In addition, lepisosteid and semionontiform teeth were also reported from L'Espinau, Serrat del Rostiar-1, Serrat del Pelleu and Camí del Soldat (Blanco and Bolet, 2014). Turtles are also diverse in the Basque locality of Laño including solemydids, bothremydids and dortokids (Lapparent de Broin and Murelaga, 1999). Bothremydid turtles have been also reported in the fluvial settings of the neighbouring upper Maastrichtian locality of Barranc de Torrebilles, also in the Tremp Basin (Marmi et al., 2012a). However, turtles are surprisingly absent in the fossil assemblage of Molí del Baró-1. Different forms of crocodylomorphs and theropod dinosaurs are shared between the Molí del Baró-1 and Laño localities (e.g. *Allodaposuchus* eusuchians and dromaeosaurid theropods) (Pereda-Suberbiola et al., 2000 and present study). In fact, the Molí del Baró-1 would be one of the most diverse crocodylomorph assemblages reported in the Maastrichtian of Europe (Puértolas-Pascual et al., this volume). The ten different morphotypes might represent from seven to nine different species. However, this assumption should be taken with caution, due to the limited diagnostic value of the teeth. In turn, the five morphotypes of theropod teeth might represent about five or six dinosaur species (Table 1). The high number of shed teeth found in Molí del Baró-1 indicates on-site predatory activity by crocodylomorphs and theropod dinosaurs in the form of prey carcass consumption and scavenging (Csiki et al., 2010 and references therein). Regarding other dinosaur groups, ankylosaurs and rhabdodontids are absent in Molí del Baró-1 while hadrosauroid ornithopods are present and represented by at least two forms (a basal hadrosauroid and a lambeosaurine), as it is expected from the diversity patterns inferred in the area during the Maastrichtian (Riera et al., 2009). Although direct remains of sauropods were lacking, megaloolithid eggshells suggest sauropod nesting areas away from the depositional setting. Several upper Campanian–lower Maastrichtian localities from southern France interpreted as fluvial environments share faunal elements with Laño (e.g. lepisosteids, chelonians, ankylosaurs and rhabdodontids) that are not present in Molí del Baró-1 (Table 2, Chanthasit, 2010; Ortega et al., 2015).

The upper Maastrichtian locality of Cassagnau, in southern France, is also among the most diverse in Europe (Laurent et al., 2002). There, two rich vertebrate sites situated in a transition zone between paralic and limnic deposits were reported by these authors. Within osteichthyans, the Cassagnau sites included lepisosteids, phyllodontids and likely sparids. The latter are members of Perciformes and have well-developed ctenoid scales. Like Molí del Baró-1, amphibians are hardly present in Cassagnau but represented by an albanerpetontid instead of anurans. Chelonians and squamates are found in the French locality, unlike the Molí del Baró-1. Crocodylomorphs are diverse in Cassagnau as in the Iberian localities, represented by the longirostrine *Thoracosaurus neocesariensis* Kay 1833, the genus *Musturzabalsuchus* Buscalioni et al., 1997 and many other remains referred to indeterminate crocodylomorphs (Laurent et al., 2002). However, *Thoracosaurus* Leidy 1852 and *Musturzabalsuchus* are lacking in the crocodylomorph sample from Molí del Baró-1. Dromaeosaurid-like theropods, titanosaurian sauropods and hadrosauroids are represented by teeth and bones in the French locality, being hadrosauroid remains the most abundant (Laurent et al., 2002). Other upper Maastrichtian localities from southern France are known from shallow marine to continental settings (Buffetaut et al., 1997). Peyrecave and Tricouté, also in the Petites Pyrenees, are very close to Cassagnau and belong to the same formation (Auzas Marls) (Table 2). Unlike, Molí del Baró-1, Peyrecave has yielded several chondrichthyan taxa, suggesting stronger marine influence, as well as indeterminated teiid lizards and likely therian mammals (Gheerbrant et al., 1997). It is interesting to note that, up to now, mammalian remains have never been found in the transitional to continental beds of the Tremp Formation. It is also remarkable the presence of nodosaurid

Table 2
Vertebrate taxa represented in the upper Campanian–Maastrichtian from the Iberian Peninsula and southern France compared with the Molí del Baró-1 site. Data from Lo Hueco (Ortega et al., 2015), Laño (Pereda-Suberbiola et al., 2000), Lestaillats (Laurent et al., 1999), Peyrecave (Gheerbrant et al., 1997), Cassagnau (Laurent et al., 2002), Molí del Baró-1 (this study).

Taxa	Late Campanian–early Maastrichtian		Late Maastrichtian			
	Lo Hueco (Cuenca, Spain)	Laño (Burgos, Spain)	Lestaillats (Petites Pyrénées, France)	Peyrecave (Petites Pyrénées, France)	Cassagnau (Petites Pyrénées, France)	Molí del Baró-1 (Catalonia, Spain)
Chondrichthyes			**X**	**X**		
Triakidae				X		
Rhinobatidae				X		
Rhombodontidae				X		
Dasyatoidae				X		
Osteichthyes	**X**	**X**	**X**	**X**	**X**	**X**
Albulidae	X					
Amiidae	X					
Lepisosteidae	X	X	X		X	
Palaeolabridae		X				
Phyllodontidae		X	X		X	
Pycnodontoidea	X					
Sparidae			?		?	
Amphibia		**X**		**X**	**X**	**X**
Albanerpetontidae		X			X	
Discoglossidae		X				
Palaeobatrachidae		X				
Chelonia	**X**	**X**	**X**		**X**	
Solemydidae		X				
Bothremydidae	X	X			X	
Dortokidae		X				
Squamata	**X**	**X**		**X**	**X**	
Iguania	X	X				
Lacertoidea indet.	X					
Scincomorpha		X				
Amphisbaenia		X				
Varanoidea indet.	X				X	
Madtsoidae		X				
Crocodylomorpha	**X**	**X**	**X**	**X**	**X**	**X**
Mesoeucrocodylia		X				
Atoposauridae						X
Thoracosaurus					X	
Allodaposuchia	X	X				X
Acynodon		X				
Musturzabalsuchus		X			X	
Ornithopoda	**X**	**X**	**X**		**X**	**X**
Rhabdodontidae	X	X				
Hadrosauridae		X				X
Thyreophora		**X**	**X**			
Nodosauridae		X	X			
Theropoda	**X**	**X**	**?**		**X**	**X**
Neoceratosauria	X	X				
Dromaeosauridae	X	X	?		X	X
Richardoestesia	X					?
Paronychodon	X					?
Euronychodon		X				?
Ornithomimosauria		X				
Sauropoda	**X**	**X**			**X**	**X**
Titanosauridae	X	X			X	X
Pterosauria		**X**				
Azhdarchidae		X				
Eutheria		**X**		**X**		
Zhelestidae		X				

For each group of vertebrates, the most inclusive taxon is marked in bold.

ankylosaurs in the shallow marine to marshy beds of Lestaillats, in the same area (Laurent et al., 1999). Upper Maastrichtian fluvial beds outcrop in the eastern Corbières in the northeastern Pyrenees. There, the Montplaisir site yielded remains of turtles, eusuchian crocodilomorphs, pterosaurs and hadrosauroid dinosaurs (Le Loeuff et al., 1994).

Several factors may explain the differences in composition of vertebrate fossil assemblages among these localities. As it is expected, the presence of ankylosaurs and rhabdodontids in Laño and hadrosauroids in Molí del Baró-1 and Cassagnau is consistent with the turnover of plant-eating dinosaur faunas around the early and late Maastrichtian Iberoarmorican Island (Riera et al., 2009 and references therein). Other differences may be due to environment (fluvial in Laño and Molí del Baró-1 versus paralic to limnic in Peyrecave or Cassagnau) or taphonomy (e.g. differential preservation, mode of concentration or accumulation, size-selection during transport). For instance, the microfossil samples from Molí del Baró-1 and Cassagnau are much less diverse than the ones of Laño, L'Espinau or Serrat del Rostiar-1, with herpetofauna elements almost absent in the two former localities.

8. Conclusions

The Molí del Baró-1 site represents an exceptional locality from the upper Maastrichtian of Europe. In addition to a diverse vertebrate fossil assemblage, this locality includes abundant plant remains that have allowed to reconstruct a riparian community exclusively dominated by angiosperms and a hydrophytic community formed by one of the last clavatoracean charophytes. Insect remains are reported for the first time in the Maastrichtian Iberian Peninsula, and consist of a pronotum and elythron of indeterminate coleopterans and an indeterminate insect egg. The vertebrate assemblage is very poor in herpetofauna and fish with only a few remains of anurans and possible percomorphs. Crocodylomorphs are well represented by teeth and bones revealing evidence for atoposaurids, ziphodontids and eusuchian allodaposuchians. Dinosaurs include a variety of theropods and hadrosauroid ornithopods as it is expected for this area and timespan. Most of plant and vertebrate remains are interpreted as deposited in a pool at the edges of a meander. Some bones were shortly transported from disarticulated carcasses nearby the depositional setting. Others were fragmentary and likely allochthonous. Based on taphonomical evidence, fluvial-to-tidal environments nearby the depositional setting were inhabited by hadrosauroids and a variety of crocodylilomorphs and theropods feeding on prey carcasses or scavenging. Theropod nesting areas might also be nearby the depositional setting while nesting areas of sauropods were located far away.

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THE FOSSIL RECORD OF THE UPPERMOST MAASTRICHTIAN REPTILE SANDSTONE (TREMP FORMATION, NORTHEASTERN IBERIAN PENINSULA)

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Mi contribución en este trabajo consistió en la participación en las prospecciones que se realizaron en el nivel de la Arenisca con Reptiles de las localidades estudiadas, durante dos campañas de campo (2012 y 2013), así como en la recogida del material y extracción de pequeñas muestras de sedimento para procesar y buscar fósiles de microvertebrados. Tras dicho procesamiento, los niveles muestreados resultaron estériles. Llevé a cabo la clasificación taxonómica y descripción del material perteneciente a cocodrilos, terópodos y ornitópodos. Participé activamente en el diseño y redacción de la mayor parte de secciones del artículo (Introducción, Paleontología Sistemática, Discusión y Conclusiones).

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The fossil record of the uppermost Maastrichtian Reptile Sandstone (Tremp Formation, northeastern Iberian Peninsula)

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ABSTRACT

Numerous localities with vertebrate remains, including dinosaurs (sauropods, ornithopods, theropods and ankylosaurs), crocodiles and turtles, are known in the Arén and Tremp Formations (Maastrichtian, northeastern Iberian Peninsula). This diverse fossil record is improving our understanding of the history of the latest Mesozoic faunas in Europe. A conspicuous 7 meter thick sandstone and/or microconglomerate level (the so called Reptile Sandstone) occurs near the top of the 'lower red unit' of the Tremp Formation, about 10 meters below the base of the 'Vallcebre limestone', which is Danian in age. Bone remains and ichnites are known in the Reptile Sandstone, and represent one of the youngest vertebrate records in the Maastrichtian of the Tremp Formation. New findings carried out in north Barcelona province complement the fossil assemblage of the Reptile Sandstone with turtle, crocodile, theropod and possible sauropod remains in addition to hadrosaurs.

Keywords: Late Maastrichtian, Tremp Formation, Reptile Sandstone.

RESUMEN

Numerosas localidades con restos de vertebrados, que incluyen dinosaurios (saurópodos, ornitópodos, terópodos y anquilosaurios), cocodrilos y tortugas, son conocidas en las Formaciones Arén y Tremp (Maastrichtiense, noreste de la Península Ibérica). Este diverso registro fósil está mejorando de forma notable nuestro conocimiento sobre la historia de las últimas faunas mesozoicas en Europa. Cerca del techo de la unidad roja inferior de la Formación Tremp, se encuentra una capa conspicua de areniscas y/o microconglomerados de unos siete metros de potencia, la cual se conoce como la Arenisca con reptiles. Su localización estratigráfica exacta es de unos 10 metros debajo de la base de la Caliza de Vallcebre, que es de edad Daniense. Los restos óseos y las icnitas son conocidos en la Arenisca con reptiles, los cuales representan uno de los registros más recientes de vertebrados de la sección maastrichtiense de la Formación Tremp. Nuevos hallazgos realizados en el norte de la provincia de Barcelona complementan el registro fósil de la Arenisca con reptiles con restos de tortugas, cocodrilos, terópodos y posibles saurópodos, además de hadrosaurios.

Palabras clave: Maastrichtiense superior, Formación Tremp, Arenisca con reptiles.

1. INTRODUCTION

In the southern Pyrenees, marine-transitional to fully continental rocks of the Arén Sandstone and Tremp Formations (Maastrichtian-Thanetian) (Mey *et al*., 1968) have yielded a diverse vertebrate fauna with fishes, amphibians, squamates, turtles, crocodiles and dinosaurs (Riera *et al*., 2009; Marmi *et al*., 2012a). The Tremp Formation is widely exposed from the Vallcebre syncline (north Barcelona province, Catalonia, Spain) to the Huesca province (Aragón, Spain) and encompass the Cretaceous-Palaeogene boundary (K-Pg). Research works carried out over the last decades have considerably improved our knowledge on the diversity of some groups of dinosaurs that inhabited the Pyrenean region during the last 6 millions of years before the end-Cretaceous mass extinction (Riera *et al*., 2009; Vila *et al*., 2012, 2013). However, the diversity of other groups of vertebrates is partially known (Marmi *et al*., 2012a).

Within the Maastrichtian portion of the Tremp Formation, those localities closest to the K-Pg boundary are of great interest. The precise position of the K-Pg boundary is not fixed in the Tremp Formation. However, in the Vallcebre syncline, charophyte biostratigraphy (Feist & Colombo, 1983) and magnetostratigraphy (Oms *et al*., 2007) suggest that the K-Pg boundary is located within a less than 10 meters thick pale red mudstone over a conspicuous sandstone and/or conglomerate level (the Reptile Sandstone of Masriera & Ullastre, 1982) and beneath the Vallcebre limestone, which is of Danian age. The Reptile Sandstone crops out in numerous localities in the Vallcebre and Àger synclines and occurs within the magnetochron C29r (Galbrun *et al*., 1993; Oms *et al*., 2007). In the Pyrenees, some of the youngest records of dinosaurs have been reported in the Reptile Sandstone beds and consist of fragmentary bones (Masriera & Ullastre, 1983; Ullastre & Masriera, 1998; Pereda-Suberbiola *et al*., 2003) and footprints (Vila *et al*., 2013). Up to now, very few authors have paid attention on the description of vertebrate fossils from the Reptile Sandstone except Pereda-Suberbiola *et al*. (2003), who described a distal epiphysis of a right femur assigned to an indeterminate hadrosaurid, and Vila *et al*. (2013), who reported hadrosaur footprints.

In this paper, new vertebrate remains from the Reptile Sandstone exposed in several localities of the Berguedà region (north Barcelona province) are described. In addition, their relevance to the uppermost Maastrichtian fossil record of the Tremp Formation is discussed.

2. GEOLOGICAL SETTING

The Tremp Formation (south-central and southeastern Pyrenees) (Mey *et al*., 1968) consists of Maastrichtian to Thanetian materials deposited in an E–W foreland trough connected to the Atlantic Ocean, which was close to the boundary between the Iberian and European plates. It is also informally known as 'Garumnian' (Leymerie, 1862). The Tremp Formation sediments were deposited following a marine regression that began near the Campanian–Maastrichtian transition (Oms *et al*., 2007 and references therein). After the uplift of the Pyrenean range, these deposits were separated into four synclines: Vallcebre, Coll de Nargó, Tremp and Àger from the east to west. The Tremp Formation was divided into four lithologic units by Rosell *et al*. (2001), which are from the base to the top: i) a transitional 'grey unit' (marls, coals, limestones, and sandstones), ii) a fluvial 'lower red unit' (mudstones, sandstones, oncoids, and palaeosols), iii) the lacustrine 'Vallcebre limestone' and laterally equivalent strata and, iv) a fluvial 'upper red unit' (mudstones, sandstones, conglomerates and limestones). According to charophyte biostratigraphy (Feist & Colombo, 1983) and magnetostratigraphy (Oms *et al*., 2007), the two former units are Maastrichtian in age whereas the two later are Palaeocene.

The Reptile Sandstone, 7 m thick, occurs near the top of the 'lower red unit', about 7-10 m below the base of the Danian 'Vallcebre limestone' (Figs 1b-c). The Reptile Sandstone (Facies F10 in Oms *et al*., 2007) is composed of texturally and lithologically mature sediments (i.e., coarse-grained sandstones and microconglomerates rich in feldspars) displaying medium and large-scale cross-bedding (Fig. 2). These features, together with the lenticular cross-bedded sandstones, the scarce mudstone interbeds and the absence of fining-up sequences and lateral accretion surfaces suggest deposition on braided streams under high-energy hydric regime (Oms *et al*., 2007). The Reptile Sandstone represents a period of high-energy flow in the basin and marks a change in the sedimentation regime from a previous muddy flood plain to a sandy braidplain. In the southern Pyrenees, this facies can be traced all over the Pedraforca thrust sheet (Oms *et al*., 2007) and in the Àger syncline, where it is eight meters thicker (Astibia *et al*., 2012). The Reptile Sandstone can be correlated with similar French Galante and Fleurie sandstone units and in all cases provenance is from the south and southwest extant massifs of Sardinia (Westphal & Durand, 1990) and Ebro (Masriera & Ullastre, 1982).

In the Vallcebre syncline, Feist & Colombo (1983) located the K-Pg boundary in the mudstone separating the Reptile Sandstone and the base of the 'Vallcebre limestone', at the last occurrence of non-reworked *Peckichara sertulata*. Oms *et al*. (2007) found a strong correlation between polarities inferred from the Vallcebre section and the magnetic polarity time scale of Cande & Kent (1995), from C32n.1n to C29r magnetochrons. Accordingly, these authors inferred a constant sediment accumulation rate of 77 m/Ma through most of the

Maastrichtian section in the Vallcebre syncline. Assuming this value, the Reptile Sandstone deposited between 130 and 220 ka before the K-Pg boundary.

3. MATERIALS AND METHODS

In October-November 2012 and April-June 2013, we conducted prospecting works in several localities at the north Barcelona province (localities 1 to 4 in Fig. 1a). Bone remains were collected from several exposures of the Reptile Sandstone. They consisted of bone fragments attributed to dinosaurs, partial, isolated plates belonging to turtles and a crocodile tooth. The material was restored by technicians from the Institut Català de Paleontologia Miquel Crusafont. Specimens preserving some diagnostic features were described and compared with published material from the Maastrichtian of southern Pyrenees. Unpublished specimens housed at the Museu Municipal de Berga from El Torrent del Jou (locality 5 in Fig. 1a) were also described and compared. All of them were photographed with digital camera and details were photographed under Leica EZ4D stereomicroscope integrating digital camera. Measurements were made on the pictures using the freeware ImageJ v. 1.40g (Rasband, 1997-2008). The distal fragment of an hadrosaur femur reported by Pereda-Suberbiola *et al*. (2003) from Peguera (locality 6 in Fig. 1a) and footprints reported by Vila *et al*. (2013) from Cingles del Boixader (locality 7 in Fig. 1a) were not described in the present work. However, these specimens were taken into account in order to complete the database of the fossil record of the Reptile Sandstone. Studied material is stored in the collections of the Institut Català de Paleontologia Miquel Crusafont and Museu Municipal de Berga.

4. GENERAL COMMENTS ON TAPHONOMY

Vertebrate fossils are usually isolated and sparse through the Reptile Sandstone. Fossils occurred in different horizons at the most extended exposures (e.g., locality 2, Cingles de Cal Ros, Fig. 1c), but in several cases they were found in detached rough stones at the base of Reptile Sandstone cliffs or in small exposures of the Reptile Sandstone. This made difficult a precise stratigraphic correlation between fossil-bearing horizons belonging to different exposures or localities of the Reptile Sandstone. On the other hand, the lithological composition of the Reptile Sandstone is heterogeneous ranging from sandstones to microconglomerates, with oncolite layers interbedded, indicating heterogeneity of sedimentary environments. In this sense, only a general description on the state of preservation of vertebrate fossils from the Reptile Sandstone and the implications on taphonomy is provided.

A total of 44 bone remains and a tooth from the Reptile Sandstone were documented in the present fieldwork and previous studies (e.g., Pereda-Suberbiola *et al*., 2003). Due to their fragmentary nature and bad preservation, many remains (56 %) were classified as indeterminate. However, the remaining samples reveal a diversity of elements including a crocodile tooth, turtle plates (plastron and carapace) and bones attributed to dinosaurs. Turtles and dinosaurs represent the 27 % and 15 % of the sample respectively. Remains attributed to dinosaurs consisted of one transverse apophysis of a vertebra and several appendicular bones (two partial ischia, one epiphysis and one diaphysis belonging to two femora and some undetermined diaphyses). Fossils mostly appeared in coarse matrices (i.e., microconglomerate) showing a wide range of sizes, from less than one centimeter fragments (Fig. 2a) to a partial hadrosaur femur 45 cm long (Figs 2g-h, 6). However, most bones consisted of small sized fragments (74 % of the sample was less than 3 cm^2) with clear evidence of weathering and abrasion (Figs 2b, d, f-h). Largest bones were heavily damaged with the medullar cavity sometimes infilled by the same sediment than the matrix (Figs 2h, 6). Some bones were covered by oncoids (Fig. 2c). All these evidence suggest that, as a rule, bone remains from the Reptile Sandstone were probably largely exposed and transported far away before their burial. This is consistent with sedimentology, which indicates deposition under a high-energy hydric regime (Oms *et al*., 2007). The only autochthonous remains of the Reptile Sandstone correspond to hadrosaur tracks (*Hadrosauropodus*) from the Cingles de Boixader locality (Fig. 1, Vila *et al*., 2013).

5. SYSTEMATIC PALAEONTOLOGY

Order CHELONII Latreille, 1800
Chelonii indet.
(Figs 3a-d)

Material. IPS-81874, IPS-81875.

Locality. Cingles de Cal Ros (Cercs, Barcelona).

Description. Both specimens consist of fragments of turtle plastrons. IPS-81874 (Fig. 3a) probably corresponds to a left side fragment of a plastron including the bridge and the inguinal notch. It measures 11 cm long and 5.8 cm wide. The inguinal notch opening is slightly obtuse (95.3º).

