Universitat Autònoma de Barcelona

Registre geològic, paleoambients i successió dels darrers dinosaures del sud-oest europeu

Víctor Fondevilla Moreu

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Registre geològic, paleoambients i successió dels darrers dinosaures del sud-oest europeu

Memòria presentada per Víctor Fondevilla Moreu per optar al títol de Doctor en Geologia.

La tesi doctoral ha estat dirigida per:

- Dr. Oriol Oms Llobet, Departament de Geologia de la Universitat Autònoma de Barcelona
- Dr. Àngel Galobart Lorente, Institut Català de Paleontologia Miquel Crusafont.

Dr. Oriol Oms Llobet

Dr. Àngel Galobart Lorente

Víctor Fondevilla Moreu

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Lo pus bell catalanesc del món

Lentes alzines, maternals figueres,
pollancres cristal·lins, dring de font viva,
esclarissades ombres de l'oliva,
armat esvolot mut de romegueres,
el pomerar pintat, fresques pereres,
arrodonida eufòrbia, pleta freda,
amb flors l'albó com d'engruixada seda,
roques llises, capblaus, esparregueres,
pedra amb un liquen, groc com la moneda
del temps que calla entre les caderneres,

blaus, espigats espígols, llentrisqueres
mates enceses, escanya-rossins,
fua aturada dels cabridencs pins
que s'enfilen amb xiulo a les voreres
d'arran de mar, esmusses carritxeres,
escambuixades penyes, vent gregal,
mar: esperit escènic, fonda sal,
roques brescades, conques salineres…
Ran de rel com llengua romanial
pateix flor el romaní de les caeres.

Blai Bonet
El jove (1987)

A la meva família i amics

Índex

ABSTRACT / RESUM

Abstract

The terrestrial Campanian/Maastrichtian geological and paleontological record from southwestern Europe is one of the best outside North America to study the last 15 milion years previous to the Cretaceous-Paleogene mass extinction. The narrative of the last dinosaur communities from the Ibero-Armorican Island (European Archipelago) is addressed by studying their occurrences, associated paleoenvironments and magnetostratigraphic dating.

Such integrated works in the Mesozoic portion of the Tremp Group (South-Pyrenean Basin) includes the study of footprints of the ichnogenus *Hadrosauropodus,* linked to hadrosaur dinosaurs. These tracks are abundant in the fluvial coastal plains of the upper Maastrichtian. In addition to the fluvial ecosystem, hadrosaurs also colonized the coastal environment (e.g. lagoons), as reveals the L'Espinau site (amongst other localities). In contrast, sauropods were dominant in the Campanian and the lower Maastrichtian coastal and inland environments of the region, but were still present in those settings until the uppermost Maastrichtian, as evidenced by bones, eggshell and tracks, and skin impressions. However, their remains were much scarcer than those of hadrosaurs at this age.

The dinosaur faunal succession of southwestern Europe has been improved by means of: 1) habitat understanding, 2) dating and integrating the Aude record (northern Pyrenees), 3) improving of the age calibration of the Isona sector (southern Pyrenees), and 4) integrationg of the Campanian-Maastrichtian dinosaur fossil record from the rest of France, Spain and Portugal (Provence and Iberian areas). Dating refinements permit a new model for the Maastrichtian dinosaur faunal succession. Instead of a rapid faunal shift from titanosaurian-dominated herbivorous assemblages to hadrosaur-dominated communities around the early-late Maastrichtian boundary, the achieved data show that the extinction of major clades and the apparition of new ones took place diachronously and was not time coincident. On the contrary, a coexistence period of about two milion years between older and newer Ibero-Armorican dinosaur inhabitants have been identified. This dinosaur turnover was not the response to environmental changes, but probably to faunal migration episodes after geographical barriers disappeared.

Resum

El registre geològic i paleontològic del Campanià i Maastrichtià del sud-oest europeu ofereix una de les millors oportunitats per estudiar els darrers 15 milions d'anys abans de l'extinció del Cretaci-Paleogen més enllà del registre de Nord Amèrica. En aquesta tesi doctoral s'ha estudiat i caracteritzat el registre de dinosaures i els seus paleoambients associats, i s'han datat successions sedimentàries mitjançant magnetostratigrafia amb l'objectiu d'aprofundir en el coneixement sobre les darreres comunitats de dinosaures de l'illa Ibero-Armoricana de l'Arxipèlag europeu.

Els treballs integrats realitzats a la part mesozoica del Grup Tremp (Conca sud-pirinenca) inclouen l'estudi de les petjades de l'icnogènere *Hadrosauropodus*, associat a dinosaures hadrosaures. Aquestes empremtes són molt abundants en les planes costaneres fluvials del Maastrichtià superior. A més de l'ambient fluvial, els hadrosaures també van colonitzar l'ecosistema costaner (per exemple llacunes), tal com mostra el jaciment de L'Espinau, entre d'altres localitats. Per contra, els sauròpodes van ser dominants en els ambients costaners i continentals de la regió durant el Campanià i el Maastrichtià inferior, tot i que van persistir fins el Maastrichtià terminal tal i com evidencia el seu registre osteològic, oològic i de petjades, incloent-hi impressions de pell. Amb tot, les seves restes fòssils són molt més escasses que les d'hadrosaure en aquesta edat.

La successió faunística de dinosaures del sud-oest europeu s'ha millorat gràcies a 1) la millora del coneixement sobre la distribució paleoambiental dels diferents grups, 2) la integració del registre paleontològic de de l'Alta Vall de l'Aude, una important zona fossilífera del nord dels Pirineus, gràcies al seu estudi magnetostratigràfic, 3) la millora de la calibració del sector Isona del sinclinal de Tremp, a la banda sud dels Pirineus, i 4) la integració de dades provinents del registre campano-maastrichtià de la resta d'àrees fossilíferes de França, Espanya i Portugal (Provença i Ibèria). Amb la millora de les datacions, s'ha pogut desenvolupar un nou model de canvi faunístic de dinosaures durant el Maastrichtià. Enlloc d'un reemplaçament ràpid de faunes herbívores dominades per sauròpodes cap a comunitats dominades per hadrosaures concentrat al voltant del límit entre el Maastrichtià inferior i el superior, les noves dades d'aquesta tesi mostren que les extincions i noves aparicions de clades no van coincidir en el temps. Ans al contrari, el reemplaçament faunístic entre grups de dinosaures va durar uns dos milions d'anys a la regió, existint un període de coexistència entre formes antigues i els nous habitants de l'illa Ibero-Armoricana. El canvi faunístic no es va produir com a conseqüència d'esdeveniments climàtics concrets, sinó per successives migracions durant episodes de trencament de barreres geogràfiques a Europa.

INTRODUCCIÓ

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1.1. Els dinosaures en el Cretaci Superior d'Europa

Allò que diferencia el registre continental del Cretaci superior europeu de la resta és la seva singular configuració i disposició en forma d'arxipèlag. Això, i el fet que la posició d'Europa es troba a mig camí de les grans masses terrestres de Nord Amèrica i Àsia, va conferir a les faunes de vertebrats europees una distintiva i complexa paleobiogeografia i evolució (Csiki-Sava et al., 2015).

La formació de l'arxipèlag europeu té el seu origen en la fragmentació de Pangea iniciada durant el Triàssic, la qual s'accelerà i prengué força durant el Juràssic i el Cretaci Inferior. L'expansió del fons oceànic que provocà l'obertura de l'Atlàntic central i nord es va propagar al territori europeu, dividint-lo en una sèrie de masses continentals (Seton et al., 2012). Aquest fenomen, sumat a l'increment del nivell del mar durant els inicis del Cretaci Superior (Haq et al., 1987; Miller et al., 2003) va afavorir l'aïllament d'aquestes masses, configurant l'arxipèlag d'illes en el qual van viure els darrers dinosaures d'Europa (Fig. 1.1). Aquestes illes incloien masses d'origen cratònic (situades al nord, com ara l'area Bàltica) o bé petites masses terrestres que emergien en la zona on es produïa la compressió alpina. Els canvis eustàtics i tectònics que es van produir durant el Cretaci Superior van provocar que la paleogeografia de la regió anés variant en el temps. Així, les àrees emergides s'expandien o es retreien depenent dels canvis en el nivell del mar, malgrat alguns massissos van romandre emergits durant tota l'època. Entre el Santonià i el Campanià, la convergència continental entre Ibèria i el cratό europeu, que donaria lloc a l'aixecament dels Pirineus, va provocar que diversos massissos, com el Massís Ibèric, el Massís de l'Ebre i el Massís Central francès quedessin units formant l'illa Ibero-Armoricana, la massa emergida de majors dimensions de l'Europa occidental (veure referències a Csiki-Sava et al., 2015). La present tesi doctoral agafa per tant aquest marc de referència.

En aquest context paleogeogràfic en forma d'arxipèlag, molt diferent de les grans àrees continentals de Nord Amèrica i Àsia, convivien faunes de vertebrats originàries d'Europa juntament amb representants d'altres parts del món.