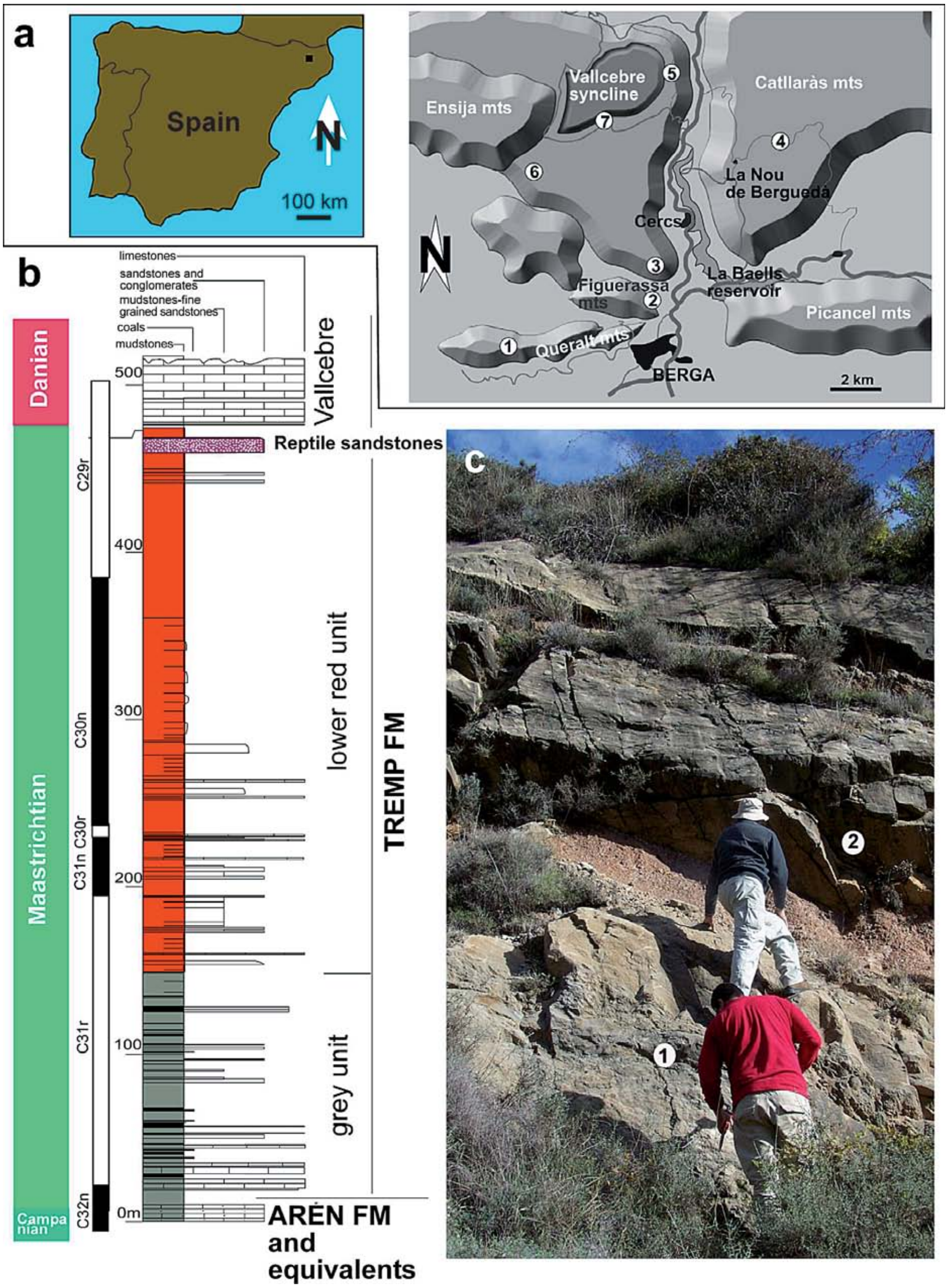

Figure 1. Geographical and geological setting of the studied area. **a)** Geographical location of the Reptile Sandstone outcrops where studied fossils were found: 1, El Portet; 2, Cingles de Cal Ros; 3, Tossal de la Guàrdia; 4, Cingles de la Creueta; 5, Torrent del Jou; 6, Peguera; 7, Cingles de Boixader. **b)** Synthetic section of the Tremp Formation from the Vallcebre syncline showing the location of the Reptile Sandstone (modified from Vila *et al*., 2005). **c)** Picture of the Reptile Sandstone outcropping at the Cingles de Cal Ros locality showing the horizons where two isolated bone remains were found: 1, small bone fragment from an oncoid level (see Fig. 2a); 2, fragment of an hadrosaur femur (see Fig. 6).

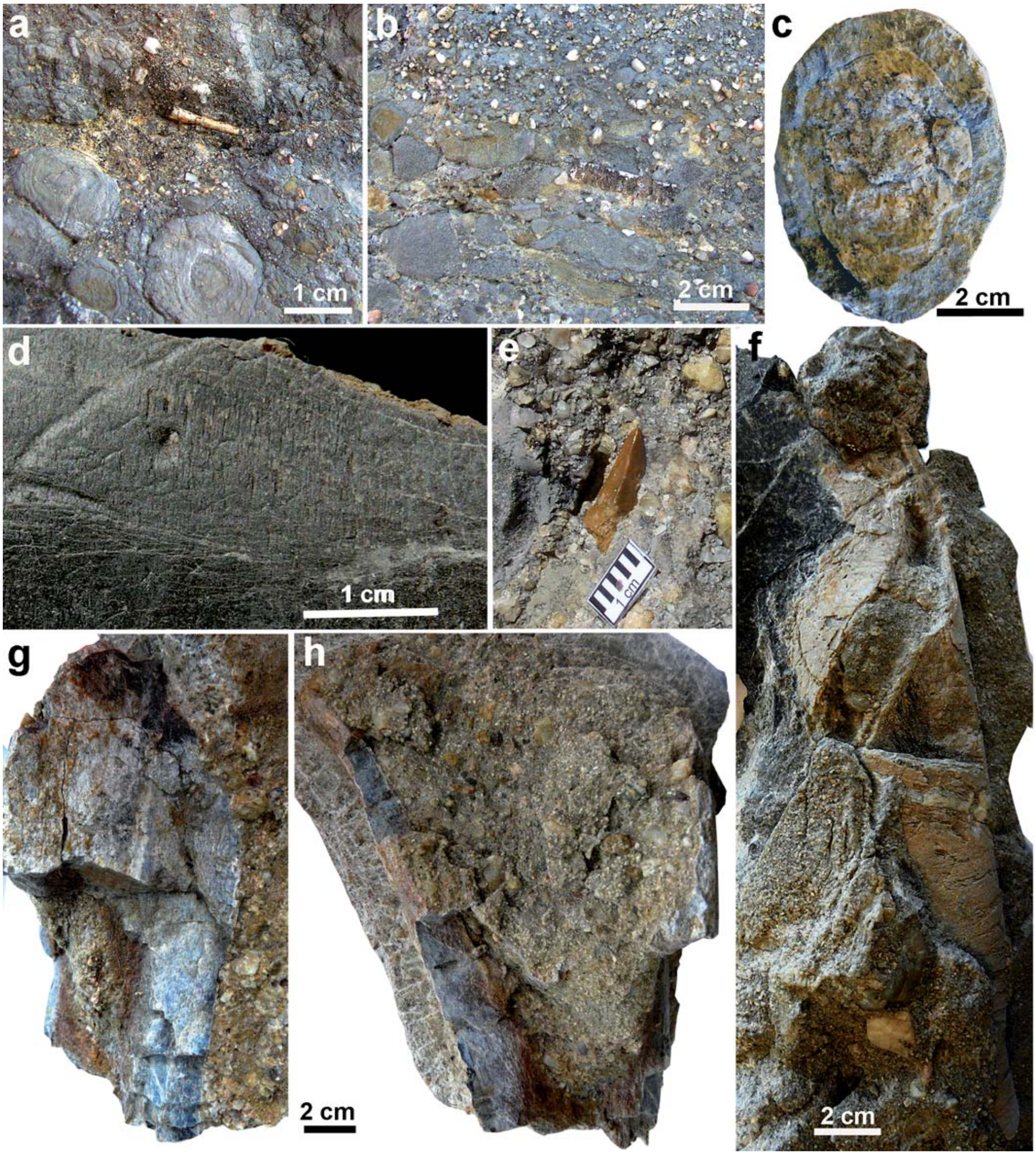

Figure 2. Examples of preservation in fossils from the Reptile Sandstone. **a)** Tiny bone in coarse-grained siliciclastic hybrid arenites rich in feldspars including oncoids. **b)** Section of a turtle plate in the transition from conglomerates to sandstones. **c)** Section of a bone covered by an oncoid. **d)** Detail of a turtle plate (see Fig. 3e for details) showing marks of abrasion. **e)** Crocodyle tooth (see Fig. 4 for details) within a microconglomerate matrix (scale equals 1 cm). **f)** Elongated bone showing clear evidence of weathering and abrasion. **g)** Fragment of an hadrosaur femur (see Fig. 6 for details) included in a microconglomerate matrix. **h)** Another view of the same specimen showing the medullar cavity infilled by microconglomerate.

IPS-81875 (Figs 3b-d) is flat and trapezoid in shape. It might correspond to a hyoplastron or hypoplastron based on the straight edge, which is interpreted as the hyo-hypoplastron suture, and the absence of pelvic girdle scar marks in the inner side. The edge opposite to the hyo-hypoplastron suture is strongly weathered. The bone is wider (5.5 cm) than longer (4.6 cm) and slender in section (0.4 cm).

Infraorder PLEURODIRA Cope, 1864
Family **Bothremydidae** Baur, 1891
Bothremydidae indet.
(Figs 3e-f)

Material. IPS-81876.

Locality. Cingles de Cal Ros (Cercs, Barcelona).

Description. It corresponds to the first right peripheral plate of a turtle carapace (Fig. 3e). It is trapezoid in shape and measures 7.9 cm long and 5.5 cm wide. The anterior edge is longer (5.2 cm) than the posterior (3.1 cm). The sulcus between marginals 1 and 2 and the first vertebral scute is almost straight and not reaches the suture between peripheral 1 and costal 1. The sulcus between first and second marginals is partially preserved. The surface is smooth and ornamented with very fine sulci, dichotomized and sometimes united forming small polygons (Fig. 3f).

Comparison. The well developed net consisting of dichotomic sulci suggests a highly vascularized shell bones. This feature has been used to recognize shell material of the Bothremydidae (e.g., Lapparent de Broin & Murelaga, 1996; Murelaga & Canudo, 2005). Elongated peripheral 1 with short posterior margin has been observed in bothremydids from the Campanian-Maastrichtian of the Pyrenees, such as *Elochelys convenarum* (Laurent *et al*., 2002), *Foxemys mechinorum* (Tong *et al*., 1998), *Polysternon provinciale* Matheron, 1869 (Gaffney *et al*., 2006) and *P. isonae* (Marmi *et al*., 2012b). In *Elochelys* and *P. provinciale*, the first pleural scute partially reaches the posterior end of the first peripheral, unlike the IPS-81876, *Foxemys* and *P. isonae*. In *P. isonae*, the marginal scutes cover almost all the surface or the first peripheral (Marmi *et al*., 2012b). However, in the studied specimen, marginals are shorter and the posterior third of the first peripheral is covered by the anterior edge of the first vertebral scute, as in *F. mechinorum*. The suture between the marginals and the first vertebral scute is almost straight in the IPS-81876 and *F. mechinorum* but it is curved in *Polysternon* species.

Order CROCODYLIFORMES Hay, 1930 (*sensu* Benton & Clark, 1988)
Suborder EUSUCHIA Huxley, 1875
Unranked CROCODYLIA Gmelin, 1789 (*sensu* Benton & Clark, 1988)
(Figs 4a-e)

Material. IPS-81877.

Locality. Cingles de la Creueta (La Nou del Berguedà, Barcelona).

Description. Conical tooth, with high crown, acute apex, and subcircular section (Fig. 4). It measures 1.71 cm in height and 0.8 cm wide and it is slightly labiolingually compressed (Fig. 4b). The tooth shows two well-developed mesodistal keels that converge at the apex. They are limited on the lingual side by two longitudinal grooves (Fig. 4c). The tooth is very slightly sloping towards the lingual side. The enamel is very smooth, without ornamentation, although fine ridges can be observed, under magnification, next to the mesodistal carinae, conforming a very soft false ziphodont dentition (Fig. 4d).

Comparison. This tooth lacks denticles and lateral compression, property of true ziphodont dentition. Based on the absence of these features, its inclusion within ziphosuchians can be rejected. The tooth morphology and size are similar to those described in Campanian-Maastrichtian eusuchians from the Iberian Peninsula, such as *Musturzabalsuchus* and *Allodaposuchus*. The IPS-81877 shares with teeth attributed to these genera the following characters: conical shape with labiolingual compression and mesodistal keels or carinae limited by two prominent vertical grooves in the lingual side (Buscalioni *et al*., 1997, 2001; Delfino *et al*., 2008; Puértolas-Pascual *et al*., 2013). However, unlike IPS-81877, *Musturzabalsuchus* teeth show crown surfaces profusely ridged with the margins crenulated (Buscalioni *et al*., 1997, 1999). In *Allodaposuchus*, the enamel may be ridged (Delfino *et al*., 2008; Blanco *et al*., 2014), delicately wrinkled (Buscalioni *et al*., 2001) or smooth (Puértolas-Pascual *et al*., 2013). The species *A. palustris* (Blanco *et al*., 2014) has false ziphodont teeth but, unlike IPS-81877, their enamel is completely ridged. On this basis, the tooth herein described might correspond to a member of the genus *Allodaposuchus*.

Order SAURISCHIA Seeley, 1887
Suborder THEROPODA Marsh, 1881a
Theropoda indet.
(Figs 5a-b)

Material. IPS-81878.

Locality. Cingles de Cal Ros (Cercs, Barcelona).

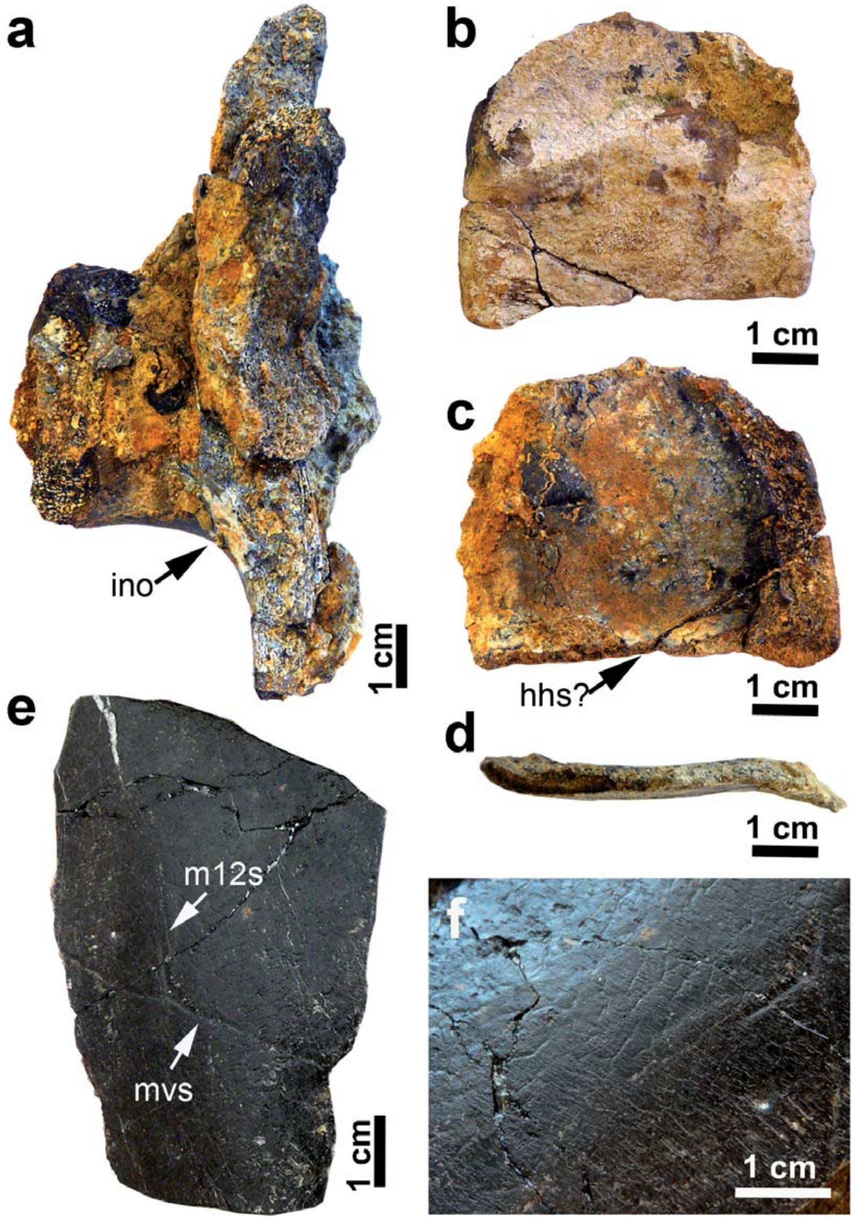

Figure 3. Turtle remains from the Cingles de Cal Ros. **a)** Fragment of a plastron showing the bridge and the inguinal notch (ino) (IPS-81874). **b, c, d)** Possible hyoplastron or hypoplastron (IPS-81875) in ventral, dorsal and transversal views, respectively, indicating the likely hyo-hypoplastron suture (hhs?). **e)** Peripheral plate of a bothremydid (IPS-81876) indicating the sulci between marginals 1 and 2 (m12s) and between the marginals and the first vertebral scute (mvs). **f)** Detail of the previous picture showing fine dichotomized sulci.

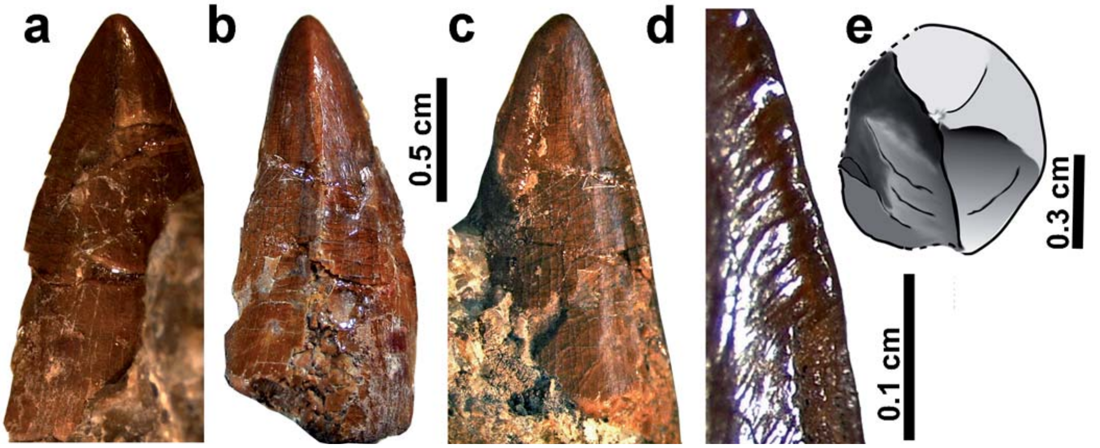

Figure 4. Crocodile tooth (IPS-81877) from Cingles de la Creueta. **a)** Labial view. **b)** Lateral view showing the carina. **c)** Lingual view showing longitudinal grooves. **d)** Detail of the lateral carina showing a very soft false ziphodont dentition. **e)** Drawing in apical view showing the outline of the section and carinae.

Description. It is a small long bone that only preserves the diaphysis (Fig. 5a). It measures 3.96 cm long and 0.49 cm wide. It has a subcircular section with a slim cortical bone (0.015 cm in section) (Fig. 5b). The high vascularisation is patent in the broken end (Fig. 5b). There is a nutritional foramen in the medial part of the bone (Fig. 5a).

Comparison. The bone is difficult to classify due to it only preserves the diaphysis. However, the high vascularisation, the thin cortical bone, the elongated shape, the subcircular section and the presence of a nutritional foramen are shared with limb bones (e.g., ulna and humerus) of theropod dinosaurs. Although, the size of the bone is similar to those of small-sized theropods or birds, more diagnostic material is needed to confirm the presence of these dinosaurs in the Reptile Sandstone.

Order ORNITHISCHIA Seeley, 1887
Suborder ORNITHOPODA Marsh, 1881b
Family **Hadrosauridae** Cope, 1869
Hadrosauridae indet.
(Figs 6a-d)

Material. IPS-81879.

Locality. Cingles de Cal Ros (Cercs, Barcelona).

Description. The specimen consists of a robust long bone, broken at both ends. It measures 45 cm long and preserves the diaphysis, which measures 7.96 cm wide, and the basalmost part of the proximal epiphysis (Fig. 6a). The bone is interpreted as a right femur exposed in posterior view. The end of the proximal epiphysis is eroded, and no femur head is preserved. The base of the fourth trochanter can be observed, but it is not complete (Figs 6a-b). A wide, deep, longitudinal groove is present (Figs 6 a-b) from the

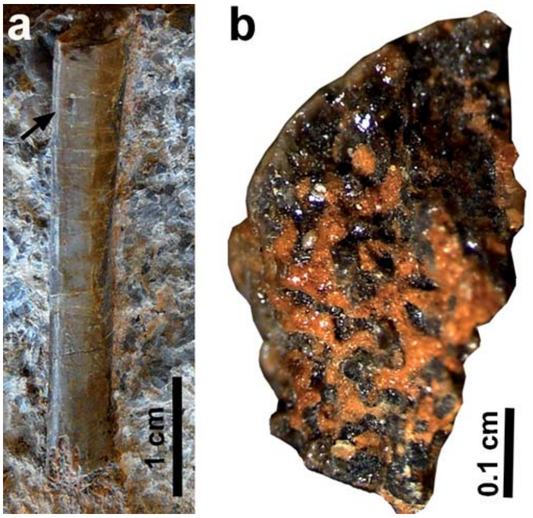

Figure 5. a) Diaphysis of a limb bone attributed to a theropod dinosaur (IPS-81878) from Cingles de Cal Ros. The nutritious foramen can be observed in the upper part of the bone (arrowed). **b)** Cross-section of IPS-81878 showing a very thin cortical bone.

forth trochanter to the distal end of the preserved diaphysis, and could be the posterior intercondylar groove in the distal epiphysis (Figs 6a-c). The distal epiphysis is eroded, and no description is possible for the distal condyles or the anterior intercondylar groove for the *ilio-tibialis* tendons.

Comparison. Although the bone is broken and eroded, the general shape is preserved, and it is different from that of a sauropod limb bone. On the other hand, the cortical bone is thicker (1.32 cm) (Fig. 6d) than it is expected in a theropod limb bone. Tyreophora dinosaurs are no present throughout the entire stratum. Thus, all these evidence and general description suggest that this specimen correspond to an hadrosaurid limb bone. Hadrosaur bone remains are known in the Reptile Sandstone level. Pereda-Suberbiola *et al*. (2003) cited a right distal femur and Vila *et al*. (2013) described hadrosaur footprints in the Reptile Sandstone outcropping at the neighboring localities of Peguera and Cingles del Boixader, respectively. The deep longitudinal groove below the forth trochanter of the specimen herein studied has been observed in other hadrosauroid femora from Maastrichtian sites in the Pyrenees such as MPZ2007/933 from Blasi (fig. 2f in Cruzado-Caballero *et al*., 2009), and an uncoded specimen from Magret (fig. 16.4s in Dalla-Vecchia *et al*., 2014a). This latter specimen is similar in outline and size to the partial femur IPS-81879

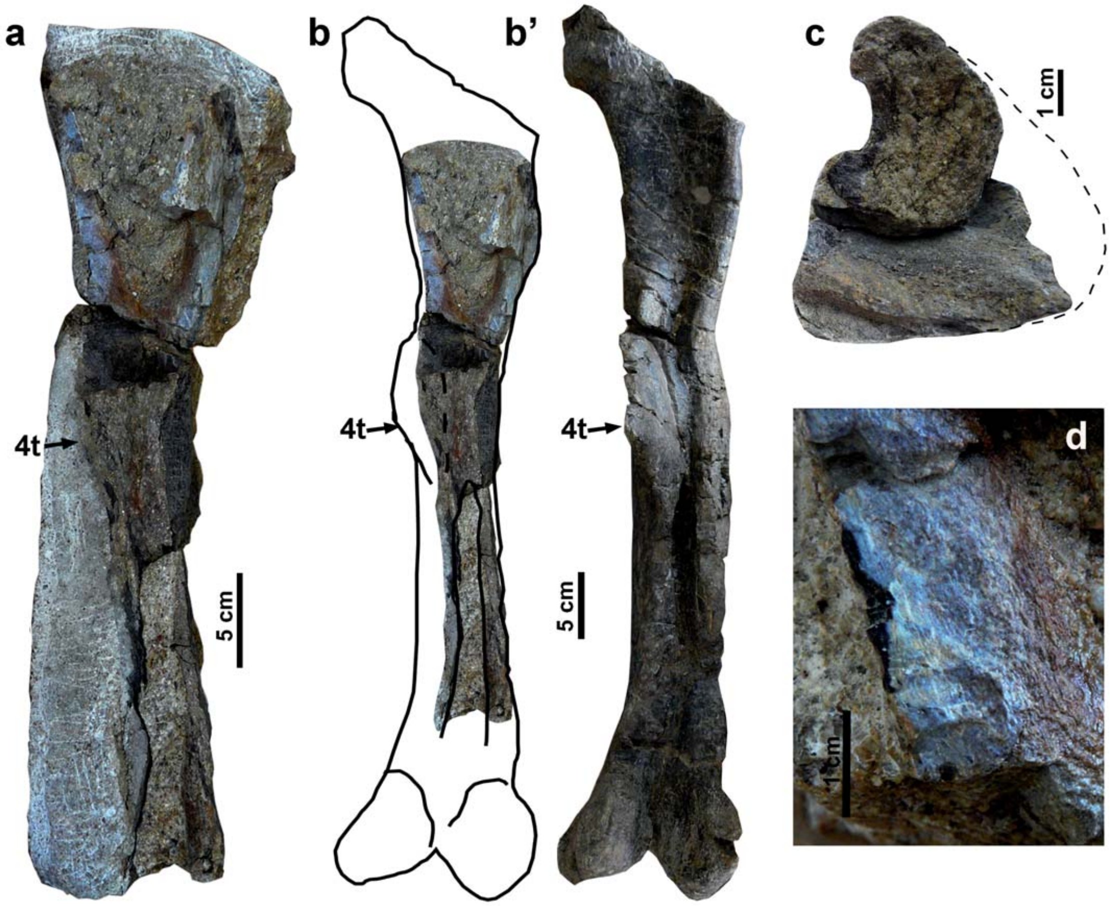

Figure 6. Partial hadrosaur femur (IPS-81879) from Cingles de Cal Ros. **a)** Posterior view of the fossil within the rock matrix. The base of the fourth throcanter (4t) is preserved and the deep longitudinal groove between the fourth throcanter and the condyles is clearly visible. **b)** Outline of an hadrosaur femur from the upper Maastrichtian locality of Magret (Tremp syncline), figured in **b'** and Dalla Vecchia *et al*. (2014a, fig. 16.4s), including IPS-81879 for its interpretation. **c)** Cross section of the distal end of IPS-81879 showing the outline of the longitudinal groove (left). **d)** Detail of the thick bone cortex in the proximal end of IPS-81879.

(Fig. 6b-b'). The diaphysis of IPS-81879 is wider (~ 8 cm) compared to the specimen reported by Pereda-Suberbiola *et al*. (2003) from Peguera, which is 3.2 cm wide.

Hadrosauridae indet.
(Figs 7a-i)

Material. MMB-1944, MMB-1476.

Locality. Torrent del Jou (Guardiola de Berguedà, Barcelona).

Description. The MMB-1944 (Figs 7a-e) is thin, elongated and slightly curved like the ischiadic shaft of an hadrosauroid ischium. It is 24.65 cm long and 2.6 cm wide. Its proximal end is wider in lateral view and measures 6.28 cm (Figs 7a-b). In dorsal-ventral views, the proximal end becomes narrow (Figs 7c-d). The section is elliptic at the distal end of the bone (Fig. 7e). The MMB-1476 (Figs 7f-i) is flat and trapezoidal. It measures 8.6 cm long and 6.64 cm wide. In its broken edge, it is almost circular in section and measures 3.3 cm (Fig. 7i). In one side, an ovoid, shallow concavity can be observed (Fig. 7g).

Comparison. MMB-1944 is very similar in shape to a partial lambeosaurine left ischium from Serrat del Corb in the Tremp syncline (fig. 15 in Prieto-Márquez *et al*., 2013). However, MMB-1944 cannot be assigned to Lambeosaurinae because it lacks the distal end. There, taxa included within Lambeosaurinae have a characteristic foot-like structure, expanding 90º ventrally from the main structure of the shaft (Horner *et al*., 2004). MMB-1476 might represent a distal end of hadrosaur ischia. Its trapezoidal outline and the shallow depression resembles those of a lambeosaurine ischium (e.g., fig. 15 in Prieto-Márquez *et al*., 2013; fig. 16.8c in Dalla-Vecchia *et al*., 2014a).

6. DISCUSSION

The Reptile Sandstone records one of the youngest vertebrate fossil assemblages from the Late Cretaceous in Europe (Vila *et al*., 2013). These sandstone and/or microconglomerate beds are included within the geomagnetic chron C29r (Oms *et al*., 2007) and, according to available data, deposited between 130 and 220 ka before the K-Pg boundary in the Vallcebre syncline. Bilotte *et al*. (2010) described two hadrosaur fragments (maxilla and quadrate) from the uppermost Maastrichtian marine sediments of Larcan (Haute-Garonne, France), only one meter below the K-Pg boundary in this area. Thus, remains herein described would be slightly older than those from the French locality.

Turtles are reported through the Tremp Formation materials both in the coastal environments of the 'grey unit' and the fluvial environments of the 'lower red unit' (Marmi *et al*., 2012a). Up to now, the youngest turtle remains of the Tremp Formation were found in the Barranc de Torrebilles site (Isona i Conca Dellà, Lleida province), which also corresponds to C29r, being less than 300 ky older than the K-Pg boundary (Marmi *et al*., 2012b; Dalla Vecchia *et al*., 2013). Previously, Murelaga & Canudo (2005) described isolated turtle plates, some of them assigned to bothremydids, from the Blasi and Rim sites (Arén and Serraduy, Huesca province), corresponding to the upper part of C30n or near the C30n-C29r transition (according to Oms & Canudo, 2004). Several turtle bones were found in the Reptile Sandstone, representing 27 % of the sample. These remains may be coeval or even younger than turtle remains from the Barranc de Torrebilles site. One specimen corresponds to a first peripheral of a bothremydid (Figs 3e-f) and it is clearly different (see description above) from *Polysternon isonae* from Barranc de Torrebilles, which was described by Marmi *et al*. (2012b). This suggests that several bothremydid forms inhabited fluvial environments from northwestern Iberia in the uppermost Maastrichtian.

Crocodile teeth and bones are also common throughout the whole Cretaceous portion of the Tremp Formation, but they seem more frequent in the fluvial environments of the 'lower red unit' (Marmi *et al*., 2012a). Uppermost Maastrichtian crocodile remains from the Tremp Formation were found at the Molí del Baró-1 site (Isona i Conca Dellà, Lleida province) and consist of isolated teeth (Marmi *et al*., 2012a). Recent magnetostratigraphic analyses suggest that this locality also falls within the C29r (Dalla Vecchia *et al*., 2014b). The study of the Molí del Baró-1 crocodile teeth is now in process and several morphotypes are preliminarly distinguished. However, IPS-81877 shows clear differences in shape, size and ornamentation compared to crocodrile tooth types from Molí del Baró-1. In fact, its morphology seems very close to the teeth described for genus *Allodaposuchus*, which is present in the Upper Cretaceous of the Iberian Peninsula and southern France (Buscalioni *et al*., 2001; Puértolas-Pascual *et al*., 2013). Up to now, the youngest remains correspond to *Allodaposuchus subjuniperus* (Puértolas *et al*., 2013) from the upper Maastrichtian of Serraduy del Pon (Huesca). Accordingly, IPS-81877 would represent one of the youngest records for this genus. On the other hand, the fossil record of theropods from the Tremp Formation is represented by scarce teeth, one locality with tracks, eggs, Prismatoolithidae-type eggshell fragments and rarely bones (Galobart *et al*., 2012; López-Martínez & Vicens, 2012). The specimen IPS-81878 would represent the first unequivocal theropod bone remain from the uppermost Maastrichtian of the Pyrenees.

The chronostratigraphic analysis of the ichnological record from the Tremp Formation revealed that all

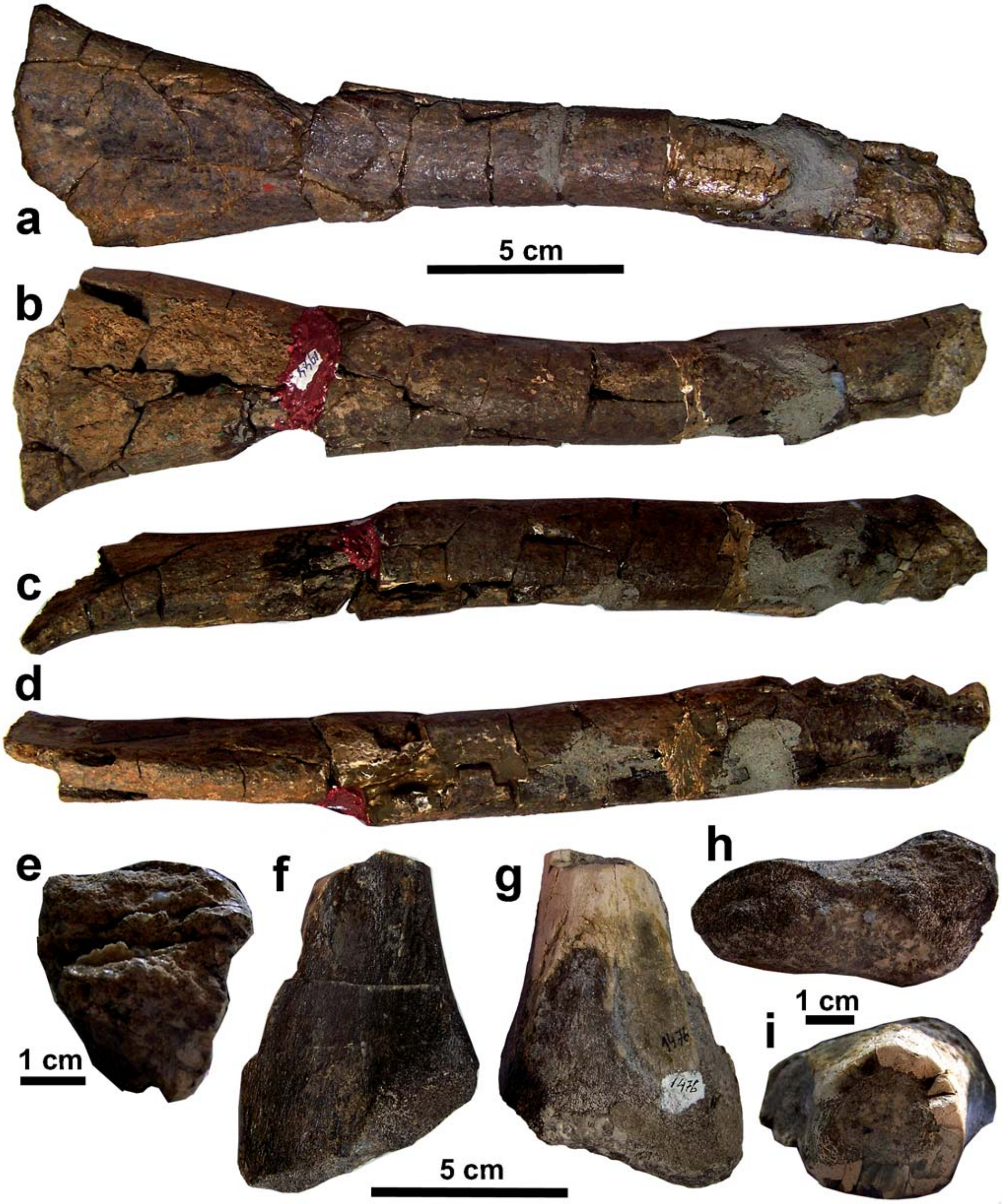

Figure 7. Ischiadic shaft of an hadrosauroid ischium (MMB-1944): **a)** Lateral view. **b)** Medial view. **c)** Ventral view. **d)** Dorsal view. **e)** Cross section. Possible foot-like expansion of a likely lambeosaurine right ischium (MMB-1476). **f)** Medial view. **g)** Lateral view. **h)** Dorsal view. **i)** Cross section.

hadrosaur tracks occurred within the late Maastrichtian and the highest abundance was found in the last 300 thousand years of this time stage (Vila *et al*., 2013). This ichnological record includes hadrosaur tracks from the Reptile Sandstone exposed at Cingles de Boixader (locality 7 in fig. 1a, Vila *et al*., 2013). This finding demonstrates that hadrosaurs walked on channel muds during low water stage conditions in those braided stream environments (Vila *et al*., 2013). On the contrary, hadrosaur bone remains reported in the present study and Pereda-Suberbiola *et al*. (2003) showed clear evidence for allochthony. The partial femur IPS-81879 is similar to that reported by Dalla Vecchia *et al*. (2014a) from Magret locality (Tremp syncline), which falls within C31n, between 2.5 and 2.0 My older than the Reptile Sandstone.

Sauropod remains are also found in the latest Maastrichtian but they seem to be more frequent in the marine-to-continental transitional beds from the lower part of the succession (i.e., the 'grey unit' of the Tremp Formation) (Riera *et al*., 2009; Vila *et al*., 2013). López-Martínez *et al*. (1999) reported the youngest sauropod footprints from the Pyrenees, at the Mas de Morull and Santa Maria de Meià sites (Lleida Province). These authors estimated an age of 200-350 ka before the end of chron C29r, indicating that the sites correspond approximately to the K-Pg boundary. However, Vila *et al*. (2013) considered both sites too poorly preserved to be of ichnotaxonomic significance. A sauropod bone was previously cited in the Reptile Sandstone outcropping at El Portet locality (Fig. 1a) by Ullastre & Masriera (1998). These authors stated in their report that the material was identified by the French palaeontologist Phillip Taquet (Muséum National d'Histoire Naturelle de Paris) as a neural arch of a dorsal or sacral vertebra belonging to a sauropod. Unfortunately, the study of this specimen was not possible because it is not currently stored in any public research institution; it is probably lost or housed in a private collection.

7. CONCLUSIONS

The fossil record of the Reptile Sandstone does not show remarkable differences in taxonomic composition [at least at higher taxon level (i.e., from family to order)] compared to the remaining 'lower red unit' of the Tremp Formation. The vertebrate association of the Reptile Sandstone includes turtles (with members of Bothremydidae), possible *Allodaposuchus* crocodiles, possible sauropods, hadrosaurid ornithopods (with likely members of Lambeosaurinae) and possible theropods. Bone and tooth remains were strongly damaged by biostratinomic processes indicating long exposure and distant transport along braided stream systems. The only evidence of autochthony is found in hadrosaur footprints. Thus, ichnological record suggests that hadrosaurs inhabited braided river environments from the uppermost Maastrichtian Iberia. Vertebrate fossils from the Reptile Sandstone are among the youngest of the Ibero-Armorican domain (a large island that included emerged lands of Iberia and most of France in the westernmost part of the Upper Cretaceous southern European archipelago) (Dercourt *et al*., 2000). Reptile Sandstone beds probably deposited less than 220 ka before the K-Pg boundary.

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Chapter 9. DISCUSSION

Art by Óscar Sanisidro

9. DISCUSSION

9.1 Microvertebrate fossil record from the Maastrichtian of the southern Pyrenees

The southern Pyrenean area has yielded an extensive and diverse assemblage of microvertebrates composed of chondrichthyans, osteichthyans, lissamphibians, lepidosaurs and crocodylomorphs (Table 1 and 2). Although most members of these clades are present in other coeval Ibero-Armorican localities (*i.e.*, Laño, Albaina, Quintanilla la Ojada, Chera and several sites in southern France), this thesis has contributed substantially to the knowledge of Maastrichtian microvertebrates and reflects a hidden taxonomic diversity, especially of teleosteans (Chapter 5, Blanco *et al.*, 2017), anurans and squamates (Chapter 6, Blanco *et al.*, 2016), and crocodylomorphs (Chapter 7, Blanco *et al.*, 2014b, 2015a, in prep.; Marmi *et al.*, 2016a).

It is striking, however, the apparent absence of bird and mammalian fossils in the Tremp Formation. Although an enigmatic diaphysis of an appendicular bone recovered from the Reptile Sandstone might belong to an avian taxon (Blanco *et al*, 2015b), no diagnostic remains testify confidently the presence of birds in the Maastrichtian of north-eastern Spain. Nevertheless, fossil birds are well represented in some fossil *Lagerstätten* from the Lower Cretaceous of Spain, such as Las Hoyas (Buscalioni & Poyato-Ariza, 2016) and Santa Maria de Meià (Lacasa-Ruíz, 1989; Chiape & Lacasa-Ruíz, 2002). Thus, their absence in other Cretaceous localities is likely produced by taphonomic biases related to the fragility of hollow bones. On the other hand, mammals are known from the Late Jurassic and Early Cretaceous (e.g., Las Hoyas, Galve and other localities of Teruel; Buscalioni & Sanz, 1987; Canudo & Cuenca-Bescós, 1996; Cuenca-Bescós & Canudo, 2003; Sánchez-Hernández *et al.*, 2007; Buscalioni & Poyato-Ariza, 2016) to the uppermost Campanian of Spain (*i.e.*, Laño) and the Maastrichtian of southern France (*i.e.*, Provence) (Tabuce *et al.*, 2004, 2013; Gheerbrant *et al.*, 1997; Gheerbrant & Astibia, 1999; Pereda-Suberbiola *et al.*, 2015). Their apparent absence in the Late Cretaceous ecosystems of the southern Pyrenean area is disconcerting. However, their presence in other coeval localities points to a possible environmental selection. The Tremp Formation records a marine regression from transitional environments ('grey' unit) to fluvial and continental deposits ('lower red' unit), but even the continental sites in the area show marine or tidal influence. In turn, Spanish and French localities yielding mammalian remains (e.g., Laño and Aix-en-Provence) are interpreted as fluvial and lacustrine settings, respectively (Tabuce *et al.*, 2013; Pereda-Suberbiola *et al.*, 2015). Nevertheless, apparently there are minor differences between mammal-bearing *vs* non-mammal-bearing depositional settings. Thus, more research is needed to resolve this conundrum.

9.1.1 Ichthyofauna

The diversity of chondrichthyans from the Maastrichtian of the southern Pyrenees is significantly lower than in other coeval Ibero-Armorican localities. Based on the batoid material studied in this thesis, the assemblage is composed by *Igdabatis indicus* Prasad & Cappetta 1993 and *Rhombodus ibericus* Kriwet, Soler-Gijón & López-Martínez 2007. These taxa have also been reported in previous works carried out in similar beds from the Àger and Tremp synclines (Soler-Gijón & López-Martínez, 1998; Kriwet *et al.*, 2007). This thesis also reveals the presence of an indeterminate anacoracid shark in the coastal settings of L'Espinau. In addition, Kriwet *et al.* (2007) also described two other batoid species from the Orcau-2 site (a dinosaur track-site located in the 'grey' unit) – *Coupatezia trempina* Kriwet, Soler-Gijón & López-Martínez 2007 and *Paratrygonorrhina amblysoda* Kriwet, Soler-Gijón & López-Martínez 2007 – as well as the presence of *Hemiscyllium* sp. and other different lamniform shark. On the contrary, Albaina has yielded ten different selachian and nine batoid species based on a similar number of fossil remains as collected in the Tremp Fm, whereas Quintanilla la Ojada has yielded at least seven different sharks and six rays with approximately a half of the amount of the fossil material (Cappetta & Corral, 1999; Corral *et al.*, 2016; Blanco *et al.*, 2017). On the other hand, the diversity of chondrichthyans collected from the Maastrichtian of southern France is even lower than that of the southern Pyrenees, being limited to one shark and three batoid species (Gheerbrant *et al.*, 1997; Laurent, 2003).

The osteichthyan assemblage from the Tremp Fm is more diverse than those from other Campanian and Maastrichtian localities in Spain. One chondrostean, at least eight basal neopterygians and up to five teleosteans were recovered from the southern Pyrenean localities. The holostean assemblage is composed by *Atractosteus* sp., *Lepisosteus* sp., a possible ?macrosemiid semionotiform, an indeterminate amiiform, cf. *Caturus* sp., cf. *Coelodus* sp., another indeterminate pycnodontiform and *Belonostomus* sp. Likewise, the teleost assemblage comprises two indeterminate osteoglossiforms, *Paralbula* sp., *Pseudoegertonia granulosus* (Arambourg 1952), cf. *Phyllodus* sp., indeterminate cypriniforms and perciforms. Of these osteichthyan taxa, chondrosteans, osteoglossiforms, cypriniforms and perciforms are not present in other Campanian or Maastrichtian sites in the Ibero-Armorican Island. Osteoglossiforms of the Tremp Fm represent the oldest evidence of the group in Europe, whereas the cypriniforms correspond to the oldest record worldwide. In comparison, the ichthyofauna of Laño is mostly dominated by lepisosteids as evidenced by some vertebrae, a supracleitrum and thousands of scales, whereas only four teeth testify the presence of phyllodontids and five tooth plates were referred to ?*Palaeolabrus* sp (Cavin, 1999; Pereda-Suberbiola *et al.*, 2015). Likewise, the ichthyofauna of Albaina is composed by pycnodontiforms, phyllodontids, enchodontids and indeterminate acanthomorphs recovered from a sample of twice the fossil material collected in the Tremp Fm. (Poyato-Ariza *et al.*, 1999; Pereda-Suberbiola *et al.*, 2015). Furthermore, pycnodontiforms, amiids, phyllodontids and enchodontids were identified in Quintanilla la Ojada based on a similar sample size than that collected in the Tremp Fm (Berreteaga *et al.*, 2011). Furthermore, the fish assemblage reported from the Maastrichtian of southern France is less diverse, including confidently lepisosteids and phyllodontids, although pycnodontids, amiiforms, enchodontids and salmoniforms might have occurred (Laurent *et al.*, 2002; Laurent, 2003).

9.1.2 Herpetofauna

This thesis also reveals a diverse herpetofaunal assemblage, similar to other coeval localities from the Ibero-Armorican landmass. Lissamphibians of the Tremp Formation are represented by indeterminate albanerpetontids and four anurans: two alytids (alytines and discoglossines), palaeobatrachids and a possible pelobatid or gobiatid. These taxa, compared at high taxonomic level, also occur in the amphibian fossil record of Laño, Blasi-2, Chera, La Solana and the poorly-known herpetofauna of southern France (Buffetaut *et al.*, 1997; Laurent *et al.*, 2002; Blain *et al.*, 2010; Company & Szentesi, 2012; Pereda-Suberbiola *et al.*, 2015; Szentesi & Company, 2017). However, several sites show some peculiarities. For example, members of the subfamily Alytinae are only present in the Tremp Fm and represent the first Mesozoic record in Europe. Likewise, except Laño and La Solana, none of the aforementioned sites have yielded remains of Caudata; whereas L'Espinau and Chera are the only localities with Pelobatidae/Gobiatidae occurrences (Company & Szentesi, 2012; Blanco *et al.*, 2016). Furthermore, the anuran from L'Espinau does not likely correspond to the same pelobatid/gobiatid form.