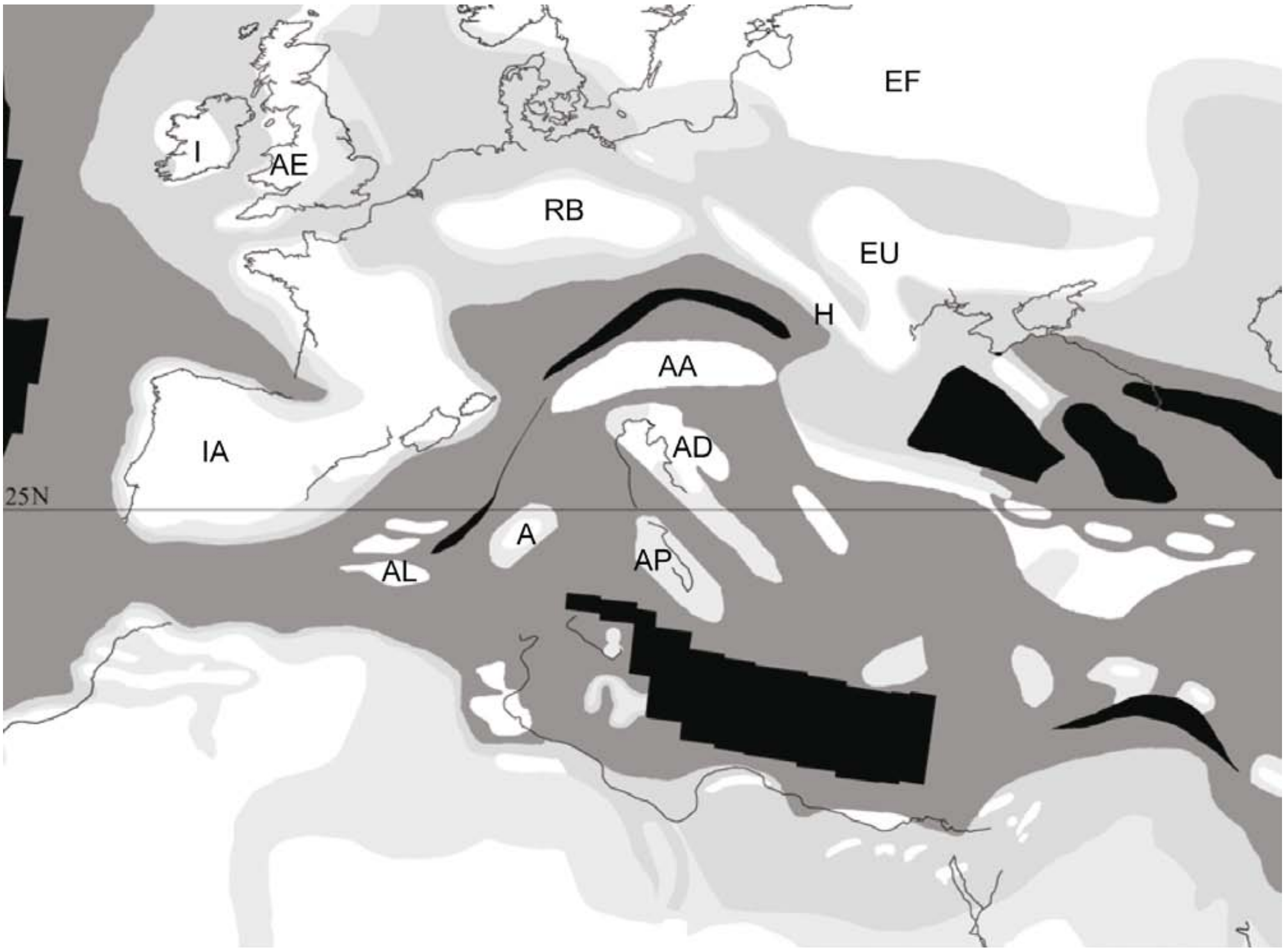

Figura 1.1. Paleogeografia d'Europa durant el Maastrichtià. Les àrees emergides estan representades en blanc, mentre que les zones oceàniques en expansió es mostren en negre. A, plataforma apenina; AA, illa Austro-Alpina; AD, illa Adriatico-Dinàrica; AE, illa Anglo-Escocesa; AL, illes de l'Alborà; AP, plataforma d'Apúlia; EF, escut fennoscandià; EU, escut ucraïnès; H, illa de Haţeg; I, illa d'Irlanda; IA, illa Ibero-Armoricana; RB, illa de Renània-Bohèmia. Modificat de Dalla Vecchia et al. (2011), modificat al seu temps de Philip et al. (2000).

Així, les faunes de dinosaures i altres grups trobades en cadascuna de les illes generalment estan caracteritzades per un tronc comú representat per llinatges autòctons o endèmics de la regió europea, com ara els amfibis paleobatràcids i discoglòssids, tortugues del clade dels solemídids i dortòkids (entre d'altres), cocodriliformes hylaeocàmpsids i atoposàurids i alguns mamífers com ara els multituberculats kogaiònids (per exemple Le Loeuff, 1991; Holtz et al., 2004; Csiki i Grigorescu, 2006; Buscalioni et al., 2008, 2011; Pereda-Suberbiola, 2009; Martin et al., 2010; Weishampel et al., 2010; Joyce et al., 2011; Wuttke et al., 2012; Pérez-Ga8rcia et al., 2014). Es considera que el grup dels anquilosaures nodosàurids és autòcton d'Europa (Weishampel et al., 2010). En canvi, dinosaures ornitòpodes basals com els rhabdodòntids, malgrat ésser presents a Europa al Cretaci Inferior (Torcida Fernández-Baldor et al., 2005), podrien ser relictes de grups amb una distribució també americana (Ősi et al., 2012). Els grups típicament europeus s'haurien disseminat per l'arxipèlag mitjançant vicariança, durant la formació del mateix a inicis del Cretaci Superior (veure revisió a Csiki-Sava et al., 2015).

A aquests grups endèmics d'Europa cal afegir-hi clades originaris del continent americà i asiàtic (Pereda-Suberbiola, 2009) que van arribar a l'arxipèlag en diverses onades o migracions durant el Cretaci Superior. Aquí s'hi inclouen els llangardaixos poliglifanodontins, aligatòrids i crocodiloids basals, alguns mamífers com els zhelèstids lainodontins i possibles marsupialiformes (Nydam et al., 2013; Puértolas et al., 2011; Archibald i Averianov, 2012; Vullo et al. 2009). Respecte els dinosaures, alguns dels tàxons d'hadrosaures lambeosarins lambeosaurinis trobats al Maastrichtià superior del sud-oest d'Europa, *Arenysaurus ardevoli* i *Blasisaurus canudoi* (Pereda-Suberbiola et al., 2009; Cruzado-Caballero et al., 2010) tenen un origen nord-americà (Cruzado-Caballero et al., 2013; Prieto-Márquez et al., 2013), mentre que altres lambeosaurins estan emparentats amb representants asiàtics (Prieto-Márquez et al., 2013), com ara el tsintaosaurini *Pararhabdodon isonensis* i l'aralosaurini *Canardia garonnensis* (Casanovas-Cladellas et al., 1993; Prieto-Márquez et al., 2013). De la mateixa manera, hadrosaures més basals del Campanià-Maastrichtià com ara *Telmatosaurus transsylvanicus* i *Tethyshadros insularis*, de les illes Adriatico-Dinàrica (Itàlia) i Haţeg (Romania, conques de Transilvània, Rusca Montana i Haţeg) tindrien també un origen a Àsia (Dalla Vecchia, 2009; Prieto-Márquez, 2010). Altres dinosaures com el dromeosàurid del Maastrichtià romanès *Balaur bondoc* també tindrien un origen asiàtic (Csiki et al., 2010; Brusatte et al., 2013). Finalment, altres grups menys documentats a Europa com ara possibles alvarezsàurids, ceratòpsids, ovirraptorosaures i therizinosauroides també podrien correspondre's amb dispersions provinents d'Àsia (Csiki-Sava et al., 2015).