The studied squamate assemblage includes an iguanid, an indeterminate 'scincomorph', an anguid and probably a gekkotan. Anguids and iguanians have been also reported from Laño and Blasi-2, although some morphological differences likely reflect specific variation between these specimens (Rage, 1999; Blain *et al.*, 2010). Besides the southern Pyrenean basin, only the locality of Laño has yielded scincomorph record in the Upper Cretaceous of the Ibero-Armorican landmass. In addition, some peculiarities should be remarked in the lepidosaurian record of the Ibero-Armorican Island. Despite the abundant findings referred to 'Scincomorpha' in other Upper Cretaceous sites of Europe – e.g., the four different taxa from the Iharkút locality (Santonian of Hungary; Makádi, 2006, 2008, 2013a, 2013b; Makádi & Nydam, 2015) – the 'scincomorph' from Serrat del Rostiar-1 does not show similar dental morphology to any described taxon and likely represents a new species. Unfortunately, only 3 tooth-bearing bone fragments are not enough to formally erect a new taxon. Furthermore, if the assignment of the tiny frontal from Serrat del Rostiar-1 to Gekkota is correct, it would be the first fossil record in Ibero-Armorica, and one of the few findings in the Mesozoic record of Europe (Evans, 2003; Daza *et al.*, 2014; Caldwell *et al.*, 2015). Regarding snakes, two madtsoiids (*Herensugea* and *Menarama*) were found at Laño (Pereda-Suberbiola *et al.*, 2015), and one alethinophidian was recovered in Blasi-2 (Blain *et al.*, 2010), but no occurrence was registered in the studied localities. The Laño assemblage also includes three indeterminate squamates, of which two of them might represent a paramacellodidae and a possible varanoid (Pereda-Suberbiola *et al.*, 2015), which seem absent in the Tremp Fm beds.

Besides of contributing to the knowledge of the squamate diversity, this thesis reveals a diverse crocodilian assemblage in the southern Pyrenean basin during the Maastrichtian (Blanco *et al.*, 2014b, 2015a, in prep.; Marmi *et al.*, 2016a). Two new species were erected based on partial skeletons: *Allodaposuchus palustris* Blanco, Puértolas-Pascual, Marmi, Vila & Sellés 2014 from the lower Maastrichtian of the Fumanya Sud site (Vallcebre syncline, Barcelona province) and *Allodaposuchus hulki* Blanco, Fortuny, Vicente, Luján, García-Marçà & Sellés 2015 from the lower Maastrichtian of the Casa Fabà site (Tremp syncline, Lleida province). In addition, two species previously described in the westernmost sector of the Tremp Basin should be taken into account: *Allodaposuchus subjuniperus* Puértolas-Pascual, Canudo & Moreno-Azanza 2014 from the upper Maastrichtian of the Amor-3 site (Serraduy, Huesca Province) and *Arenysuchus gascabadiolorum* Puértolas-Pascual, Canudo & Cruzado-Caballero 2011 from the upper Maastrichtian of Elías site (Arén, Huesca Province). Moreover, digging works in the Molí del Baró-1 site together with the screenwashing processing of samples collected in other palaeontological sites have yielded isolated teeth belonging to notosuchians (?*Doratodon* sp. and other indeterminate ziphosuchian), atoposaurids (cf. *Theriosuchus* sp.) or paralligatorids (cf. *Sabresuchus* sp.), eusuchians (two indeterminate allodaposuchids, *A. palustris*, and ?*Acynodon* sp.), one gavialoid (cf. *Thoracosaurus*) and other indeterminate crocodylomorph, revealing several crocodilian taxa unrecorded by the macrofossil remains excavated in the area up to now. Most of the taxa identified from this microfossil record match with macrofossils recovered in other Spanish and French localities. In comparison, Laño site has yielded macrofossil remains of *Acynodon* and *Musturzabalsuchus*, although one allodaposuchid and ?*Ischyrochampsa* also might have occurred (Buscalioni *et al.*, 1999; Pereda-Suberbiola *et al.*, 2015). *Acynodon* has also been reported in several Campanian-Maastrichtian localities in southern France (Martin, 2007). Allodaposuchids were broadly distributed in the Iberian plate. Macrofossils of this group are known from the lower Maastrichtian of Fumanya (Blanco *et al.*, 2014), Casa Fabà (Blanco *et al.*, 2015) and Vilamitjana (Buscalioni *et al.*, 1986), the upper Maastrichtian of Arén and Serraduy (Puértolas-Pascual *et al.*, 2011, 2014), and the Campanian-Maastrichtian of Lo Hueco (Narváez *et al.*, 2015, 2016a) and Armuña (Pérez-García *et al.*, 2016). Allodaposuchids also occurred in few French Campanian localities (Narváez *et al.*, 2015; Martin *et al.*, 2016) suggesting a wide range of distribution in the Ibero-Armorican Island at the end of the Cretaceous. The presence of *Thoracosaurus* during the Maastrichtian of Ibero-Armorica is testified by a skull from Cassagnau (France) and occasional shed teeth in coastal and marine-influenced sediments in Cassagnau (France), Barranco de Extremadura and Blasi-1 (Huesca, Spain) (Puértolas-Pascual *et al.*, 2016). In turn, the macrofossil record of sebecosuchians (*i.e.*, *Doratodon*), paralligatorids (*i.e.*, *Sabresuchus*) and atoposaurids (*i.e.*, *Theriosuchus*) in the Iberian Peninsula is stratigraphically older than Maastrichtian (Company *et al.*, 2005; Puértolas-Pascual *et al.*, 2015, 2016; Tennant *et al.*, 2016).

Table 2. Faunal list of fishes, amphibians, squamates and crocodylomorphs from the studied Tremp Fm sites. Casa Fabà, Barranc de la Boïga, Les Torres-2, Porrit-6 and Reptile Sandstone sites are not included because of their little diverse assemblage (see Table 1). Other Iberian localities are included for comparisons (in grey), modified from Blain *et al.* (2010); Pereda-Suberbiola *et al.* (2015); Berreteaga *et al.* (2011) & Corral *et al.* (2016); Szentesi & Company (2016); Company & Szentesi (2012); respectively.

	Vallcebre syncline	Tremp syncline					Àger syncline		Tremp s. (Huesca)	Basque-Cantabrian region			Iberian range	
	early Maastrichtian			late Maastrichtian			early M	late M	late Maast	late Camp	late Maast		Late Maast	Cam-Maas
	Fumanya	Els Nerets	Serrat del Rostiar-1	Serrat del Pelleu	Camí del Soldat	Molí del Baró-1	Fontllonga-6	L'Espinau	Blasi-2	Laño (L1A)	Albaina	Quintanilla la Ojada	La Solana	Chera
Chondrichthyes														
Selachii														
Anacoracidae														
Squalicorax pristodontus											X	X		
Squalicorax kaupi											X	X		
Anacoracidae indet.								X						
Otodontidae														
Cretolamna appendiculata											X	?		
Serratolamnidae														
Serratolamna serrata											X	X		
Odontaspididae														
Carcharias heathi											X	X		
Carcharias aff. *gracilis*											X			
Odontaspis bronni											X			
Ginglymostomatidae														
Plicatoscyllium lehneri											X	X		
Hemiscylliidae														
Chiloscyllium sp.											X			
Triakidae														
Palaeogaleus faujasi											X	X		
Batoidea														
Rhinobatoidei														
Rhinobatos echavei											X	X		
Rhinobatos ibericus											X	X		
Ataktobatis variabilis											X			
Vascobatis albaitensis											X	X		
Sclerorhynchidae														
Dalpiazia stromeri											X			
Ganopristis leptodon											X	X		
Dasyatoidea														
Coupatezia fallax											X	X		
Myliobatoidea														
Rhombodus binkhorsti											X	X		
Rhombodus andriesi											X			
Rhombodus ibericus	X						X							
Igdabatis indicus	X						X							

Table 2. Continuation.

Osteichthyes											
Chondrostei											
?Palaeoniscidae indet.							X	X			
Neoptertgii (non teleosteans)											
Lepisosteiformes											
Atractosteus sp.			X		X		X	X			
Lepisosteus sp.			X								
Lepisosteidae indet.				X			X		X		
Semionotiformes											
?Macrosemiidae indet.							X	X			
Amiiformes											
Amiidae indet.		X						X			X
cf. *Caturus* sp.								X			
Pycnodontiformes											
cf. *Anomoedus* sp.										X	X
cf. *Paramicrodon* sp.										X	
cf. *Coelodus* sp.		X						X			
Pycnodontiform. indet.			X		X		X			X	
?Pycnodontif. indet.							X	X			X
Pycnodontoidei indt. A										X	
Pycnodontoidei indt. B										X	X
Pycnodontoidei indt. C											X
Aspidorhynchiformes											
Belonostomus sp.					X			X			
Teleostei											
Osteoglossiformes											
Osteoglossidae indet. 1								X			
Osteoglossidae indet. 2	X					X					
Phyllodontidae											
Paralbula sp.					X			X		X	
Pseudoegertonia granulosus								X			
Paralbulinae indet.							X	X			X
cf. *Phyllodus* sp.								X		X	X
Phyllodontidae indet.									X		
Palaeolabridae											
?*Palaeolabrus* sp.									X		
Cypriniformes											
Cypriniformes indet.		X	X					X			
Aulopiformes											
Enchodus sp. A										X	X
Enchodus sp. B										X	X
Acanthomorpha											
Acanthomorpha indet.								X		X	X
Percomorpha indet.						X					
Sciaenidae indet.								X			
Teleostei indet.					X			X			

Table 2. Continuation.

Lissamphibia												
Allocaudata												
Albanerpetontidae												
Albanerpetont. indet.	X	X				X	X	X			X	X
Caudata												
Salamandridae												
Salamandridae indet.								X			X	
Anura												
Alytidae												
Discoglossinae indet.	X	X					X				X	
Alytinae indet.	X					X						
Alytidae indet.								X				?
Palaeobatrachidae												
Palaeobatrach. indet.	X					X	X	X			X	
Pelobatidae/Gobiatidae												
P./G. indet.						X						X
Anura indet.	X		X			X		X			X	X
Lepidosauria												
Sphenodontia												
?Eilenodontinae indet.								X				
Squamata												
Iguania												
Iguanidae indet.	X					X	X	X				
Gekkota												
Gekkota indet.	X											
'Scincomorpha'												
'Scincomorpha' indet.	X						X	X				
Anguimorpha												
Anguidae indet.	X						X	X				
Serpentes												
Alethinophidia indet.							X					
Menarama								X				
Herensugea								X				
Squamata indet. sp. 1								X				
Squamata indet. sp. 2								X				
Squamata indet. sp. 3								X				
Squamata indet.	X											
Crocodyliformes												
Notosuchia												
Ziphosuchia												
Ziphosuchia indet.	X			X		X						
cf. *Doratodon* sp.	X					X						
Neosuchia (non eusuchians)												
Atoposauridae												
cf. *Theriosuchus* sp.	X	X	X	X		X						

Table 2. Continuation.

Eusuchia								
Hylaeochampsidae								
Acynodon sp.		X	?	X			?	X
Allodaposuchidae								
Allodaposuchus palustris	X				X		X	
Allodaposuchus hulki		?	?	?	?		?	
Agaresuchus subjuniperus		?	?	?	?		?	
Arenysuchus gascabadiol.		?	?	?	?		?	
Allodaposuchidae sp. 2				X	X	X	X	
Allodaposuchidae ind.		X						X
Gavialoidea								
cf. *Thoracosaurus* sp.							X	
Crocodylomorpha form 1					X			
Musturzabalsuchus								X
?*Ischyrochampsa*								X

9.1.3 Status and controversy of *Allodaposuchus*

Allodaposuchus is probably the most emblematic eusuchian from the Campanian and Maastrichtian of Europe due to its broad distribution along the archipelago. However, its history is not exempt of controversy. *Allodaposuchus precedens* Nopcsa 1928 was described on the basis of fragmentary cranial and postcranial material from the Densus Ciula Formation at Vălioara (Transylvania, Romania; Nopcsa, 1915, 1928). Buscalioni *et al.* (2001) reviewed the material from Romania and described new fragmentary remains from Spain (Armuña, Vilamitjana and Laño localities) and France (Bellevue locality), which they referred to *Allodaposuchus precedens* based on several characters broadly distributed among basal eusuchians, but absent in Crocodylia (Puértolas-Pascual *et al.*, 2014, 2016; Narváez *et al.*, 2015). Later, Delfino *et al.* (2008a) reported a complete skull from Oarda de Jos (Romania) undoubtedly referred to *A. precedens.* These authors related the new discovery to the material from Vălioara, suggesting that *Allodaposuchus* from western Europe could be distinguished at the species level from *A. precedens.*

In the last few years, new skulls and partial skeletons referable to *Allodaposuchus* or closely related forms have been recovered from several sites in France and Spain (Blanco *et al.*, 2014b, 2015a; Puértolas-Pascual *et al.*, 2014; Narváez *et al.*, 2015, 2016a; Martin *et al.*, 2016) leading to a hotspot in the research focused on the taxonomy, diversity and phylogenetic relationships of basal European eusuchians. In this sense, three new species were described from different units in the Tremp Formation: *Allodaposuchus subjuniperus* Puértolas-Pascual, Canudo & Moreno-Azanza 2014, from the fluvial settings of Serraduy (Huesca, Spain); *Allodaposuchus palustris*, from the brackish lacustrine settings of the Fumanya Sud site (Barcelona, Spain); and *Allodaposuchus hulki*, from the ephemeral pond settings of Casa Fabà site (Lleida, Spain). Additionally, Narváez *et al.* (2015, 2016a) erected three additional species: *Lohuecosuchus megadontos* Narváez, Brochu, Escaso, Pérez-García & Ortega 2015 and *Agarecushus fontesi* Narváez, Brochu, Escaso, Pérez-García & Ortega 2016 from Lo Hueco (Cuenca, Spain), as well as *L. mechinorum* Narváez, Brochu, Escaso, Pérez-García & Ortega 2015 from Fox-Amphoux (France). With the addition of these two new genera, the family Allodaposuchidae was formally described (Narváez *et al.*, 2015). On the basis of such diversity, the former material reported by Buscalioni *et al.* (1986, 2001) was revised and reinterpreted as Allodaposuchidae indet. (Narváez *et al.*, 2016b).

On the contrary, Martin *et al.* (2016) referred two new skulls and five fragmentary cranial remains from the Velaux-La Bastide Neuve (France) site to *Allodaposuchus precedens*. Based on this material, these authors defend that *A. precedens* is the only valid species of *Allodaposuchus*, arguing that purported differences between *A. subjuniperus, A. palustris* and *A. precedens* reflect pathology or insufficient preservation in the Spanish forms. In addition, Narváez *et al.* (2015, 2016a) also questioned the validity of *A. palustris* and *A. hulki* due to their fragmentary nature. However, after the revision of the morphological variability amongst allodaposuchids, this thesis demonstrates that most of the diagnostic characters supporting these species do not fall into the range of intraspecific variability (see Appendix, Blanco & Brochu, in press) and therefore these species should be considered as valid, whereas the new material reported by Martin and collaborators likely represents a new form. Our study provides an exhaustive morphological discussion, contributing to the knowledge of intra- and interspecific variability on the European allodaposuchids, distinguishing a vast taxonomic diversity in the European archipelago also supported by different chronological occurrences and palaeoecological frameworks.

Simultaneously to the advance on the *Allodaposuchus*-topic, several studies remarked that three other fossil eusuchians – *Massaliasuchus affuvelensis* (Matheron 1869) Martin & Buffetaut 2008, *Arenysuchus gascabadiolorum* Puértolas, Canudo & Cruzado-Caballero 2011, and *Musturzabalsuchus buffetauti* Buscalioni, Ortega & Vasse 1997 – could be more closely related to *Allodaposuchus* than previously thought. For instance, *Arenysuchus* was initially considered a basal crocodyloid (Puértolas *et al.*, 2011). However, subsequent phylogenetic analyses recovered *Arenysuchus* as the sister taxa of *A. subjuniperus* and more derived than *A. palustris* (Chapter 7, Blanco *et al.*, 2014b, 2015a). In order to reflect their phylogenetic relationships, this clade was informally named 'Allodaposuchia' (Blanco *et al.*, 2014b) and finally *Arenysuchus* was formally included into Allodaposuchidae (Narváez *et al.*, 2015). On the other hand, both *Massaliasuchus* and *Musturzabalsuchus* are based on poorly-preserved or very fragmentary remains, respectively. Although their proximity to *Allodaposuchus* has been suggested through descriptive approaches, these taxa are usually excluded from the phylogenetic analyses due to the lack of anatomical information (Narváez *et al.*, 2016a).

Another important controversy is the phylogenetic emplacement of *Allodaposuchus* and its relatives. The classical approaches, proposed a basal eusuchian position (1) in an intermediate step between Hylaeochampsidae and Crocodylia (Buscalioni *et al.*, 2001); (2) included within the family Hylaeochampsidae (Delfino *et al.*, 2008a; Brochu *et al.*, 2012); or (3) as the sister taxon of Hylaeochampsidae (Puértolas-Pascual *et al.*, 2014). One exception was the result of Puértolas *et al.* (2011), in which *Allodaposuchus precedens* was considered a member of Crocodylia. But all of these hypotheses are exclusively based on cranial remains. The results reported in this thesis are the only ones including postcranial features in the phylogenetic analyses and the first with morphological characters of the lower jaw (Chapter 7, Blanco *et al.*, 2014b; 2015a). When these features were considered, the phylogenetic position shifted to a more derived position within Crocodylia, as the sister taxon of Brevirostres (Alligatoroidea + Crocodyloidea). In order to test the effects of the addition of the postcranial characters, we performed different phylogenetic analyses with (1) the cranial characters only, (2) with cranial and postcranial characters as a whole and (3) constraining the phylogenetic result forcing Hylaeochampsidae and *Allodaposuchus* to appear together (Blanco *et al.*, 2014a). The derived position was the most parsimonious result if the postcranial features are considered. Furthermore, some mandibular features also support this hypothesis (Blanco *et al.*, 2014b). Posteriorly, Martin *et al.* (2016) defended again the inclusion of *Allodaposuchus precedens* in Hylaeochampsidae on the basis of a phylogenetic analysis with a much reduced number of taxa and lacking any other allodaposuchid species for comparisons. Likewise, Narváez *et al.* (2015, 2016a) suggested an intermediate position for Allodaposuchidae, between Hylaeochampsidae and Crocodylia. But these three latest analyses are again based on cranial remains exclusively. Therefore, the phylogenetic status of Allodaposuchidae seems still unresolved, far from reaching an agreement, and pending of new findings of postcranial skeletons and their inclusion in the phylogenetic analyses.

Another important point to discuss of the phylogenetic analyses performed by Narváez *et al.* (2015) is the proposal that the genus *Allodaposuchus* includes only the species *A. precedens*. These authors argued that *A. precedens* (and therefore the genus) should be restricted to eastern European specimens and that *A. subjuniperus, A. palustris* and *A. hulki* should be reclassified in a new genus or genera. Posteriorly, *A. subjuniperus* was relocated into the genus *Agaresuchus*, leaving no representative of the genus *Allodaposuchus* in the western European archipelago (according to Narváez *et al.*, 2016a), and reinforcing the hypothesis proposed by Narváez *et al.* (2015). However, this hypothesis lies once again in a phylogenetic analysis exclusively based on cranial remains and in the exclusion of *A. palustris* and *A. hulki* from the test. Although we agree that the species *A. precedens* is limited to the specimens from eastern Europe (Blanco & Brochu, in press), there is not a significant larger number of autapomorphies in such specimens in comparison with the western taxa to justify the restriction of the genus *Allodaposuchus* to *A. precedens*.

9.2 Palaeoecological implications

Although chondrichthyans may often occur in freshwater environments, those recovered from the Maastrichtian of Ibero-Armorica are marine representatives (Cappetta, 1987). The differences in chondrichthyan diversity between the southern Pyrenean localities and the Basque-Cantabrian region (*i.e.*, Albaina and Quintanilla la Ojada sites) might mostly be due to environmental factors. Because of the marine regression that underwent the Pyrenean area since the Campanian-Maastrichtian boundary, the Tremp Formation records from lagoonal and transitional environments ('grey' unit) to fluvial and terrestrial settings with some marine influence ('lower red' unit); whereas both Albaina and Quintanilla la Ojada are interpreted as open-coastal and in-shore settings, respectively. Rays and sharks of the Tremp Fm were found in sites placed in the 'grey' unit (Fumanya, Figuerola-2 and Orcau-2) or sites located in the 'lower red' unit interpreted as coastal lagoons, estuaries or mangrove swamps (L'Espinau, Fontllonga-6). All of them correspond to shallow coastal environments close to the sea, which some neritic batoids probably inhabited, being the sharks very rare. On the contrary, in totally marine environments like Albaina or Quintanilla la Ojada sites chondrichthyans became diverse and sharks were important components of the ichthyofaunas.

Most of the basal actinopterygians are little informative from a palaeoenvironmental viewpoint because of their euryhaline nature. 'Chondrosteans', lepisosteids, semionotiforms, amiids and pycnodontiforms have fresh- and saltwater occurrences. However, some taxa are considered primarily marine, like *Caturus* and *Belonostomus*, although the latter was eventually reported in freshwater settings (Brinkman, 1990; Brinkman *et al*., 2014). On the other hand, pycnodontiforms are not well-adapted to upstream waters independently of the salinity (Poyato-Ariza, 2005). It is congruent with the expected lentic environments of the Pyrenean basin (*i.e*., lagoons, estuaries, floodplains). Regarding teleosteans, perciforms include freshwater and marine members; phyllodontids are a primarily marine group in littoral and estuarine environments (Estes, 1969); Mesozoic osteoglossiforms are considered freshwater faunas (Nelson, 1969; Gayet *et al*., 2001); and cypriniforms have never developed tolerance for saltwater (Nelson, 2006; Alves-Gomes, 2010). Thus, as an overview, the diverse environments of the southern Pyrenean basin (e.g., lagoons, estuaries, coastal swamps, floodplains, fluvial meandering and braided river systems) promoted a decrease in chondrichthyan diversity but a rich and mixed osteichthyan fauna of euryhaline, salt- and freshwater taxa.

Amphibians and lizards have been mostly recovered from the 'lower red' unit of the Tremp Fm. This fact reflects that they were more terrestrial and freshwater faunas, but they were also able to tolerate brackish or marine tidal influence. Together with other Iberian occurrences, albanerpetontids, alytids, palaeobatrachids, anguids and iguanids seem to have been present in both freshwater and coastal environments, whereas pelobatids or gobiatids would be restricted to coastal swamps (*i.e*., Chera and L'Espinau sites) and 'scincomorphs' to fluvial environments (*i.e*., Laño and Serrat del Rostiar-1) as well as salamanders (*i.e*., Laño and La Solana). Additional environmental preferences could also be assessed for the anurans, since the palaeobatrachids are dominant in freshwater depositional settings (e.g., they represent about 70% of the lissamphibian assemblage from Laño; Pereda-Suberbiola *et al*., 2015; Csiki-Sava *et al*., 2015), whereas alytids exceed them in abundance in low-salinity waters (*i.e*., Blasi-2, representing southern Pyrenean coastal wetlands). Moreover, the abundance of aquatic and semiaquatic frogs, even of iguanids, probably reflects different lifestyles, meaning that they were local residents whereas other digging and terrestrial amphibians (albanerpetontids and salamanders) as well as heliophile reptiles (geckos, anguids and 'scincomorphs') used to live (as nowadays they do) in more terrestrial environments far away from swamps; where water floods transported their remains to the aquatic depositional sites, producing low abundances in their fossil record. These taphonomic and environmental biases were also noted by Szentesi & Company (2017), who did not find fossil remains of squamates in Chera nor La Solana sites. Anyway, because of the fragility of the microfossil remains and the absence of abrasion marks, all these taxa are supposed to have lived in, or nearby, the depositional environments.

Crocodiles broadly occupied all the ecosystems of the southern Pyrenean area. Based on macrofossil evidences, *Doratodon* and *Theriosuchus* are considered terrestrial crocodiles (Buscalioni & Sanz, 1990; Rabi & Sebők, 2015), *Acynodon* occurs in fluvial ecosystems (Buscalioni *et al*., 1999; Delfino *et al*., 2008b), *Thoracosaurus* is a marine species (Puértolas-Pascual *et al*., 2016), whereas allodaposuchids are known from brackish and freshwater environments. However, diverse lifestyles have been suggested for the different allodaposuchid species (Blanco & Brochu, in press): *Agaresuchus*, *Lohuecosuchus* and *Arenysuchus* are supposed semiaquatic crocodiles in freshwater ecosystems (Puértolas-Pascual *et al*., 2014; Narváez *et al*., 2015, 2016a); *Allodaposuchus palustris* occured in a coastal marsh (Blanco *et al.*, 2014b); and a more terrestrial lifestyle was inferred for *A. hulki* (Blanco *et al.*, 2015a). On the other hand, microfossil remains of each crocodilian clade are present in different depositional environments, but most of them are fragmentary and/or show abrasion marks that might reflect parautochthony or allochthony. Nevertheless, their abundance could reflect environmental preferences and lifestyles: *Theriosuchus* seems commonly present in the southern Pyrenean plain, regardless the depositional environment; *Acynodon* and the indeterminate durophagous crocodile are mainly recovered from fluvial settings as well as *Doratodon* and the indeterminate ziphosuchian; one of the indeterminate allodaposuchids is also more abundant in freshwaters, but the other predominates in brackish environments; and *A. palustris* and *Thoracosaurus* are strongly related with lagoons and coastal swamps. Furthermore, the coexistence of all these crocodilian taxa is also promoted by feeding specializations. Although diets of *Acynodon* have not been confidently determined, its dentition and jaw mechanisms suggest that it fed on shelled preys (Delfino *et al.*, 2008b). Similarly, Atoposaurids were considered cursorial entomophagues (Buscalioni & Sanz, 1990), and *Doratodon* was an active predator (Rabi & Sebők, 2015), but not predatory habits can be inferred for the indeterminate ziphodont crocodile. Thus, generalist aquatic predators (allodaposuchids), marine piscivores (*Thoracosaurus*), durophagues (*Acynodon* and other indeterminate form), terrestrial predators (*Doratodon* and possibly *A. hulki*) and insectivorous small crocodiles (*Theriosuchus*) composed the diverse crocodilian assemblage that inhabited the southern Pyrenean ecosystems during the Maastrichtian.

9.3 Palaeobiogeography of the Iberian microvertebrates

The geographical emplacement of the European archipelago during the Late Cretaceous represents a unique position between Asian and North American landmasses, but at the same time, near of Gondwana (*i.e.*, Africa). The isolation from other landmasses may have allowed the survival of relict taxa, but sporadic dispersal events would have brought Asian and North American faunas in the archipelago (Pereda-Suberbiola, 2009). A few trans-Tethys dispersions also took place. Thus, the Ibero-Armorican assemblage of microvertebrates includes members of different biogeographical origins.

As inhabitants of shallow marine ecosystems, rays are considered good palaeobiogeographical indicators (Cappetta, 1987). The occurrence of the same species in two different landmasses points to an interconnection between continental platforms, whereas endemic species suggest deep oceanic basins operating as geographical barriers. Thus, the occurrence of *Igdabatis indicus* in the southern Pyrenean basin and Indian localities has been suggested as the evidence of a connection between Ibero-Armorica and India during the Maastrichtian through shallow seas (Soler-Gijón & López-Martínez, 1998). The other species of the same genus, *Igdabatis sigmodon* Cappetta 1972, is known from the Maastrichtian of Niger (Cappetta, 1987). The remains of *Igdabatis* from the Fontllonga-6 and Fumanya sites are the stratigraphically oldest, and therefore support the hypothesis that this genus probably originated in the shallow marine waters surrounding the Ibero-Armorican landmass during the early Maastrichtian, before dispersing to Africa and India through the Tethys Sea (Corral *et al.*, 2016). Even though, *Rhombodus ibericus* is currently considered a Spanish endemic taxon, but if its presence in India is finally confirmed (see Prasad & Cappetta, 1993; Kriwet *et al.*, 2007) it would also reinforce the hypothesis of a geographic interconnection.

On the other hand, some active swimmer fishes that could easily migrate through open seas likely underwent a trans-Atlantic dispersion. This would explain similarities between nektonic selachian faunas of the uppermost Campanian and Maastrichtian of Spain and those of the rest of Europe and North America (Cappetta & Corral, 1999; Corral *et al.*, 2016). Specifically, the anacoracid shark found at L'Espinau site shows strong similarities with the American *Scindocorax* (Bourdon *et al.*, 2011). Concerning osteichthyans, aspidorhynchids, phyllodontids and perciforms are also shared between European and North American ichthyofaunas (Brinkman, 1990, 2008; Neuman & Brinkman, 2005; Brinkman *et al.*, 2014; Ebert, 2014), although they also seem to have reached the Indian subcontinent through the Tethys Sea (Khosla & Verma, 2015; Halliday *et al.*, 2016). Nevertheless, the fossil record of phyllodontids and perciforms is still too scarce, fragmentary and limited to a few localities for elucidating an origin for these groups. The oldest record of the aspidorhynchid *Belonostomus* is from the Late Jurassic of Germany and England (Ebert, 2014), coinciding with the point of largest specific diversity of this genus where also cohabited with other aspidorhynchids (López-Arbarello & Schröder, 2014). Thus, northern Europe could represent the original biogeographical range of this fish, and later, *Belonostomus* reached North and South America and Morocco in the Late Cretaceous (Bogan *et al.*, 2011; Martill *et al.*, 2011). Other groups of microvertebrates with American affinities are batrachosauroidid urodeles and palaeobatrachids (Pereda-Suberbiola, 2009). Of these, only palaeobatrachids have been recovered from the southern Pyrenean localities. Although the earliest representatives might be present in the Campanian of France (Csiki-Sava *et al.*, 2015), the older palaeobatrachid fossil record is still scarce to elucidate its origin.

Taxa with Asian affinities are the subfamily Alytinae and, tentatively, Osteoglossomorpha. Alytines of the Tremp Formation are related to the Asian genus *Kizylkuma*. This genus holds the oldest record of Alytinae in the Late Cretaceous (Turonian-Santonian) of Uzbekistan (Roček & Nessov, 1993), from where dispersed to India (Prasad & Rage, 1991; Roček, 2013) and Europe during the Maastrichtian. Osteoglossomorphs have been recovered almost worldwide from Cretaceous outcrops in Asia, South and North America, Africa, India and Oceania, likely showing a vicariance pattern of an ancient cosmopolitan distribution (Nelson, 1969; Wilson & Murray, 2008). The biogeographic history of the osteoglossomorphs is controversial and still unresolved. However, despite having no living representatives, the centre of diversity of the fossil osteoglossomorphs is thought to be the Early Cretaceous of Siberia and China (Wilson & Murray, 2008), from where they rapidly expanded worldwide. Because no specific taxonomic relationships could be confidently assessed for the osteoglossiforms from north-eastern Spain, this clade might be tentatively considered as primarily Asian immigrants.

Amongst the European endemisms, there are albanerpetontid amphibians, hylaeochampsids and allodaposuchid crocodiles. Europe is the centre of diversity of the albanerpetontids. The four genera grouped within Albanerpetontidae are present in Europe, of which one species of *Anoualerpeton* migrated across the Tethys, and some members of *Albanerpeton*, the most derived representatives of the clade, migrated posteriorly towards North America and Asia (Sweetman & Gardner, 2013). Regarding hylaeochampsids, *Acynodon* is exclusively known from the Campanian-Maastrichtian of south-western part of the archipelago (Ibero-Armorica and the Austro-Alpine domains; Buscalioni *et al.*, 1999; Martin, 2007; Delfino *et al.*, 2008b). Concerning allodaposuchids, it is commonly accepted that the clade Allodaposuchidae is restricted to Europe, with its highest diversity in the Iberian plate (Delfino *et al.*, 2008a; Blanco *et al.*, 2014b, 2015a; Puértolas-Pascual *et al.*, 2014, 2016; Narváez *et al.*, 2015, 2016a). Based on phylogenetic, geographic and stratigraphic data, the S-DIVA analysis (Statistical Dispersal-Vicariance Analysis; Yu *et al.*, 2010) carried out by Blanco *et al.* (2014b, Chapter 7) was the first and innovative approach suggesting an Ibero-Armorican origin for the clade, and a later dispersal event to eastern Europe.

Other taxa commonly considered typical from Laurasia are discoglossines and squamates, except few ophidian families. Concerning geckos, they were once considered Asian immigrants, since most of their Mesozoic fossil record corresponds to the Cretaceous of Asia (Daza *et al.*, 2014). Nevertheless, after the reinterpretation of *Parviraptor*, the occurrence of gekkotans in the Middle Jurassic of England (Caldwell *et al.*, 2015) obscures their palaeobiogeographic interpretations. However, as noted in Chapter 1, the fossil record of lizards is strongly biased by the palaeontological information coming from the northern continents (Evans, 2003). Thus, the Laurasian origin for all the squamates should be taken as tentative.

In addition, most of the basal neopterygian groups were abundantly reported in the Northern Hemisphere, but also display other occurrences in far landmasses. Lepisosteiforms and semionotiforms reached an almost worldwide distribution, except Oceania and Antarctica (Wiley, 1976; Grande, 2010; López-Arbarello & Alvarado-Ortega, 2011; López-Arbarello & Sferco, 2011; López-Arbarello, 2012). Amiiforms and pycnodontiforms were mainly distributed around the western Tethys in the Northern Hemisphere during the Late Cretaceous, although they have also been reported from South America, Sub-Saharan Africa and East Asia (Grande & Bemis, 1998; Martín-Abad & Poyato-Ariza, 2013; Poyato-Ariza & Martín-Abad, 2013).

Taxa with Gondwanan affinities are clearly the ziphosuchian crocodiles. *Doratodon* is closely related to the South-American sebecids, which could have reached the European archipelago through Africa during the Santonian until the Maastrichtian (Rabi & Sebők, 2015). Moreover, if the presence of trematochampsids in Ibero-Armorica is confirmed and/or the affinities of *Ischyrochampsa* are clarified, they will represent African immigrants in Europe as well. Gondwanan amphibians and squamates seem to be absent in the Maastrichtian of the southern Pyrenean area, unlike the upper Campanian of Laño, where two madtsoiid snakes were reported (Rage, 1999). Of them, *Menarana* is a snake only present in the Maastrichtian of Madagascar besides the occurrence in Laño (Pereda-Suberbiola *et al.*, 2015). Their absence in other younger Spanish localities might suggest extinction processes affecting Gondwanan elements in the herpetofaunas from the Ibero-Armorican Island during the Maastrichtian.

9.4 Time-ranges & faunal turnovers

The southern Pyrenean localities represent a timespan of about six million years, from the beginning of the early Maastrichtian (e.g., Fumanya, 72 Ma) to the end of the late Maastrichtian (e.g., Molí del Baró-1, Camí del Soldat and those of the Reptile Sandstone, 66 Ma). In this thesis, several early Maastrichtian (Fumanya, Barranc de la Boiga, Casa Fabà, Els Nerets, Fontllonga-6, Serrat del Rostiar-1, Les Torres-2) and late Maastrichtian sites (L'Espinau, Pont d'Orrit-6, Serrat del Pelleu, Molí del Baró-1, Camí del Soldat, Cingles de Cal Ros, Cingles de la Creueta y Torrent del Jou) have been studied. The exact chronological location of those sites in the Àger syncline is still not confidently confirmed (Fondevilla *et al.*, work in progress).

Chondrichthyans are present in both lower and upper Maastrichtian localities. Nevertheless, they are mostly restricted to the lower Maastrichtian (Fumanya, Orcau-2, Figuerola-2, Fontllonga-6) and only one single shark tooth has been found in the upper Maastrichtian (at L'Espinau). This fact would be more related to the marine regression that took place during the Maastrichtian rather than and extinction event. Rays and occasional sharks (e.g., the benthonic *Hemiscyllium*) would have inhabited the shallow lagoonal ecosystems of the early Maastrichtian, but they disappeared from the southern Pyrenean area during the late Maastrichtian in consequence, although sharks might have eventually occurred in coastal swamps. Rays and sharks continued to be present in other coastal marine ecosystems of Ibero-Armorica during the late Maastrichtian (e.g., Albaina and Quintanilla la Ojada).

In addition, all the osteichthyan fish groups were present in the southern Pyrenean basin during the early and late Maastrichtian. Certainly, aspidorhynchids and perciforms, specifically, seem restricted to the late Maastrichtian, but the samples of these two taxa are too small to consider this difference statistically significant. However, the abundance of 'holosteans' and teleosteans changed throughout the Maastrichtian. 'Holosteans' were more abundant in the early Maastrichtian, whereas teleosteans dominated the late Maastrichtian ichthyofaunas. Chi-square tests revealed significant differences between the early and late Maastrichtian samples (Chapter 5, Blanco *et al.*, 2017) regardless of the palaeoenvironment. These differences are significant irrespective of whether or not chondrichthyans are considered. Moreover, teleosteans were present in all the trophic guilds of the southern Pyrenean ecosystems during the late Maastrichtian (see chi-square tests in Blanco *et al.*, 2017, Appendix 3). These observations are congruent with other palaeoichthyological records of Spain (e.g., Poyato-Ariza, 2005; Buscalioni *et al.*, 2008; Berreteaga *et al.*, 2011; Poyato-Ariza & Martín-Abad, 2013). 'Holosteans' were typical members of Jurassic faunas that were progressively replaced by teleosteans throughout the Cretaceous due to several locomotion and feeding adaptations in the latters (Poyato-Ariza, 2005; Poyato-Ariza & Martín-Abad, 2013). For example, the apparent scarcity of teleostean remains in Lower Cretaceous sites has been interpreted as a combined effect of ecological and taphonomic biases. Teleosteans were probably abundant in the fish communities of the Early Cretaceous, but occupying the lowest levels of the trophic niches. Thus, these earlier teleost faunas were probably edentulous or possessed tiny villiform teeth that have not been registered in the fossil record (Buscalioni *et al.* 2008). In contrast, teleosteans seem to be widely represented in the upper Maastrichtian of north-eastern Spain, both in number of taxa and in diversity of trophic niches. Additional chi-square tests showed no significant differences between the complete samples from the 'grey' and 'lower red' units or between the samples from different palaeoenvironments (Blanco *et al.*, 2017, Appendix 3). In other words, the increase of teleost abundance in the late Maastrichtian localities is not a result of a preservation factor related to the geological units or different depositional environments, but caused by an evolutionary event in which teleosteans have replaced holosteans.

Summarizing, two different turnovers could have taken place among the Pyrenean ichthyofaunas throughout the Maastrichtian. One related to the marine regression, against the chondrichthyans that inhabited the shallow marine lagoons; and other related to the evolution and diversification of teleost fishes, which competitively excluded the holostean groups. The fish fossil record of north-eastern Spain may represent a good example of the teleost turnover during the Late Cretaceous.

Albanerpetontids, alytids and palaeobatrachids were present in the southern Pyrenean basin during the early and late Maastrichtian. Except for Blasi-2 site (Blain *et al.*, 2010), there is a lack of fossil record in the 'grey' unit suggesting a palaeoenvironmental selection. They are present, however, in the lower Maastrichtian site of Serrat del Rostiar-1, including both alytine and discoglossine alytids, and other upper Maastrichtian localities. Concerning pelobatids or gobiatids, despite showing sparse fossil occurrences, they range from the Campanian-Maastrichtian transition to the late Maastrichtian. Szentesi & Company (2017: 49) considered discoglossines being restricted to late Maastrichtian: "*Its late presence may document an expansion of this group during the advancement of the Maastrichtian regression, or simply a preservation artefact*". However, the discoglossine fossil record from Serrat del Rostiar and the indeterminate alytid from the late Campanian of Laño (besides the fact that the alytines from L'Espinau and Serrat del Rostiar are the only European record up to now), better support the preservation artefact. In any case, regarding all the Ibero-Armorican occurrences, lissamphibians were generally composing the herpetofaunas from the Campanian onwards, adapted to different continental aquatic palaeoenvironments, as noted by Szentesi & Company (2017).

Concerning squamates, iguanids and anguids were present in the lower and upper Maastrichtian localities of the north-eastern Spain regarding the paleoenvironmental frame. Data from the late Campanian of Laño and late Maastrichtian of Blasi-2 extend and complete the chronological range. However, our knowledge about the Iberian record of geckos, 'scincomorphs' and other indeterminate lizards is biased towards two localities: Laño and

Serrat del Rostiar-1. On this basis, their chronological range goes from the late Campanian to the early Maastrichtian ('scincomorphs') or simply early Maastrichtian (geckos). Their absence in other Maastrichtian localities could be explained as a mixture of ecological and taphonomic biases. As noted by Szentesi & Company (2017), squamates tend to live beyond the aquatic depositional environments and their preservation depends of a short washing-down process bringing the carcasses, so their remains are usually rare in these types of sediments. As discussed above (section 9.2), geckos and 'scincomorphs' select terrestrial environments for living. It is, thus, expected their absence in coastal swamps (Chera, Blasi-2 and L'Espinau), but they might occur in other freshwater settings if their preservation was not prevented by taphonomic processes.

Other important components of the studied herpetofaunas, the crocodiles, also show a continuous fossil record from the early Maastrichtian to the end of the late Maastrichtian in the southern Pyrenean basin. Generalist predators, at least two allodaposuchids, inhabited coastal swamps and freshwater environments throughout this age. One of them was more abundant in fluvial settings whereas the other dominated in brackish waters. In addition, *Allodaposuchus palustris* was mainly restricted to the early Maastrichtian, although a few teeth might testify its presence in the late Maastrichtian at the L'Espinau and the Molí del Baró-1 sites. *Acynodon*, *Doratodon* and the other indeterminate ziphodont crocodile also range from the early to the late Maastrichtian. Atoposaurids are mainly present during the late Maastrichtian, although a few teeth testify their presence in the fluvial settings of Serrat del Rostiar-1 during the early Maastrichtian. As for lissamphibians and squamates, this fact could be related to an environmental change rather than an expansion of the group during the late Maastrichtian, since the clade is known from earlier periods in the Ibero-Armorican Island (e.g., Puértolas-Pascual *et al*., 2015; Tennant *et al*., 2016). The few occurrences of *Thoracosaurus* in the southern Pyrenean basin are late Maastrichtian in age (Barranco de Extremadura, Blasi-1 and L'Espinau). These three localities belong to different geological units (Arén Sandstone, 'grey' unit and 'lower red' unit, respectively), but all of them underwent strong marine influence during the late Maastrichtian. It is remarkable, however, the absence of *Thoracosaurus* remains in the coastal settings of the 'grey' unit during the early Maastrichtian.

Summarizing, there is no clear evidence for an herpetofaunal turnover in northeastern Iberia during the Maastrichtian, but an increase of their geographical distribution related to the expanded areas of freshwater and terrestrial ecosystems due to the marine regression. This environmental change promoted the adequate habitats for most lissamphibian groups, squamates and some terrestrial crocodiles (atoposaurids, sebecosuchians), instead of other marine representatives.

Chapter 10. CONCLUSIONS

Art by Aina & Agnès Amblàs (ICRA)

10. CONCLUSIONS

I. The microvertebrate localities of the southern Pyrenean area have yielded a large and diverse assemblage composed of chondrichthyans, osteichthyans, lissamphibians, lepidosaurs and crocodylomorphs. Although the taxonomic composition at high taxonomic level resembles those of other coeval localities from Spain and France, several peculiarities have been found within each clade:

- The diversity of chondrichthyans from the Maastrichtian of the southern Pyrenees is significantly lower than in other coeval Ibero-Armorican localities. They are represented by four batoids (*Igdabatis indicus*, *Rhombodus ibericus*, *Coupatezia trempina*, *Paratrygonorrhina amblysoda*) and up to three selachians (*Hemiscyllium* sp., an indeterminate lamniform shark and other *Scindocorax*-like anacoracid).

- The osteichthyan assemblage from the Tremp Fm is more diverse than those from other Campanian and Maastrichtian localities from Spain and France. It is composed by one chondrostean, *Atractosteus* sp., *Lepisosteus* sp., a possible ?macrosemiid semionotiform, an indeterminate amiiform, cf. *Caturus* sp., cf. *Coelodus* sp., another indeterminate pycnodontiform, *Belonostomus* sp., two indeterminate osteoglossiforms, *Paralbula* sp., *Pseudoegertonia granulosus*, cf. *Phyllodus* sp., indeterminate cypriniforms and perciforms.

    - Osteoglossiforms from the Tremp Fm represent the oldest evidence of the group in Europe, whereas the cypriniforms are the oldest record worldwide.

- The lissamphibian assemblage is similar to other Campanian and Maastrichtian sites from the Ibero-Armorican landmass. It includes indeterminate albanerpetontids, alytines, discoglossines, palaeobatrachids and a possible pelobatid or gobiatid.

    - The alytines represent the first Mesozoic record in Europe.

- The squamate assemblage comprises, at least, an iguanid, an indeterminate 'scincomorph', an anguid and probably a gekkotan.
  - The 'scincomorph' from Serrat del Rostiar-1 likely represents a new species. Furthermore, the gekkotan would be the oldest record in Ibero-Armorica, and one of the few findings in the Mesozoic of Europe.

- Crocodylomorphs are represented by microfossil remains referred to notosuchians (?*Doratodon* sp. and other indeterminate ziphosuchian), atoposaurids (cf. *Theriosuchus* sp.) or paralligatorids (cf. *Sabresuchus* sp.), eusuchians (two indeterminate allodaposuchids, *A. palustris* and ?*Acynodon* sp.), one gavialoid (cf. *Thoracosaurus*) and other indeterminate crocodylomorph.
  - Additionally, two new species were described based on partial skeletons: *Allodaposuchus palustris* from the lower Maastrichtian of the Fumanya Sud site (Vallcebre syncline, Barcelona province) and *Allodaposuchus hulki* from the lower Maastrichtian of the Casa Fabà site (Tremp syncline, Lleida province).

  - The phylogenetic status of Allodaposuchidae remains still unresolved, far from reaching an agreement, and pending of new findings of postcranial skeletons and their inclusion in the phylogenetic analyses.

II. Environmental changes in the Pyrenean region related to a marine regression that began in the Campanian-Maastrichtian transition, affected the geographic and ecological ranges of fishes, lissamphibians, squamates and crocodylomorphs:

- The diversity of chondrichthyans decreased whereas a diverse mixture of euryhaline, salt- and freshwater faunas of osteichthyans expanded through transitional and continental habitats.

- Amphibians and lizards are mainly restricted to the 'lower red' unit suggesting that they were more terrestrial and freshwater faunas, but they were also able to tolerate brackish or marine tidal influence.
  - Even between amphibians it is possible to distinguish environmental preferences: the palaeobatrachids were dominant in freshwater settings whereas alytids exceed them in abundance in low-salinity waters. On the other hand, pelobatids/gobiatids apparently were restricted to coastal swamps and salamanders to fluvial environments.