Brikiatis (2014) proposa que l'arribada de faunes Americanes a Europa s'hauria produït per rutes situades a latituds elevades. En aquests connexions hi haurien influït canvis climàtics i eustàtics que es van produir durant el Cretaci Superior, afavorint un filtratge taxonòmic. D'aquesta manera, alguns grups van aconseguir arribar a Europa (per exemple els lambeosaurinis) mentre que d'altres com els tiranosàurids no (Csiki-Sava et al., 2015). Pel que fa a les dispersions provinent d'Àsia, Dalla Vecchia (2009) proposa una ruta a través de les illes volcàniques que hi havia al llarg de l'oceà de Tethys.

A més de la connexió biòtica entre Àsia i Nord Amèrica, el registre paleontològic del Cretaci Superior europeu mostra moltes afinitats amb les faunes de vertebrats de Gondwana. Així, s'han documentat peixos caraciformes, lepisosteiformes i mawsòniids, amfibis neobatracis o tortugues botremídides (per exemple Cavin et al., 1996, 2005; Pereda-Suberbiola, 2009; Szentesi i Venczel, 2010; Csiki-Sava et al., 2015). Entre els dinosaures, la connexió entre les províncies faunístiques de Gondwana i Europa està confirmada per la presència de diverses formes del clade dels teròpodes abelisàurids, incloent-hi l'espècie *Arcovenator scotae* (Tortosa et al., 2014), els quals són alhora absents en el registre asiàtic i nord americà (Carrano i Sampson, 2008). Per contra, els sauròpodes titanosaures, malgrat haver estat considerats inicialment com la prova paradigmàtica de la connexió dinosauriana amb Gondwana (per exemple Le Loeuff, 1993), mostren en ocasions formes relictes o afinitats poc clares amb formes contemporànies del sud (veure Curry Rogers, 2005 i Csiki-Sava et al., 2015), tal i com s'observa en els tàxons *Atsinganosaurus velauciensis* del Campanià superior de la Provença, i *Lirainosaurus astibiae* del Campanià superior d'Ibèria (Garcia et al., 2010; Sanz et al., 1999).

En la seva extensa revisió del registre paleontològic europeu durant el Cretaci Superior, Csiki-Sava et al. (2015) assenyalen dues qualitats que caracteritzen les faunes de vertebrats de la regió. La primera és que molts clades típicament europeus són rars o absents en altres parts del món, i la segona, que dins aquest registre hi ha un elevat grau d'endemisme en cadascuna de les masses emergides que conformaven l'arxipèlag. Així, sovint les faunes de vertebrats que van habitar una illa no es troben en les masses terrestres veïnes.

A més a més, s'ha proposat, i en alguns casos demostrat amb estudis osteohistològics, que les condicions d'insularitat sota les quals vivien els dinosaures europeus podrien haver influït en la seva evolució (Nopcsa, 1915, 1923; Pereda-Suberbiola i Galton, 2009; Benton et al., 2010; Dalla Vecchia, 2014; Csiki-Sava et al., 2015). Algunes de les formes trobades en aquesta regió presenten mides més petites que els seus parents que habitaven en les grans masses continentals d'Àsia i Amèrica. Aquest fet pot ser indicatiu d'un enanisme insular com a resposta a la manca de recursos que els ambients insulars imposen. Mentre que alguns casos de l'illa de Haţeg semblen ben justificats amb la presència de formes adultes de mida petita, com el sauròpode titanosaure *Magyarosaurus dacus*, l'hadrosaure *Telmatosaurus transsylvanicus,* el rhabdodòntid *Mochlodon vorosi* i el nodosàurid *Struthiosaurus* (Pereda-Suberbiola i Galton, 2009; Stein et al., 2010; Benton et al., 2010; Ősi et al., 2012, 2014) altres tàxons de la mateixa illa presenten mides grans o estàndards (veure Stein et al., 2010). Dalla Vecchia (2009) va descriure adaptacions a un hàbitat insular en *Tethyshadros insularis* (Itàlia). A l'illa Ibero-Armoricana també s'ha proposat una condició d'enanisme pel sauròpode titanosaure del Campanià Superior *Lirainosaurus astibiae* (Company, 2011). Amb tot, altres titanosaures de la mateixa regió i de similar època, com

Ampelosaurus atacis no són nans (Klein et al., 2012). Referint-se als hadrosaures de l'illa, Dalla Vecchia (2014) i Dalla Vecchia et al. (2014) comenten que si bé generalment les restes trobades en l'àrea dels Pirineus presenten mides més petites que les formes adultes nord americanes, hi ha alguns exemplars amb mesures comparables a aquests, cosa que posa en dubte un escenari de faunes nanes generalitzat al sud-oest europeu.