○ Other digging and terrestrial amphibians (albanerpetontids and salamanders) as well as heliophile reptiles (geckos, anguids and 'scincomorphs') used to live in more terrestrial environments far from swamps.

- Crocodiles were widely distributed through the diverse ecosystems of the southern Pyrenean area. Both habitat and feeding specializations might have allowed the coexistence of several crocodilian clades: generalist aquatic predators (several allodaposuchids), marine piscivores (*Thoracosaurus*), durophagues (*Acynodon* and other indeterminate form), terrestrial predators (*Doratodon* and possibly *A. hulki*) and insectivorous small crocodiles (*Theriosuchus*).

III. The geographical emplacement of the European archipelago during the Late Cretaceous and the isolation from other landmasses allowed the coexistence of taxa with American affinities (an anacoracid shark, ?aspidorhynchids, phyllodontids, ?perciforms, batrachosauroidids and palaeobatrachids), Asian immigrants (alytines and, tentatively, osteoglossomorphs), typical Laurasian faunas (discoglossines and squamates), Gondwanan immigrants (*Doratodon* and probably the other ziphodont crocodile, ?*Ischyrochampsa* and madtsoiid snakes) and European endemisms (?*Rhombodus ibericus*, albanerpetontids, hylaeochampsids and allodaposuchids).

- As it was suggested by previous works, the co-occurrence of *Igdabatis indicus* in the southern Pyrenean basin and Indian localities suggests a connection between Ibero-Armorica and India during the Maastrichtian through shallow seas. However, the oldest evidences of *Igdabatis* reported in this thesis could complement the latter hypothesis, indicating that this genus originated in the Iberian plate and later migrated towards the Indian subcontinent.

- Unlike the uppermost Campanian of Laño, the absence of Gondwanan elements in the herpetofaunas from other younger Spanish localities might suggest extinction processes affecting these taxa in the Ibero-Armorican Island during the Maastrichtian.

IV. Some faunal replacements can be assessed throughout the timespan of six million years registered, from the early Maastrichtian to the end of the late Maastrichtian, in the southern Pyrenean area:

- Two different turnovers could have taken place among the Pyrenean ichthyofaunas throughout the Maastrichtian. One related to the marine regression, against the chondrichthyans that inhabited the shallow marine lagoons; and other related to the evolution and diversification of teleost fishes, which competitively excluded the holostean groups.

- In turn, there is no evidence for a turnover affecting the herpetofaunas during the Maastrichtian, but an increase of their geographical distribution related to the advance of freshwater and terrestrial ecosystems. This marine regression promoted suitable habitats for most lissamphibian groups, squamates and some terrestrial crocodiles (atoposaurids, sebecosuchians).

Chapter 11. APPENDIX

INTRA- AND INTERSPECIFIC VARIABILITY IN ALLODAPOSUCHID CROCODYLOMORPHS AND THE STATUS OF WESTERN EUROPEAN TAXA

Historical Biology, in press (I.F.: 2,059; Q1 2015, Palaeontology)

Mi trabajo consistió en la revisión y re-descripción de los caracteres morfológicos de los taxones incluidos en este trabajo en colaboración con un especialista en cocodrilos eusuquios (Dr. Christopher Brochu, Universidad de Iowa, EE.UU.), así como llevar a cabo los diversos análisis estadísticos, la redacción completa del manuscrito, y la creación de las figuras y tablas. Este estudio sirve para consolidar la variabilidad morfológica interespecífica entre las diferentes especies de eusuquios del Cretácico Superior de Europa criticadas en trabajos recientes, al tiempo que se pretende mejorar el conocimiento de la diversidad de eusuquios en los ecosistemas del Cretácico Superior, para facilitar la posterior clasificación y descripción de los morfotipos compuestos por restos dentales aislados.

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Intra- and interspecific variability in allodaposuchid crocodylomorphs and the status of western European taxa

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ABSTRACT
The genus *Allodaposuchus* is an endemic eusuchian from the Late Cretaceous of Europe. This genus was erected in 1928 by Baron Franz Nopcsa based on *Allodaposuchus precedens* from the Maastrichtian of Romania. Fragmentary skulls recovered from France and Spain were later referred to *A. precedens*, but three new species of *Allodaposuchus* have since been described: *A. subjuniperus, A. palustris* and *A. hulki*. A set of remains from Velaux, France, was recently interpreted as an ontogenetic series of *A. precedens*, prompting the argument that other species referred to *Allodaposuchus* are synonyms of *A. precedens*. Here, we review intra- and interspecific variability among allodaposuchids. Diagnostic characters for different allodaposuchids are outside the ranges of variation for modern species. Ontogenetic (intraspecific) variation observed in the allodaposuchid from Velaux is not in conflict with the presence of at least four taxa in the European Archipelago during the Late Cretaceous.

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Introduction

Allodaposuchus precedens Nopcsa 1928 was described on the basis of fragmentary cranial and postcranial material from the Densus Ciula Formation at Vălioara (Transylvania, Romania; Nopcsa 1915, 1928). Buscalioni et al. (2001) reviewed the material from Romania and described new fragmentary remains from Spain (Armuña, Vilamitjana and Laño localities) and France (Bellevue locality), which they referred to *Allodaposuchus precedens* based on several characters broadly distributed among basal eusuchians, but absent in Crocodylia (Buscalioni et al. 2001; Narváez 2015; Puértolas-Pascual et al. 2016). Later, Delfino et al. (2008) reported a complete skull from Oarda de Jos (Romania) undoubtedly referred to *A. precedens*. These authors related the new discovery to the material from Vălioara, and suggested that *Allodaposuchus* from Western Europe could be distinguished at the species level from *A. precedens* (Delfino et al. 2008; Narváez 2015). Later, Martin (2010) referred a new skull from Fox-Amphoux (France) to *Allodaposuchus*. Although noting morphological differences with Romanian *Allodaposuchus*, Martin (2010) classified this skull as *Allodaposuchus* cf. *precedens*. Others have suggested that Fox-Amphoux skull might represent a new species (Puértolas-Pascual et al. 2014; Narváez 2015), and finally Narváez et al. (2015) named the specimen *Lohuecosuchus mechinorum* Narváez, Brochu, Escaso, Pérez-García and Ortega 2015, which is closely related to *Allodaposuchus* within Allodaposuchidae.

In the last few years, new skulls and partial skeletons referable to *Allodaposuchus* or closely related forms (Allodaposuchidae) have been recovered from several sites in France and Spain (Blanco et al. 2014; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015; Marmi et al. 2016; Martin et al. 2016; Narváez 2015; Narváez et al. 2015; Ortega et al. 2015; Canudo et al. 2016; Puértolas-Pascual et al. 2016). *Allodaposuchus subjuniperus* Puértolas-Pascual, Canudo and Moreno-Azanza 2014 is from the fluvial settings of Serraduy (Huesca, Spain); *Allodaposuchus palustris* Blanco, Puértolas-Pascual, Marmi, Vila and Sellés 2014 was described from the brackish lacustrine settings of the Fumanya Sud site (Barcelona, Spain) and *Allodaposuchus hulki* Blanco, Fortuny, Vicente, Luján, García-Marçà and Sellés 2015 was recovered from the ephemeral pond settings of Casa Fabà site (Lleida, Spain). These three species come from different units in the Tremp Formation (northeastern Spain; Blanco et al. 2014; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015; Puértolas-Pascual et al. 2016). Narváez et al. (2015) named two additional allodaposuchids – *Lohuecosuchus megadontos* Narváez, Brochu, Escaso, Pérez-García and Ortega 2015 from the Lo Hueco site in Cuenca, Spain, and *L. mechinorum* from Fox-Amphoux. They argued that *A. precedens* should be restricted to Eastern European material and that *A. subjuniperus*, *A. palustris* and *A. hulki* (whose diagnosability they questioned) should be reclassified in a new genus or genera.

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Simultaneously, several studies suggested that three other fossil eusuchians – *Massaliasuchus affuvelensis* (Matheron 1869). Martin and Buffetaut 2008, *Arenysuchus gascabadiolorum* Puértolas, Canudo & Cruzado-Caballero 2011, and *Musturzabalsuchus buffetauti* Buscalioni, Ortega & Vasse 1997 – could be more closely related to *Allodaposuchus* than previously thought. *Massaliasuchus* was originally described and named '*Crocodylus affuvelensis*' by Matheron (1869) based on isolated mandibular and postcranial material from the Fuveau Basin (southern France). Later, new, fragmentary and poorly-preserved material with uncertain phyllogenetic relationships allowed the erection of *Massaliasuchus affuvelensis* (Martin and Buffetaut 2008), including the previously material described by Matheron (1869). *Arenysuchus* was recovered from the Elías site (Huesca, Spain) in the lower red unit of the Tremp Formation and was initially considered as a basal crocodyloid (Puértolas et al. 2011). Subsequent phylogenetical analyses included *Arenysuchus* within the informal clade 'Allodaposuchia' (Blanco et al. 2014; Blanco, Fortuny et al. 2015) and finally was formally included in the subsequently erected clade Allodaposuchidae (Narváez et al. 2015). *Musturzabalsuchus* was discovered at the Laño site (Vitoria Formation; Basque-Cantabrian Region, Spain), and was initially considered an alligatoroid (Buscalioni et al. 1997). Several authors pointed similarities between *Musturzabalsuchus* and *Allodaposuchus* (Ortega et al. 2008; Blanco et al. 2014; Narváez et al. 2014; Narváez 2015; Puértolas-Pascual et al. 2016) and it was also formally included in Allodaposuchidae (Narváez et al. 2015). In fewer than five years, we have gone from perceiving a single pan-European species (*A. precedens*) to recognizing a diverse clade of up to five genera and nine species.

The significance of this material cannot be understated. Allodaposuchids are either basal crocodylians (e.g. Martin 2010; Puértolas et al. 2011; Blanco et al. 2014; Blanco, Fortuny et al. 2015) or proximate outgroups to Crocodylia (e.g. Buscalioni et al. 2001; Delfino et al. 2008; Pol et al. 2009; Brochu et al. 2012; Puértolas-Pascual et al. 2014; Turner & Pritchard 2015; Martin et al. 2016; Narváez et al. 2015). In either case, allodaposuchids will play a central role in optimizing ancestral character states for Crocodylia and resolving long-standing debates in crocodylian phylogenetics (e.g. Brochu 2003; Gatesy et al. 2004; Piras et al. 2010; Oaks 2011; Gold et al. 2014) and understanding eusuchian biogeography and diversity patterns across the Cretaceous–Paleogene boundary (Le Loeuff 1991; Pereda-Suberbiola 2009; Canudo et al. 2016; Puértolas-Pascual et al. 2016).

Recently, Martin et al. (2016) referred seven specimens (two nearly complete and one fragmentary skulls, one skull table, two maxillae and one fragmentary dentary) from the Velaux-La Bastide Neuve (VBN) site to *Allodaposuchus precedens*. These authors regarded the specimens as an ontogenetic series and performed a regression analysis to assess ontogenetic (intraspecific) variation. They also compared the ontogenetic traits of the VBN form with other eusuchians. On this basis, Martin et al. (2016) recognized *A. precedens* as the only valid species of *Allodaposuchus*, arguing that purported differences between *A. subjuniperus, A. palustris,* and *A. precedens* reflect pathology or insufficient preservation in the Spanish forms.

Their study comes at a critical time in the history of crocodyliform systematics. Phylogenomic studies are showing that many modern 'species' may actually be comprised of two or more very similar species (Ray et al. 2001; Eaton et al. 2009; Hekkala et al. 2011; Milián-García et al. 2011; Franke et al. 2013; Shirley et al. 2014; Escobedo-Galván et al. 2015; Smolensky et al. 2015). The delimitation of fossil crocodyliform species rests on knowing the ranges of variation within modern lineages. If differences between two fossils lie outside the known ranges of variation for living species, we assume they are from different species. These assumptions are bolstered if the fossils are from different sites and horizons.

Martin et al. (2016) described important new material and conducted one of the few allometric studies of a Late Cretaceous eusuchian in the literature. However, we question whether their analysis can be used to synonymize allodaposuchids from eastern and western Europe. Here, we discuss morphological variability among allodaposuchids and demonstrate that most of the diagnostic characters of other species of *Allodaposuchus* do not fall into the range of intraspecific variability of the VBN eusuchian.

Materials and methods

In the present paper, we follow Narváez et al. (2015) and restrict *Allodaposuchus precedens* to eastern European specimens. Material referred to *Allodaposuchus precedens* from VBN (Martin et al. 2016) is here named the VBN form. *Allodaposuchus subjuniperus, A. palustris* and *A. hulki* are considered as members of *Allodaposuchus* pending revision. We acknowledge arguments that *A. palustris* and *A. hulki* may not be diagnosable, and that *A. subjuniperus* may not be referable to *Allodaposuchus* (Narváez et al. 2015), but all will be treated as species of *Allodaposuchus* for purposes of this study.

Morphometric data provided by Martin et al. (2016; see supplementary data) were analyzed in the statistical package PAST (Hammer et al. 2001). The data-set contains measurements of length and width of the skull from several individuals of *Acynodon* (n = 3), *Allodaposuchus* (n = 7), *Osteolaemus* (n = 13) and *Crocodylus* (n = 5). The *Crocodylus* specimens were all referred to *C. niloticus*. Linear regression analyses (Ordinary Least Square regression, OLS) relating both measurements were carried out with (1) the whole data-set and (2) one regression for each taxon in order to compare the statistical parameters. To assess homogeneity (equality) of the slopes of obtained models, analyses of covariance (ANCOVA) were performed to compare (1) the slopes of the four taxa, (2) the slopes of the brevi- and mesorostrine eusuchians (without *Crocodylus*), and (3) the slopes of the fossil taxa (*Acynodon* and *Allodaposuchus*) (e.g. Quinn & Keough 2002; Moncunill-Solé et al. 2015; Blanco, Prieto-Márquez et al. 2015; Moncunill-Solé et al. Forthcoming 2016).

Referral of a specimen to a species requires three things: a species concept, a diagnostic combination of character states (preferably including autapomorphies) distinguishing a species, and an understanding of the range of variation for a species, or at least for close relatives. An extensive discussion of the first is beyond the scope of this paper; here, we regard smallest diagnosable units (phylogenetic 'species') as approximations of lineages of ancestor-descendent populations (evolutionary species; Wiley 1978). The second and third are more straightforward, though the third can become circular in the absence of comparative data from close relatives – differences are viewed as ontogenetic variation if they occur within a sample we have circumscribed

Table 1. Results of OLS: skull length (premaxilla-supraoccipital distance, mm) – skull width (distance between condyles, mm).

	Regression analysis for *Acynodon*	Regression analysis for *Allodaposuchus*	Regression analysis for *Osteolaemus*	Regression analysis for *Crocodylus*	Regression analysis (all groups)
Slope (*a*)	1.3652	0.94667	0.78603	0.76917	0.69706
Interception (*b*)	−71	−53.625	−13.488	−56.191	2.1473
Correlation coef. (*r*)	0.96674	0.98818	0.97375	0.99733	0.97697
Determination coef. (r^2)	0.93459	0.97649	0.94818	0.99467	0.95447
t	3.7799	14.412	14.187	23.668	23.347
p (uncorrelated)	0.16465*	2.9013E−05	2.0454E−08	0.00016526	5.7198E−19

*Non-significant values.

as a species, but we consider the sample to be a single species because the variation is viewed as ontogenetic. In this case, we can draw from our knowledge of ontogenetic variation in living crocodylians closely related to allodaposuchids (e.g. Mook 1921; Müller 1924; Kälin 1933; Monteiro et al. 1997; Gold et al. 2014; Watanabe & Slice 2014; Foth et al. 2015), as well as fossil crocodylians with large samples across multiple ontogenetic stages (e.g. Erickson 1976).

Results

The single regression analyses for each genus shows a robust fit to the linear model ($r_{Allodaposuchus} = 0.988$; $r_{Acynodon} = 0.967$; $r_{Osteolaemus} = 0.974$; $r_{Crocodylus} = 0.997$; Table 1, Figure 1(A)). The probability that length and width of the skull are uncorrelated is low in all groups ($p_{Allodaposuchus} = 2.901 \times 10^{-5}$; $p_{Acynodon} = 0.165$; $p_{Osteolaemus} = 2.045 \times 10^{-8}$; $p_{Crocodylus} = 0.0002$). These results are the same that those of Martin et al. (2016), although, the p-value for the *Acynodon* regression is not significant ($p > 0.05$) (Quinn & Keough 2002). The regression analysis using the whole data-set is similarly robust (Table 1, Figure 1(B)); the 28 specimens fit a linear model ($r = 0.977$) and the probability that skull length and width are correlated is significant ($p = 5.720 \times 10^{-19}$).

Concerning the results of ANCOVA analyses (Table 2), the first test shows significant differences among the slopes of the regression analyses when the four groups are considered ($p = 0.006$). To avoid differences due to the inclusion of both longirostrine and brevirostrine crocodiles in the sample, the ANCOVA test was repeated without *C. niloticus* to compare only the brevi- or mesorostrine taxa. The result of the second ANCOVA analysis does not show significant differences among the regression slopes of *Allodaposuchus*, *Acynodon* and *Osteolaemus* ($p = 0.087$). Finally, the third ANCOVA test, comparing the slopes of *Acynodon* and *Allodaposuchus*, also shows no significant differences ($p = 0.278$) (Quinn & Keough 2002).

Discussion

Ontogenetic scaling

The results of the linear regression analyses were plotted considering the genera separately (Figure 1(A)) and together (Figure 1(B)). These results show a high correlation between the length and width of the skull, even when we consider genera individually or collectively (Table 1). If the four genera are considered individually, the first ANCOVA suggests significant differences among their slopes (or ontogenetic trends). However these differences disappear when *C. niloticus* (the longest-snouted taxon in the sample) is removed from the second and third analyses. Both second and third ANCOVAs do not show significant differences among the ontogenetic trajectories of *Allodaposuchus, Acynodon* and *Osteolaemus* (Table 2). It means that these three taxa grow in similar way, and the skull of *C. niloticus* grows proportionally longer (Figure 1(A)).

In their study, Martin et al. (2016) plotted the results of the linear regression analyses to demonstrate that all included *Allodaposuchus* skulls belong to an ontogenetic series and to justify their referral to a single species (Figure 15 in Martin et al. 2016). But this was not tested statistically. This is based on two complete and one fragmentary skulls from the VBN site, as well as other two skulls available from the literature and assigned to *A. precedens*. These two skulls are *A. precedens* from Oarda de Jos (Delfino et al. 2008) and *Allodaposuchus* cf. *precedens* from Foux-Amphous (Martin 2010), which was recently reconsidered as *Lohuecosuchus mechinorum* (Narváez et al. 2015). They also included the skull of *Allodaposuchus subjuniperus* and one supposed *Musturzabalsuchus* skull from Lo Hueco (actually referable to *Lohuecosuchus megadontos*; see Narváez et al. 2015; Ortega et al. 2015) to calculate the ontogenetic trajectory of *Allodaposuchus precedens.* The use of specimens to calculate an equation and subsequent classification of these specimens to the same species based on the equation can be viewed as circular.

However, the regression plot provided by Martin et al. (2016) does not support the attribution of the *Allodaposuchus* skulls to a single ontogenetic trajectory if the data-set is analyzed in detail. None of the brevirostrine taxa (*Allodaposuchus, Acynodon* and *Osteolaemus*) can be distinguished from the skull length-width data. This weakens the referral of *Allodaposuchus precedens, A. subjuniperus*, *Lohuecosuchus mechinorum,* and *L. megadontos* to the trajectory of the VBN form. Moreover, there is a non-significant probability ($p_{Acynodon} = 0.165$) of correlation between skull length and width on the *Acynodon* trajectory, despite the good

Table 2. Results of ANCOVAs. Test for homogeneity (equality) of slopes.

	ANCOVA analysis (all groups)	ANCOVA analysis (without C*rocodyuls*)	ANCOVA analysis (*Acynodon* and *Allodaposuchus*)
F	5.554	2831	1.42
p (same)	0.006126	0.08685*	0.2783*

*Non-significant value.

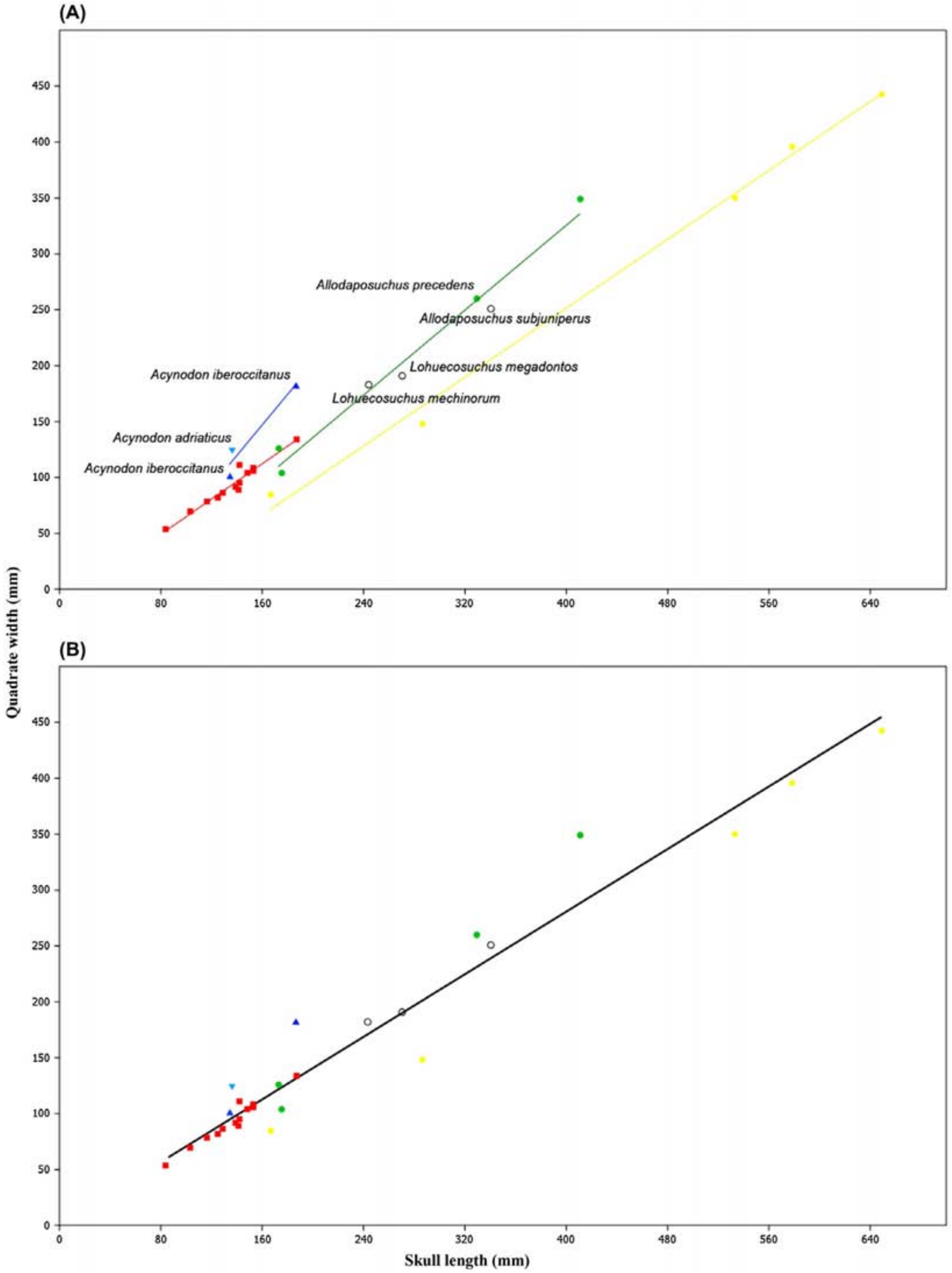

Figure 1. Plots of the quadrate width vs. skull length (mm.) resulted from the regression analyses (A) for each single taxon and (B) grouping all taxa. Filled circles: *Allodaposuchus precedens* and the VBN crocodylomorph. Open circles: Other allodaposuchids included in the sample (*A. subjuniperus, Lohuecosuchus megadontos* and *L. mechinorum*) Regular triangles: *Acynodon iberoccitanus.* Inverted triangle: *Acynodon adriaticus*. Squares: *Osteolaemus tetraspis.* Pentagons: *Crocodylus niloticus*.