1.2. El registre de l'illa Ibero-Armoricana

La present tesi doctoral centra el seu estudi en la successió dels dinosaures i el seu marc geològic al sud-oest europeu, el qual conformava l'illa Ibero-Armoricana durant el Cretaci Superior. Per qüestions pràctiques, es divideix en les àrees d'Ibèria, que inclou la major part del registre espanyol i el de Portugal, els Pirineus, tant la vessant nord com la sud, i la Provença al sud-est de França (Fig. 1.2). A continuació es fa un repàs històric del descobriment dels diferents jaciments i restes de dinosaures i es planteja l'estat del coneixement pel que fa a la recerca d'aquest grup durant el Cretaci terminal de la regió.

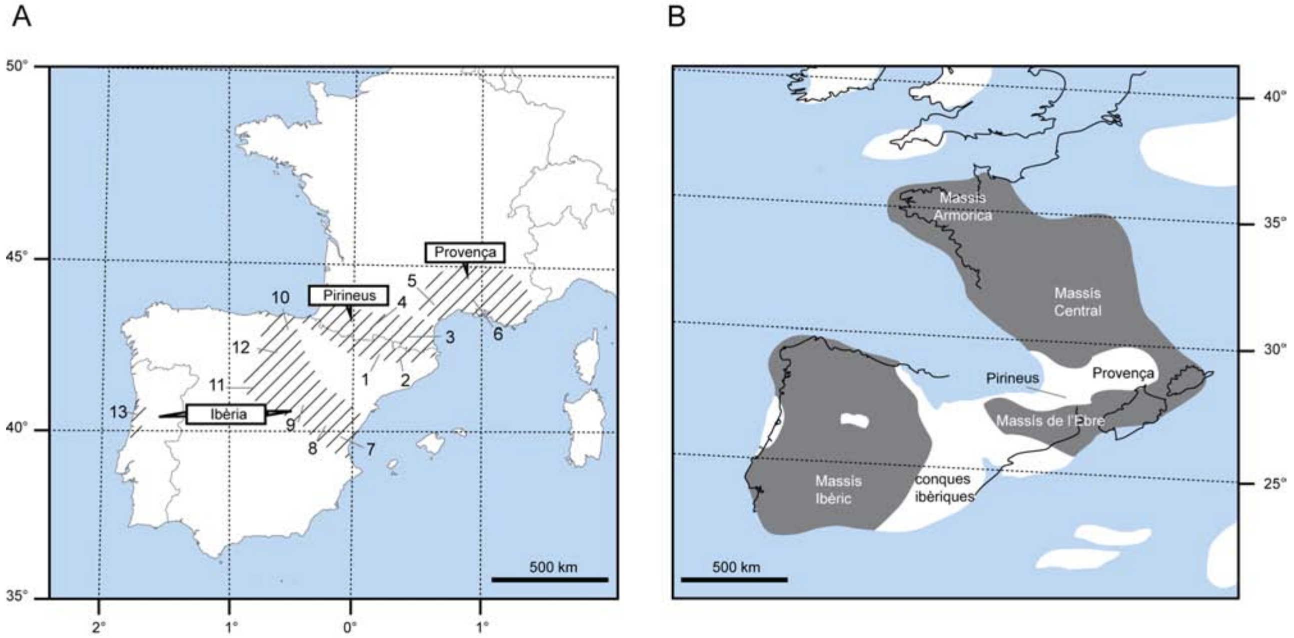

Figura 1.2. El sud-oest europeu. **A**, situació geogràfica de les principals zones fossilíferes. 1, sinclinals de Tremp, Àger i Coll de Nargó; 2, Sinclinal de Vallcebre; 3, Plantaurel, Aude i Corberes; 4, Petits Pirineus i Alta Garona; 5, Hérault-àrea del Llenguadoc; 6, Sinclinal de l'Arc-Provença; 7, La Solana; 8, Chera; 9, Lo Hueco i Sacedón; 10, Laño-Condado de Treviño; 11, Armuña; 12, jaciments de Burgos; 13, Viso, Aveiro i Taveiro. **B**, paleogeografia de l'illa Ibero-Armoricana durant el Maastrichtià. Modificat de Vila et al. (2016). Cortesia de Bernat Vila i Albert Garcia Sellés.

1.2.1. Breu història dels descobriments

Les primeres restes de dinosaures del Cretaci Superior trobades a la regió van ser documentades per Matheron (1846, 1869) als departaments francesos de les Bouches-du-Rhône i Var, a la Provença. A partir del 1850 es van començar a citar i documentar ossos i ous de dinosaures al nord dels Pirineus (departaments d'Ariège i Aude) i Hérault (Le Loeuff, 1992; Csiki-Sava et al., 2015). A la Península Ibèrica, les primeres restes de dinosaures d'aquesta edat van ser citades a Portugal per Sauvage (1897-1898) a la localitat de Viso. Depéret (1900) va ampliar els descobriments de restes de dinosaure al departament de Hérault. Alguns fòssils trobats a la zona serien posteriorment descrits per Nopcsa (1929).

Les primeres troballes de dinosaures al sud dels Pirineus no es documentarien fins el 1927 en una nota de l'enginyer Joaquín Maluquer sobre restes de rèptils a la Conca de Tremp (Catalunya). Marín i Bataller (1929) van citar restes de rèptils pels voltants de la central hidroelèctrica de Tremp. Les prospeccions petrolíferes fetes en aquesta zona cap al 1940 van permetre recuperar restes prop de Suterranya, les quals van ser donades a l'Instituto Geológico i Minero de España. També a la zona, Walter Khüne va conduir prospeccions i excavacions entre el 1953 i el 1954 que van resultar en el descobriment de restes de sauròpode al jaciment d'Orcau-1 (Talens, 1955a i b). També durant els anys 50, Dughi i Sirugue (1957) van centrar-se en l'estudi de les restes d'ous fòssils dels voltants d'Aix-en-Provence.