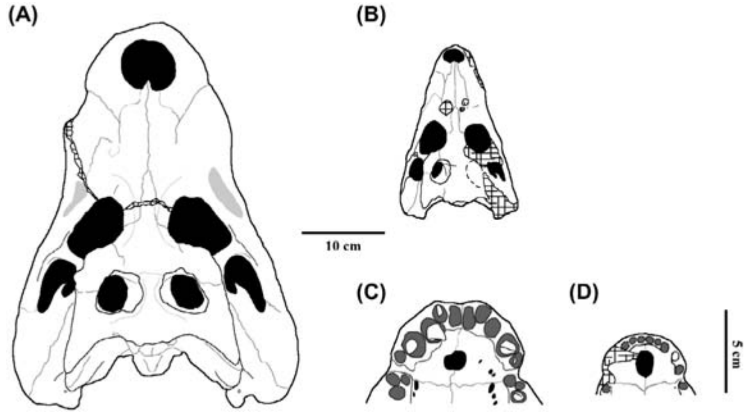

Figure 2. Allodaposuchid crocodyliform from VBN site (modified from Martin et al. 2016). (A) Adult specimen (MMS/VBN-12-10A). (B) Juvenile specimen (MMS/VBN-12-42). (C–D) Maxillae of both specimens, respectively, in palatal view.

fit of the specimens to the model ($r_{Acynodon} = 0.967$). This could be due to the low size of the sample ($n = 3$) of the *Acynodon* specimens or to the inclusion of two different species of *Acynodon* in the sample, or both. Martin et al. (2016) do not provide any reason about this issue.

Regression analyses support the long-recognized correlation between skull length and width as a general trait among eusuchians (e.g. Erickson & Brochu 1999; Verdade 2000; Wu et al. 2006; Piras et al. 2010; Erickson et al. 2012), but particular conclusions about *Acynodon* or *Allodaposuchus* would be based on statistically insignificant results and small heterogeneous samples that combine multiple species. For this reason, this trend is better illustrated in the analysis considering the whole data-set (Figure 1(B)) than in the analysis provided by Martin et al. (2016).

Comments on intraspecific and interspecific variability

Regression analyses

Although their regression analysis of Allodaposuchidae includes seven skulls, Martin et al. (2016) based their description of discrete ontogenetic changes primarily on two skulls from VBN (MMS/VBN-12-42 and MMS/VBN-12-10A; Figure 2). For a few characters, a third fragmentary skull was considered (MMS/VBN-93–28). These skulls were regarded as an ontogenetic series with MMS/VBN-12–42 a juvenile and MMS/VBN-12-10A an adult.

Discrete ontogenetic and intraspecific variation

Because of the absence of intermediate sizes, one cannot fully exclude the possibility that multiple species are represented in the same site. Different allodaposuchid species co-occur at Lo Hueco (Narváez 2015) and Molí del Baró-1 (Marmi et al. 2016). Still, we agree that referral to one species from this locality is most parsimonious, and the differences between smaller and larger specimens may reflect ontogenetic variation. But whether these differences consistently vary ontogenetically across all named allodaposuchids is another matter.

Martin et al. (2016) listed sixteen characters as ontogenetically variable in the VBN sample (Table 3). Of these, seven vary ontogenetically in living crocodylians (Mook 1921; Müller 1924; Kälin 1933; personal observation) and show patterns among allodaposuchids consistent with ontogenetic variation: rostral expansion at largest maxillary alveolus, width of the quadrate ramus, relative size of the orbit, prominence of the paroccipital process, prominence of the paroccipital boss, size of the adductor tuberosity on the ventral surface of the quadrate ramus and deflection of the medial quadrate hemycondyle (see suplementary Figures S1, S2). In addition, other three characters are consistent with trends in modern crocodylians, although they cannot be confirmed in allodaposuchids: the apparent decrease in incisive foramen size, elevation of the orbit and supratemporal fenestral margins and sloping skull table surface in larger VBN *Allodaposuchus* are shared with other adult allodaposuchids, but also with the only other possible juvenile specimen, the type of *Arenysuchus gascabadiolorum*. According to Narváez (2015), the small size of the type specimen of *Arenysuchus*, as well as its gracile appearance and overall proportions of the skull, could indicate that the unique representative of the genus *Arenysuchus* is a juvenile, which contrasts with the presence of shared adult characters.

Martin et al. (2016) listed orientation of the external naris as an ontogenetically varying feature in the VBN sample. However, the naris seems to open anterodorsally in both larger (adult) and smaller (juvenile) specimens from Velaux (Figure 8 in Martin et al. 2016). This is consistent with the orientation in other allodaposuchids – it is dorsally oriented in *Allodaposuchus subjuniperus*, but anterodorsally in *A. precedens, A. hulki, Arenysuchus* and *Lohuecosuchus* (Delfino et al. 2008; Puértolas-Pascual et al. 2014; Martin et al. 2016; Narváez et al. 2015; Blanco, Fortuny et al. 2015) (Figure 3(A)). Narial orientation generally does not vary ontogenetically in living crocodylians except for the earliest stages; and whatever changes occur the naris may open anterodorsally somewhat in hatchlings, but adopts its dorsal orientation fairly early in posthatching ontogeny (personal observation). Thus, the differences observed among the narial orientation

Table 3. Distribution of the ontogenetic morphological characters among allodaposuchids.

	VBN form (adult)	VBN form (juvenile)	*A. precedens* (adult)	*A. subjuniperus* (adult)	*A. palustris* (adult)	*A. hulki* (adult)	*Ar. gascabadiolorum* (juvenile?)	*L. mechinorum* (adult)	*L. megadontos* (adult)	
Morphological characters regarded as ontogenetic variation by Martin et al. (2016)										
Rostral expansion at largest alveolus	Broad	Slender	Broad	Broad	?	?	Slender	Broad	Broad	Ontogenetic
Depression on dorsal jugal surface	Present	Absent	?	?	?	?	?	?	?	Intraspecific?
Attenuation of nasals proximate to naris	Acute	Gradual	Acute	Gradual	?	?	Gradual	Gradual	Acute	Not ontogenetic. Intraspecific?
Quadrate ramus	Wide	Narrow	Wide	Wide	Wide	Wide	Narrow	Wide	Wide	Ontogenetic
Margin of orbit, STF	Elevated	Not elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Only VBN?
Dorsal surface of the skull table	Sloping	Planar	Sloping	Planar	Sloping	Sloping	Sloping	Sloping	Sloping	Only VBN?*
Space between STF	Narrow (0.07)	Wide (0.16)	Narrow (0.11)	Narrow (0.10)	Narrow	Narrow (0.10)	Narrow (0.10)	Wide (0.17)	Narrow (0.08)	Intraspecific
Relative orbit size	Small	Large	Small	Small	Large?	Small?	Large	Small	Small	Ontogenetic*
Squamosal prongs/paroccipital process	Prominent	Modest	Prominent	?	Modest	Prominent	Modest	Prominent	Prominent	Ontogenetic*
Adductor tuberosity on quadrate ramus	Broad	Thin	Broad	Broad	Smooth	Broad	Thin	Broad	Broad	Ontogenetic*
Paroccipital boss	Massive	Small	Massive	Massive	Absent	Massive	Massive	Massive	Massive	Ontogenetic*
Incisive foramen	Small	Big	Small	Small	?	Small	Small	Small	Small	Only VBN?
External naris	Wider than long	Circular	Circular	Longer than wide	?	Keyhole	Longer than wide	Wider than long	Wider than long	Not ontogenetic
Orientation of naris	Anterodorsal	Anterodorsal	Anterodorsal	Dorsal	?	Anterodorsal	Anterodorsal	Anterodorsal	Anterodorsal	Not ontogenetic
Medial quadrate hemicondyle	Ventrally deflected	Not ventrally deflected	Ventrally deflected	Ventrally deflected	Ventrally deflected	Not ventrally deflected	?	Ventrally deflected	Ventrally deflected	Ontogenetic*
Postorbital bar	Slender	Massive	Slender	Massive	?	?	Slender	Massive	Slender	Not ontogenetic
Morphological characters regarded invariable through ontogeny by Martin et al. (2016)										
Premaxillary alveoli	5	5	5	4	?	4	?	5	5	Invariable
Number of maxillary alveoli	13	13	13–14	14	?	?	15	13	10	Only VBN?
Maxillary alveoli 1–7 ventral to palatal surface	Yes	Yes	Yes	Yes	?	?	Yes	Yes	Yes	Invariable
Frontoparietal suture intersects STF	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Invariable
Quadratojugal spine	Robust	Robust	?	Robust	?	Absent	Robust	?	Slender	Only VBN?
Cranioquadrate groove	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Invariable
Foramen aëreum on dorsal quadrate surface	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Invariable
Ectopterygoid does not reach posterior tip of pterygoid wing	Yes	Yes	?	?	?	?	Yes	Yes	Yes	Invariable
Ectopterygoid maxillary ramus borders last two alveoli	Yes	Yes	?	?	?	?	Yes	Yes	Yes	Invariable
Additional morphological characters										
Palatine process	Long, rectangular	Long, rectangular	Short, rounded	Short, rounded	?	?	?	Long, rectangular	Very short, rectangular	Interspecific diagnostic
Occlusion of 4th dentary tooth	Notch	Notch	Pit	Notch	?	?	Notch	Notch	Notch	Interspecific diagnostic
Medial jugal foramen	Large, posterior	Large, posterior	Large, anterior	Large, posterior	?	Large, anterior	Small	Small	Small	Interspecific diagnostic
Anterior frontal process	Short	Short?	Short	Long	Very short	?	Very long	Long	Short	Interspecific diagnostic
Transverse interorbital ridge	Absent	Absent	Absent	Present	Present	Absent	Present	Present	Absent	Interspecific diagnostic
Fossa in STE	Present	Present	Present	Present	Absent	Absent	Present	Present	Present	Interspecific diagnostic
Enamel ornamentation	Parallel ridges	Parallel ridges	Parallel ridges	Smooth	Pseudo ziphodont	?	Smooth	Smooth	Smooth	Interspecific diagnostic

Note: Asterisks indicate paedomorphic features in some supposed ontogenetic characters.

of allodaposuchids could not been assigned to ontogenetic variation.

The space between the supratemporal fenestrae is narrower in the Velaux adult with respect to juvenile specimen (Martin et al. 2016) (Figures 2(A) and (B)). This is consistent with ontogenetic variation in modern crocodylians (Figures S1, S2). However, this feature varies substantially among allodaposuchids. The interfenestral space is wide in *Lohuecosuchus mechinorum* and *Massaliasuchus affuvelensis*, but narrow in *Allodaposuchus precedens*, *A. subjuniperus*, *A. palustris*, *A. hulki*, *Lohuecosuchus megadontos* and *Arenysuchus gascabadiolorum* (Figure 3(A)). Measurements (interfenestral width/skull width index, measured at the midlength of the interfenestral bar) obtained for the juvenile specimen from Velaux and *L. mechinorum* are 0.16–0.17, whereas this index ranges from 0.07 to 0.11 in the others. This variability, however, is consistent with that observed in *C. niloticus* (0.05–0.18) and *A. mississippiensis* (0.07–0.18) (see supplementary Figures S1, S2) and should not be used as diagnostic.

The depression on the dorsal surface of the jugal in mature Velaux specimens (Martin et al. 2016) does not seem to be a widespread feature within Allodaposuchidae. This character seems to be absent in other adult allodaposuchids, and might be related to intraspecific variability. Whether the nasals gradually taper anteriorly or abruptly varies among adult allodaposuchids. This variation might also be related to intraspecific variability, but to discover more specimens of each species is needed to confirm this possibility. Elevated orbital margins are found in all allodaposuchids, including the possible juvenile *Arenysuchus gascabadiolorum*. Although relative size of the postorbital bar appears to differ between juvenile and adult specimens from Velaux (Martin et al. 2016), this feature varies in allodaposuchids; the juvenile specimen from Velaux has a massive postorbital bar similar to that of *Allodaposuchus subjuniperus* and *Lohuecosuchus mechinorum*, but the adult skull has a slender postorbital bar, as in *Allodaposuchus precedens*, *Lohuecosuchus megadontos,* and *Arenysuchus gascabadiolorum*. Although these features may reflect ontogenetic variation in the Velaux form, they may not be ontogenically variable among allodaposuchids generally. To assess if this character is related to intra- or interspecific variation in other allodaposuchids, is necessary to discover more specimens of each species.

External narial morphology varies within allodaposuchids (Figure 3(A)). Adult specimens from Velaux and *Allodaposuchus precedens* have circular external nares, *Arenysuchus gascabadiolorum* and *Allodaposuchus subjuniperus* have oval-shaped nares, *A. hulki* has a keyhole-shaped naris, and *Lohuecosuchus megadontos* and *L. mechinorum* have a wider than long nares. These differences are comparatively modest; the oval nares of *A. gascabadiolorum* and *A. subjuniperus*, for example, are not especially elongate and only slightly mediolaterally compressed, and while the *Lohuecosuchus* naris is wider than long, it does not approach the more extreme condition seen in the caimanine *Mourasuchus* (Price 1964; Langston 1965; Brochu 1999). Furthermore, the proportion between the length and width of the external naris could vary in *C. niloticus* (Figure S2). It is proportionally longer in juveniles, probably related to the variation in shape of the premaxilla which is wider in adults (S. Jouve, pers. comm.). Moreover, the shape also varies among the specimens, but the variation observed in allodaposuchids may be too large to be related to intraspecific variability. We are thus uncertain that narial outline variation should be considered as ontogenetic.

Interspecifically diagnostic characters

Although Martin et al. (2016) recognized morphological differences among the skulls recovered from France and Romania, they referred all these specimens to *A. precedens*. They also questioned the validity of *A. subjuniperus* and *A. palustris* (Figure 3). Martin et al. (2016) performed a phylogenetic analysis assessing the relationships among the VBN form and other basal eusuchians, but because they did not include any other *Allodaposuchus* specimens, their analysis did not phylogenetically test referral of the VBN material to *A. precedens.*

According to Martin and collaborators, the VBN crocodylomorph

> share diagnostic features for *Allodaposuchus precedens* such as the laterally open cranioquadrate groove, participation of the nasal into the external nares, ectopterygoid adjacent to the posterior margin of the maxillary tooth row, very large fourth maxillary alveolus and a maxillary alveolar count of 13.

However these characters are either diagnostic for Allodaposuchidae or, depending on how eusuchian relationships are resolved, plesiomorphic at a broader phylogenetic level. Close apposition of the ectopterygoid and maxillary tooth row is diagnostic for Allodaposuchidae only if the broad separation of the ectopterygoid and tooth row seen in hylaeochampsids is the ancestral condition for the last common ancestor of hylaeochampsids and allodaposuchids. The condition in allodaposuchids also pertains to paralligatorids and basal crocodylians (Brochu 1999; Turner & Pritchard 2015), suggesting that the condition in hylaeochampsids is derived.

Morphological differences between Ibero-Armorican representatives and Romanian allodaposuchids are evident (Narváez et al. 2015), however there is often exceptions and *A. precedens* share some of these differences with a few western taxa. *Allodaposuchus precedens* and *Allodaposuchus subjuniperus* have a short and rounded anterior palatine process, different from those of *Lohuecosuchus* and specimens from Velaux, whose anterior projection is wide and rectangular U-shaped. However, this process in *Lohuecosuchus megadontos* does not extend beyond the anterior margin of the suborbital fenestra, whereas it clearly exceeds these margins in *Lohuecosuchus mechinorum* and specimens from Velaux. The anterior palatine process is more elongated in the juvenile specimen from Velaux than in the adult. There is no significant differences in the length and shape of the anterior palatine process through the ontogeny of extant taxa (Figures 4(A)–(D)), therefore, the differences observed among allodaposuchids could not been related to ontogenetic changes. All the Western European allodaposuchids share the presence of a notch for the reception of the fourth mandibular tooth between the premaxilla and the maxilla. This feature is shown by all main lineages of Crocodylia except Alligatoroidea. This last clade shares the existence of a pit for the reception of the fourth mandibular tooth with *Allodaposuchus precedens* and Hylaeochampsidae. *Allodaposuchus precedens*, *A. subjuniperus*, *A. hulki,* and specimens from Velaux are the only allodaposuchids with a large medial jugal foramen, a character shared with *Borealosuchus*, *Diplocynodon*, and some crocodyloids. Other allodaposuchids possess a smaller foramen in this region. Moreover

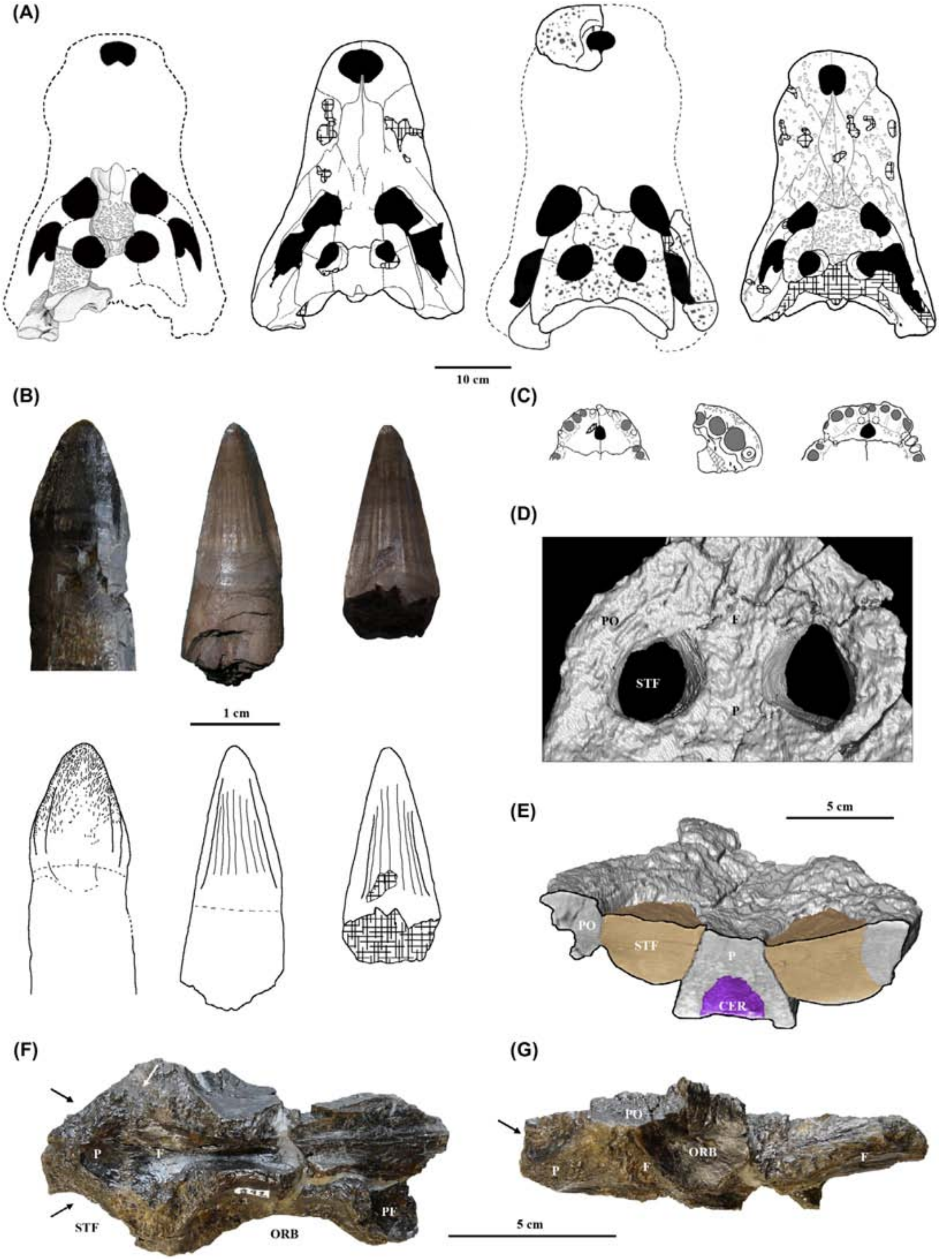

Figure 3. Comparison of *Allodaposuchus* specimens. (A) Skulls of *A. palustris*, *A. precedens*, *A. hulki* and *A. subjuniperus*, from left to right (modified from Delfino et al. 2008; Blanco et al. 2014; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015 respectively). (B) Tooth of *A. palustris* (modified from Blanco et al. 2014), VBN (modified from Martin et al. 2016) and Vălioara sites, respectively, and draws. (C) Premaxillae of *A. precedens*, *A. hulki* and *A. subjuniperus*, from left to right. (D–E) TAC reconstruction of the skull of *A. hulki* in (D) dorsal and (E) porterior view. (F–G) Frontal of *A. palustris* in (F) ventral and (G) lateral views. Black arrows indicate the anteromedial wall of the STF. White arrow indicates the fronto-parietal suture. Abbreviations: CER, cerebrum; F, frontal; ORB, orbit; P, parietal; PF, prefrontal; STF, supratemporal fenestra.

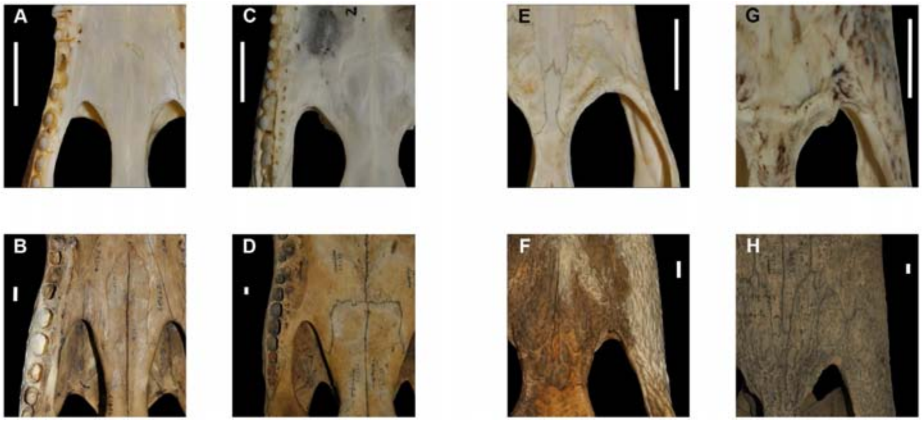

Figure 4. Ontogenetic change of (A–D) the anterior palatine process and (E–H) the anterior frontal process in *Crocodylus niloticus* and *Alligator mississippiensis.* (A, E) Post-hatchling and (B, F) adult specimens of *Crocodylus niloticus.* (C, G) Post-hatchling and (D, H) adult specimens of *Alligator mississippiensis*. Scale bar = 1 cm.

is interesting to remark the position of this foramen in relation to the postorbital bar. In the original character description of Brochu (1997), neosuchians have this foramen located anteriorly to postorbital bar. However, in the specimens from Velaux and *A. subjuniperus* is placed posteriorly to the postorbital bar, as well as other extant and fossil crocodylomorphs, and sometimes both anterior and posterior foramina are present (E. Puértolas-Pascual, pers. comm.). The anterior process of the frontal in *Arenysuchus, Allodaposuchus subjuniperus* and *Lohuecosuchus mechinorum* extends beyond the anterior margin of the prefrontals, but not in other allodaposuchids. The length of the anterior frontal process barely varies during the ontogeny of extant crocodylians (Figures 4(E)–(H)), thus, the differences observed among allodaposuchids could not been related to ontogenetic changes.