Lapparent (1947) va realitzar una important tasca de revisió del material francès, alhora que va ampliar el seu camp de recerca a Espanya (Lapparent i Aguirre, 1956; Lapparent et al., 1957) i en la revisió del material portuguès de Viso (Lapparent i Zbyszewski, 1957). Aquesta recerca va esdevenir un punt de partida per a futures investigacions en les dècades següents (Csiki-Sava et al., 2015).

En els darrers 30 anys la recerca dels dinosaures del Cretaci terminal a Espanya es va reemprendre gràcies a excavacions sistemàtiques dutes a terme en dipòstis del Campanià-Maastrichtià a les províncies de Lleida, Huesca, Barcelona, Burgos (incloent-hi el Condado de Treviño, dins Àlava), Cuenca, Segòvia i València. De la mateixa manera, els jaciments del sud de França van aquirir un renovat interès científic en les darreres dècades (veure referències a Csiki-Sava et al., 2015 i capítol 2).

1.2.2. Les faunes de dinosaures del Campanià-Maastrichtià del sud-oest europeu

El registre de dinosaures del Campanià i del Maastrichtià trobat a França, Espanya i Portugal és un dels més rics d'Europa, i es troba entre els més importants del món pel que fa al Cretaci terminal. A partir dels anys 90 un gran nombre de treballs científics van permetre avançar en el camp de la taxonomia i diversitat, la paleobiogeografia i la successió faunística en aquesta regió (per exemple, entre molts altres, Le Loeuff 1991, 1993, 1995; Le Loeuff et al., 1994; Antunes i Sigogneau-Russell, 1992, 1996; Casanovas-Cladellas et al., 1993; Casanovas et al., 1999a i b; Buffetaut et al., 1996, 1997; Laurent et al., 1997, 1999, 2001, 2002; López-Martínez et al., 1999, 2001; López-Martínez, 2003; Pereda-Suberbiola, 1999; Pereda-Suberbiola et al., 2003, 2009a i b, 2015; Garcia et al., 1999, 2000, 2010; Garcia i Pereda-Suberbiola, 2003; Allain i Pereda-Suberbiola, 2003; Ortega et al., 2015; Company et al., 2009; Riera et al., 2009; Valentin et al., 2012; Vila et al., 2012, 2016; Prieto-Márquez et al., 2013; Dalla Vecchia et al., 2014; Csiki-Sava et al., 2015; Pérez-Garcia et al., 2016; Díez Díaz et al., 2016). Gràcies a tota aquesta recerca, s'han pogut identificar dues associacions de dinosaures que es van succeir durant el Cretaci terminal a l'illa Ibero-Armoricana:

- Durant el Campanià i el Maastrichtià inferior, la regió estava dominada per una associació de dinosaures formada per sauròpodes titanosaures, ornitòpodes rhabdodòntids, anquilosaures nodosàurids i teròpodes abelisàurids, celurosàurids i dromeosàurids. Possiblement, però en freqüències molt més baixes, hi havia també hadrosaures i altres teròpodes com ara ornitomimosaures i troodòntids.

- A partir del Maastrichtià superior, hi va haver un canvi faunístic que va provocar que l'associació anterior fos reemplaçada per una altra dominada per hadrosaures. Contràriament a la idea original de Le Loeuff et al. (1994), aquesta associació també estava integrada en menor mesura per titanosaures i teròpodes. Per contra, els rhabdodòntids i els nodosàurids es van extingir a la regió en aquest període.

Aquest canvi s'hauria produït per diverses migracions de noves faunes que haurien arribat a l'illa Ibero-Armoricana durant el Maastrichtià superior (per exemple Prieto Márquez et al., 2013; Cruzado-Caballero et al., 2013; Csiki-Sava et al., 2015). En aquest sentit, l'arribada de dinosaures lambeosaurins hauria estat el principal impulsor del reemplaçament o canvi faunístic en pertorbar les poblacions de dinosaures herbívors (Vila et al., 2016). Aquests autors van analitzar numèricament els canvis que es produiren durant el Maastrichtià al sud-oest europeu (Fig. 1.3). Mentre que en l'associació del Campanià-Maastrichtià inferior els sauròpodes titanosaures eren el grup herbívor més abundant (52%), els rhabdodòntids i els nodosàurids tenien una presència substancial en les comunitats (abundàncies del 30 i 18%, respectivament). En canvi, després del canvi faunístic, els hadrosaures esdevingueren, de llarg, el clade d'herbívors dominant (75%), mentre que els sauròpodes experimentaren un fort declivi (disminuïnt a un abundància del 9%).

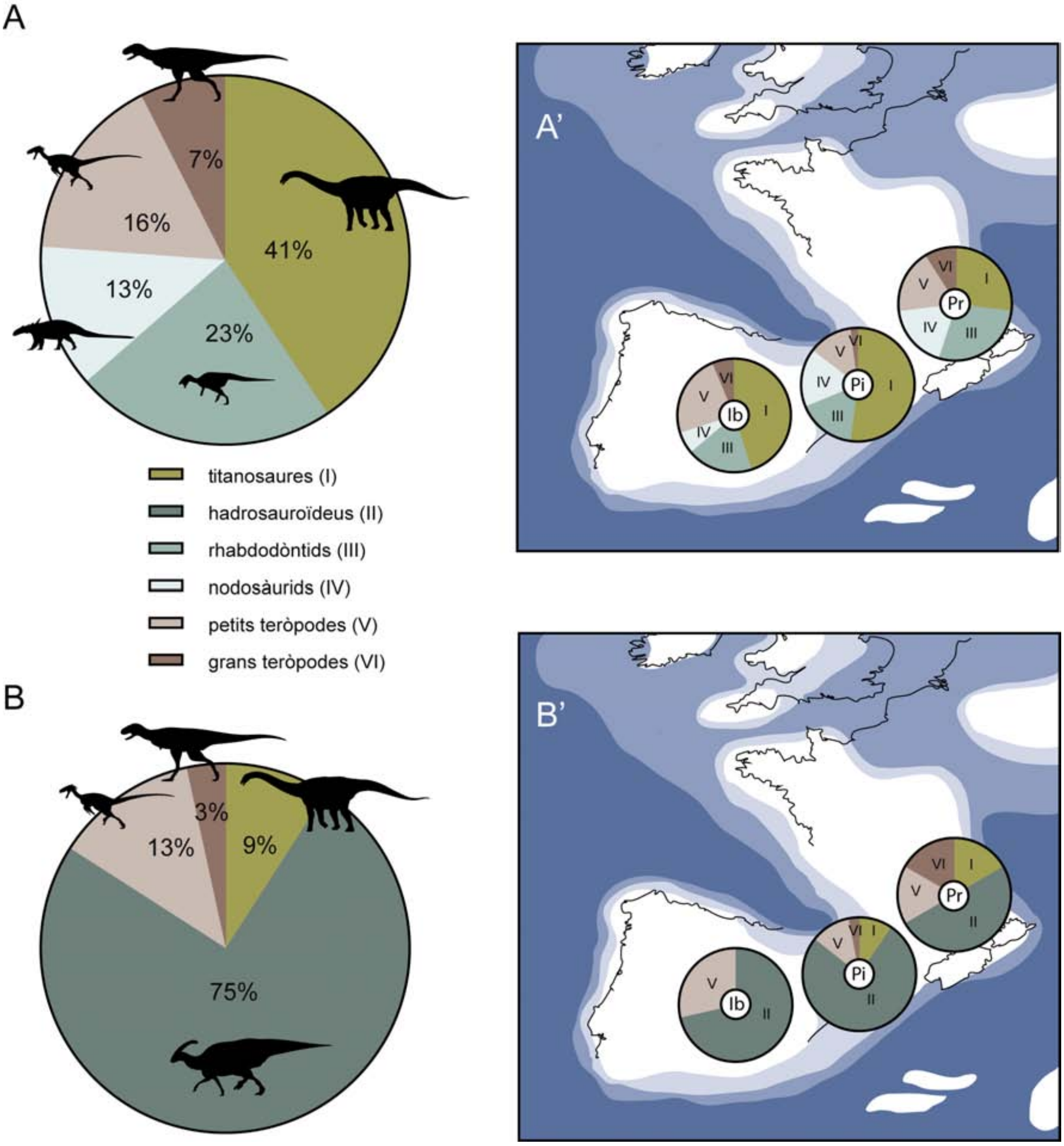

Figura 1.3. Proporcions relatives de cada grup taxonòmic durant el Cretaci terminal del sud-oest europeu (illa Ibero-Armoricana). **A**, associació faunística del Campanià-Maastrichtià inferior. A', proporcions per a cada sector (Ibèria, Pirineus i Provença). **B**, associació faunística del Maastrichtià superior. B', proporcions per a cada sector. Modificat de Vila et al. (2016). Cortesia de Bernat Vila i Albert Garcia Sellés.