Most of the morphological differences among allodaposuchids from Western Europe and *A. precedens* from Romania lie outside the observed ranges of variation within modern crocodylians and do not seem to reflect intraspecific and ontogenetic variability. They indicate a divergence within the clade, possibly due to vicariance patterns caused by isolation of the eastern and western faunas, as has been suggested for this and other vertebrate clades (Le Loeuff 1991; Weishampel et al. 2010; Blanco et al. 2014; Csiki-Sava et al. 2015; Narváez et al. 2015). Therefore, if this palaeobiogeographical scenario is true, the VBN crocodylomorph can not be referred to neither *A. precedens* nor *Lohuecosuchus mechinorum* from Foux-Amphoux (Martin 2010; Narváez et al. 2015).

Martin et al. (2016) and Narváez et al. (2015) considered that *A. subjuniperus* needs to be reviewed and questioned the validity of *A. palustris* and *A. hulki* because their poor preservation and the lack of information in the phylogenetic analyses. However, there are evident autapomorphies and combination of diagnostic characters in the know material of the three species.

Allodaposuchus subjuniperus differs from all other allodaposuchids by its wide and short premaxillae, the teardrop-shaped incisive foramen located close to the premaxillary-maxillary suture, the presence of four premaxillary alveoli, the shape and the orientation of the naris, the outline of the nasals, relatively small orbits obliquely oriented, a remarkably wide flat frontal, a low transverse interorbital ridge at the beginning of the anterior process of the frontal, a massive postorbital bar, and a relatively large maxillary foramen for palatine ramus of cranial nerve V (Puértolas-Pascual et al. 2014). Moreover, the rostrum of *A. subjuniperus* appears relatively longer than the rostra of other *Allodaposuchus*. Martin et al. (2016) acknowledge this difference, which they regard as ontogenetic; and they suggest that the morphology of the premaxilla, the position of the incisive foramen, and the number of premaxillary teeth are pathological characters, whereas they consider the interorbital ridge as an artefact of the preservation.

We agree that the number of premaxillary alveoli varies amongst modern crocodylians in a manner that can be described as either pathological or ontogenetic. The third alveolus is substantially larger, and grows more rapidly, than the second, which is often allometrically crowded out. The only living crocodylians where this is not true are *Paleosuchus*, which has four alveoli throughout ontogeny; and *Alligator*, in which the second and third premaxillary alveoli are closer in size (Mook 1921; Kälin 1933; Brown et al. 2015). However, if the second alveolus is lost, there is usually a diastema between the first and the third alveoli, and there may also be a notch in the outline of the premaxilla to indicate the position of the second alveolus (Brochu 1997, 1999). But it may depend on the allometric relationship between the premaxillary alveoli (personal observation). Therefore, the number of premaxillary alveoli should be taken with extreme caution to diagnose fossil eusuchians without an ontogenetic series.

Allodaposuchus subjuniperus, has a notch between the premaxillary–maxillary suture for the reception of the fourth dentary tooth. *Arenysuchus, Lohuecosuchus* and the VBN form also have a lateral notch, unlike *A. precedens.* This, too, should be regarded as tentatively diagnostic, as it is known to vary among some alligatoroids. The dorsolateral surfaces of an occlusal pit can wear away, leaving a notch (Kälin 1933; Norell et al. 1994).

But there is no evidence for pathology that would account for other differences in this part of the skull. In both *A. hulki* and *A. subjuniperus* the third premaxillary alveolus is the largest, unlike *A. precedens* from Romania and the VBN form, where it is the fourth (Figure 3(C)). The premaxilla of *Allodaposuchus hulki* is wider than long and rounded in outline, not straight as in *A. subjuniperus* (Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015). The position of the incisive foramen of *A. subjuniperus* close to the premaxillary-maxillary suture could be related to its extremely short premaxilla more than pathology. An interorbital ridge is also present in *A. palustris, Arenysuchus* and *Lohuecosuchus mechinorum* (Martin 2010; Puértolas et al. 2011; Blanco et al. 2014), but weakly present in *A. precedens* (personal observation) and absent in the VBN crocodylomorph and other allodaposuchids. Therefore, the interorbital ridge could not be related to an artefact of the preservation. Moreover, the dorsal surface of the skull table of *A. subjuniperus* is nearly planar and the lateral margins of the frontal are flush with the surface of the skull table, unlike other allodaposuchids (Puértolas-Pascual et al. 2014).

Blanco et al. (2014, p. 7), diagnosed *Allodaposuchus palustris* on the following autapomorphies:

> absence of a shallow fossa in the rostromedial margin of the supratemporal fenestra; slightly concavoconvex frontoparietal suture; exoccipital without boss on paroccipital process; large foramen aëreum in quadrate; short and robust teeth with two very marked longitudinal grooves close to the carinae; teeth with strong ornamentation developing false-ziphodont crenulations; anterior process of the ilium more developed.

They also discussed some ambiguous autapomorphies like the shape and position of the neural spine and keel of the axis, a rounded superior border of the iliac blade, an elevated posterior iliac process, and a large distal end of the calcaneum. Martin et al. (2016) argued that these characters are uncertain or fall into the ontogenetic variability observed in the VBN crocodylomorph.

Martin et al. (2016) assert that the development of the fossa in the supratemporal fenestra is impossible to assess in *A. palustris* because it is incomplete. Nevertheless, the frontal bone is complete, preserving the medial and part of the rostral margins of the fenestrae. There is no sign of a developed shallow fossa (or shelf) in the supratemporal fenestrae (Figures 3(F), and (G)). The anteromedial wall of the fenestra of *A. palustris* (as well as that of *A. hulki*, Figures 3(D)–(E)) is nearly vertical, unlike other allodaposuchids that bear a clearly prominent shelf (Delfino et al. 2008; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015; Martin et al. 2016; Narváez et al. 2015). Martin et al. (2016) consider the slightly concavo-convex frontoparitetal suture of *A. palustris* comparable to that of the VBN form, but in fact, the suture of *A. palustris* describes a moderate curvature which is concave anteriorly, in contrast to the more nearly linear morphology present in other allodaposuchids (Delfino et al. 2008; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015; Martin et al. 2016; Narváez et al. 2015) (Figures 3(A) and (F)). It resembles the concavoconvex condition stated in the original character description (Figure 104 in Brochu 1997), and we prefer maintain the original consideration. The frontal also bears a wider and shorter anterior process in *A. palustris* than in the rest of allodaposuchids, which is much shorter in length than the prefrontal bones and does not extend far beyond the anterior end of the orbits.

Martin et al. (2016) suggest that the expression of the boss of the paroccipital process falls into the range of variation showed in the VBN form. According to the ontogenetic changes described by Martin et al. (2016), these bosses are scarcely developed in the juveniles and become broader and weakly expressed in adults. The paroccipital boss is absent in *A. palustris* (or very smooth according to Narváez et al. 2015), and in any case, could be only compared to the juvenile condition in the VBN form.

Dental morphology varies considerably within modern crocodylians, and dental characters generally do not form robust diagnostic characters among neosuchians. As such, dental differences between any two allodaposuchids should be treated as tentative and not definitive. Nevertheless, the teeth of *A. palustris* can be distinguished from those of other allodaposuchids, such as the strong constriction in the base of the crown and the pseudoziphodont ornamentation of the enamel (Blanco et al. 2014; Narváez 2015). Martin and collaborators argued that these fall into the range of variation observed in *A. precedens* based on isolated teeth from Vălioara. These isolated teeth cannot definitively be referred to *A. precedens* (Nopcsa 1915, 1928; Buscalioni et al. 2001; Narváez 2015), but even so, the morphology of the teeth assigned to *A. palustris* differs from those referred to *A. precedens* and the VBN form (Buscalioni et al. 2001; Delfino et al. 2008; Martin et al. 2016; Figure 3(B)). The teeth of *A. precedens* bear ~7 linear apicobasal ridges in both lingual and labial views (more developed lingually), whereas teeth of *A. palustris* are furrowed by many small and irregular ridges, more concentrated at the apex. The development of these small ridges is similar in both lingual and labial sides, and conform pseudoziphodont crenulations to the contact with the carinae (Figure 3(B)).

In addition, at least the anterior region of dentary of *A. palustris* is not festooned in lateral view (Blanco et al. 2014), unlike the VBN dentary described by Martin et al. (2016) and that of *L. megadontos* (Narváez et al. 2015). The ventral surface of the quadrate also shows differences between *A. palustris* and *A. precedens.* Martin et al. (2016) noted two well-expressed muscle scars in both juvenile and adult specimens of the VBN form, but the quadrate of *A. palustris* is smooth ventrally. Martin et al. (2016) also assert that the ilia assigned to *A. precedens* and *A. palustris* do not differ from each other, but the ilium from Vălioara referred to the holotype material of *A. precedens* (Nopcsa 1915) has a visibly constricted posterior blade differing from the more rounded structure, lacking a constriction, in *A. palustris* (Blanco et al. 2014). The anterior process is also more prominent in *A. palustris* (Figure 5).

Additionally, the ontogenetic observation provided by Martin et al. (2016) about the material from Velaux helps to distinguish *A. hulki* from other allodaposuchids. This taxon is characterized by its quadratojugal forming the posteroventral corner and not extending along the posterior margin of the infratemporal fenestra, the absence of the quadratojugal spine, and the absence of fossa in the anteromedial corner of the supratemporal fenestrae (Figures 3(A), (D), and (E)). Additional characters distinguish *A. hulki* from *A. precedens,* such as the shape of the premaxilla and external naris, dermal bones of skull roof overhanging supratemporal fenestrae in *A. hulki*, the morphology of the two crests in the ventral surface of the quadrate, the orientation of the capitate processes of laterosphenoid, and dental morphology (Blanco, Fortuny et al. 2015). According to Martin and collaborators, the quadratojugal spine remains acute and robust along the ontogeny, the bones of

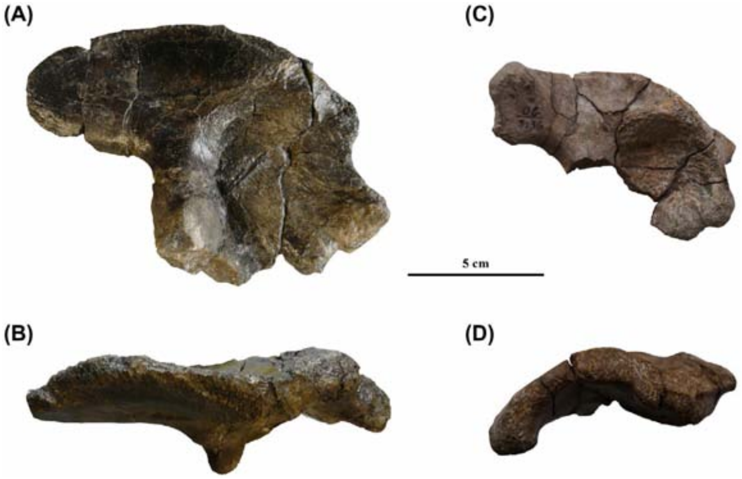

Figure 5. (A–B) Left ilium of *Allodaposuchus palustris*, in (A) lateral and (B) dorsal views. Both views were mirrored to comparisons. (C–D) Right ilium of *Allodaposuchus precedens*, in (C) lateral and (D) dorsal views.

the skull table do not overhang the supratemporal fenestrae and the shelf of the fenestra is prominent in both juvenile and adult specimens. All the other allodaposuchids, except *A. palustris,* show this shelf in the supratemporal fenestrae (Narváez 2015). Therefore, *A. hulki* is supported by three unique and an exclusive combination of character states not shown by its sister taxa, *A. subjuniperus* and *A. precedens.* In addition, Blanco, Fortuny et al. (2015) described both quadrate hemicondyles similar in size in *A. hulki*. The medial hemicondyle is not ventrally deflected, as it is in mature allodaposuchids.

If autapomorphies showed by *A. subjuniperus, A. hulki* and *A. palustris* (e.g. the plannar skull table, the expression of the boss of the paroccipital process, the size and shape of quadrate hemicondyles and the muscle scars in the quadrate) fall into the range of variation observed in the VBN form, they would represent conditions in earlier ontogenetic stages. Martin et al. (2016) claimed that Blanco et al. (2014) did not provide information about the ontogenetic state of *A. palustris.* But in fact, Blanco and collaborators described *A. palustris* as an adult specimen based on the fused neural arch of the axis (Brochu 1996; Blanco et al. 2014). The specimens of *A. subjuniperus*, *A. hulki* and *A. precedens* were also described as adults (Buscalioni et al. 2001; Delfino et al. 2008; Puértolas-Pascual et al. 2014; Blanco, Fortuny et al. 2015), and their size is similar to MMS/VBN-12-10A, a mature skull from Velaux (Figures 2(A) and 3(A)). Therefore, these characters might be better explained by paedomorphic processes during allodaposuchid phylogeny more than intraspecific variation.

On the other hand, *Arenysuchus* has been considered as a juvenile specimen based on their gracile shape and small size (Narváez 2015). This specimen shows, indeed, the juvenile condition in some morphological characters (e.g. slender rostral expansion at largest maxillary alveolus, narrow quadrate ramus with thin adductor tuberosities and large orbits). Nevertheless, it also displays a few adult characters compared to other allodaposuchids and extant crocodylians (e.g. a small incisive foramen, elevation of the orbit and supratemporal fenestral margins, sloping skull table and narrow space between the supratemporal fenestrae). Based on these morphological characters, it is not possible to assess confidently the ontogenetic stage of *Arenysuchus*, but histological approaches might shed light on it.

Allodaposuchidae is an endemic taxon of Europe and range from the Campanian to the late Maastrichtian (Buscalioni et al. 1997; Buscalioni et al. 2001; Martin and Buffetaut 2008; Ortega et al. 2008; Puértolas et al. 2011; Puértolas-Pascual et al. 2014; Blanco et al. 2014; Blanco, Fortuny et al. 2015; Csiki-Sava et al. 2015; Marmi et al. 2016; Narváez et al. 2015; Ortega et al. 2015; Puértolas-Pascual et al. 2016; Pérez-García et al. 2016). This group is known from two areas of the European Archipelago: the Transylvanian region and the Ibero-Armorican Island. Based on morphological differences among eastern and western allodaposuchids, Narváez et al. (2015) restricted the name *Allodaposuchus precedens* to specimens from Eastern Europe. *Massaliasuchus, Musturzabalsuchus, Lohuecosuchus,* the VBN crocodylomorph and other 'Allodaposuchus precedens' remains are Campanian and Campanian-early Maastrichtian in age; whereas *Allodaposuchus precedens, Allodaposuchus palustris* and *Allodaposuchus hulki* are younger and come from early Maastrichtian; while *Allodaposuchus subjuniperus* and *Arenysuchus gascabadiolorum* are the youngest representatives, both coming from the late Maastrichtian. Furthermore, different species of *Allodaposuchus* have been found in different depositional environments: *Allodaposuchus precedens* and *A. subjuniperus* were recovered from fluvial deposits (Delfino et al. 2008; Puértolas-Pascual et al. 2014); *Allodaposuchus palustris* was found in deposits interpreted like a brackish mudflat environment (Villalba-Breva et al. 2012; Blanco et al. 2014) and terrestrial habits were ascribed to *A. hulki*, recovered from ephemeral-pond deposits (Blanco, Fortuny et al. 2015). Therefore, spatiotemporal and ecological splits might contribute to reduce interespecific competition between these species in the European Archipelago.

Conclusions

Since the name *Allodaposuchus* was erected (Nopcsa 1928) several French, Romanian and Spanish discoveries were referred to the species *A. precedens*, despite differing morphologically (Buscalioni et al. 2001; Delfino et al. 2008). But in recent years, three new species were described within this genus (*A. subjuniperus*, *A. palustris* and *A. hulki*), and the clade Allodaposuchidae was formally erected to include *Allodaposuchus* and its close relatives, *Lohuecosuchus, Musturzabalsuchus* and *Arenysuchus* (Narváez et al. 2015). We reviewed arguments that Ibero-American *Allodaposuchus* can be referred to *A. precedens* (Martin et al. 2016), and conclude that the evidence does not support the presence of a single pan-European species throughout the Campanian and Maastrichtian. Morphological differences between different *Allodaposuchus* species are either outside observed ranges of variation within crocodylian species or, if they fall within the range of variation of the VBN form, they correspond to the juvenile condition.

Ongoing revision of known allodaposuchid material could increase the diversity of this clade. For example, *Allodaposuchus* from Armuña (Segovia, Spain) differs consistently from all other allodaposuchids (Narváez 2015; Pérez-García et al. 2016) and probably belongs to a new taxon. In the same way, an unnamed allodaposuchid from Lo Hueco (Cuenca, Spain) represents a new species (Narváez 2015). Rather than a single species throughout Europe, as many as five species of *Allodaposuchus* (*A. subjuniperus, A. hulki, A. palustris*, the VBN form, and the Armuña form) and five other allodaposuchids (*M. buffetauti*, *A. gascabadiolorum*, *L. megadontos*, *L. mechinorum*, and the other Lo Hueco form) may be known from western Europe alone.

Moreover, the recent discovery that some modern ‘species’ are actually two or more similar species (Eaton et al. 2009; Ray et al. 2001; Hekkala et al. 2011; Milián-García et al. 2011; Franke et al. 2013; Shirley et al. 2014; Escobedo-Galván et al. 2015; Smolensky et al. 2015) adds a level of complexity to this issue. If what we previously thought were regionally-varying species are actually cryptic species complexes, we are forced to reevaluate our preceptions of these ranges of variation. We may be approaching a paradigm shift in how we assess species-level diversity among living and fossil crocodyliforms.

Paedomorphic processes might have taken place during allodaposuchid phylogeny. Characters typical of juvenile forms in one species (the VBN form) are also found in mature specimens of other allodaposuchids. This requires more comprehensive phylogenetic analyses, at the species level, of allodaposuchids and other eusuchians.

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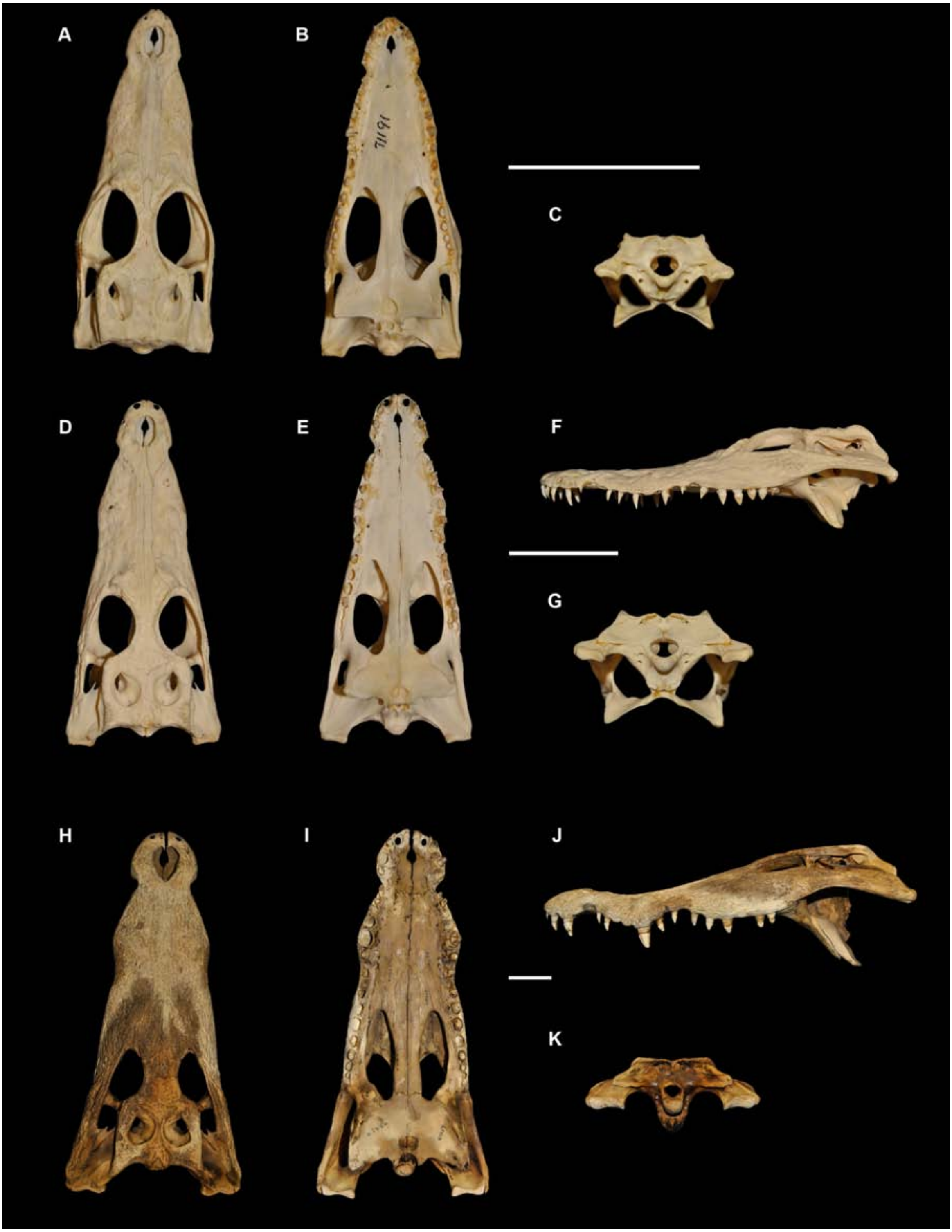
SUPPLEMENTARY MATERIAL

Figure S1. Ontogenetic series of *Alligator mississippiensis*. **A-D)** Post-hatchling specimen in (A) dorsal, (B) palatal, (C) lateral and (D) occipital views. **E-H)** Juvenile specimen in (E) dorsal, (F) palatal, (G) lateral and (H) occipital views. **I-L)** Adult specimen in (I) dorsal, (J) palatal, (K) lateral and (L) occipital views. Scale bar = 5cm.

Figure S2. Ontogenetic series of *Crocodylus niloticus*. **A-C)** Post-hatchling specimen in (A) dorsal, (B) palatal and (C) occipital views. **D-G)** Juvenile specimen in (D) dorsal, (E) palatal, (F) lateral and (G) occipital views. **H-K)** Adult specimen in (H) dorsal, (I) palatal, (J) lateral and (K) occipital views. Scale bar = 5cm.



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Chapter 13. AGRADECEMENTOS

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