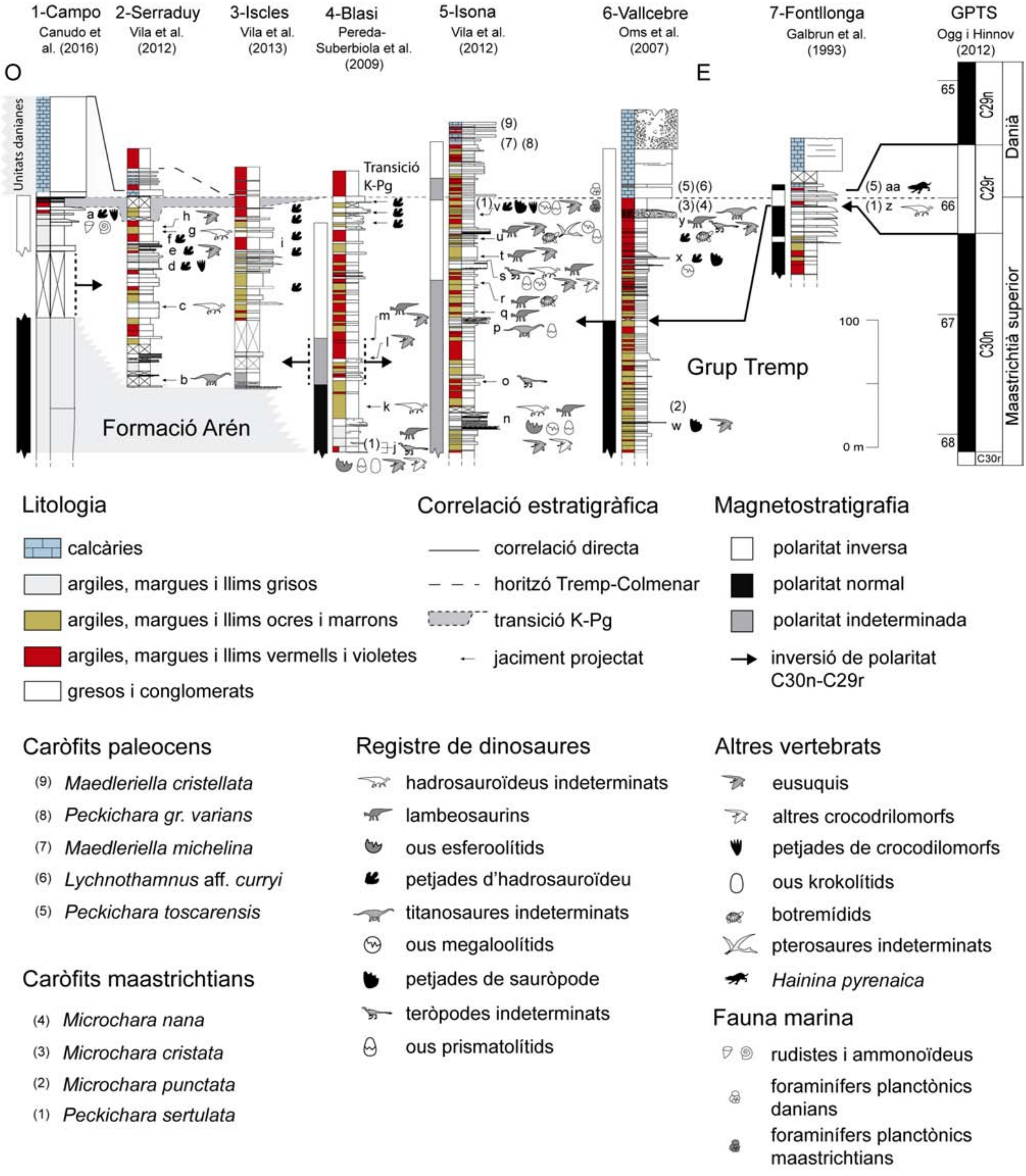

Figura 1.4. La transició K-Pg en les seccions continentals del sud dels Pirineus correlacionades amb l'escala estàndard (GPTS) i situació dels jaciments de vertebrats conjuntament amb el seu contingut paleontològic. La secció de Fontllonga, situada al sud de la resta, s'ha projectat a l'est per facilitar la correlació. Jaciments: a, Campo; b, Serraduy; c, Barranco de Serraduy 2; d, Serraduy Sur i Serraduy Norte; e, Dolor-3 i Barranco de Serraduy 4; f, Fornons 3; g, Amor 2; h, Barranco de Serraduy 5 i Amor-3; i, Iscles 1 a 5; j, Blasi 1 a 3 i Pont d'Orrit; k, Blasi 3.4; l, Elías; m, Blasi 4-5, n, Basturs Poble i Serrat del Rostiar; o, Cabana del Gori 1; p, Molí del Baró-2, q, Les Llaus; r, Euroda Nord i Costa de la Serra 2; s, Molí del Baró-1; t, Sant Romà d'Abella; u, Barranc de Torrebilles 2, 4, 5 i Serrat del Pelleu; v, Barranc de Guixers-2 i Camí del Soldat; w, Torrent de l'Esdavella; x, La Pleta Vella, La Pleta Resclosa i La Nou 1; y, jaciments

del Gres amb Rèptils (Reptile Sandstone unit); z, Fontllonga R; aa, Fontllonga-3. Referències emprades: Galbrun et al. (1993); Oms et al. (2007); Pereda-Suberbiola et al. (2009a i b); Ogg i Hinnov (2012); Vila et al. (2012, 2013); Díez-Canseco et al. (2014). Modificat de Canudo et al. (2016, Annex 1).

Malgrat aquest canvi de dominància, la proporció entre herbívors i carnívors es va mantenir sense gaires canvis en l'associació de dinosaures resultant del reemplaçament. Així, mentre els herbívors representaven un 76% i els carnívors un 24% durant el Campanià i el Maastrichtià inferior, durant el superior els primers representaven el 84% i els segons un 16%. Aquests percentatges són similars als observats en les comunitats del Cretaci terminal de Nord Amèrica (Vila et al., 2016; per exemple veure White et al., 1998 i Brinkman et al., 2005).

Segons Vila et al. (2016), aquest canvi faunístic hauria provocat una situació d'estrès en les poblacions de dinosaures de l'illa Ibero-Armoricana durant els darrers 3 milions d'anys del Maastrichtià, que les hauria deixat vulnerables de cara a l'extinció del Cretaci-Paleogen (K-Pg). Aquests autors van detectar un lleu declivi de la diversitat total de dinosaures en aquest període, malgrat el grup dels hadrosaures mostra una gran diversitat taxonòmica durant el Maastrichtià superior. Així, principalment el reemplaçament faunístic que es va produir a la regió durant el Maastrichtià va comportar un canvi en l'estructura de les comunitats d'herbívors més que no pas una disminució de la diversitat abans de l'extinció de fa 66 milions d'anys. En aquest sentit, Canudo et al. (2016, Annex 1), en la seva revisió del material paleontològic de les seccions continentals que contenen la transició K-Pg al sud dels Pirineus, van observar que les restes de dinosaures i altres vertebrats eren abundants prop del límit d'extinció, en el cron C29r (Fig. 1.4). Ara bé, aquests autors esmenten la possibilitat de que hi hagi biaixos tafonòmics en alguns grups com ara els teròpodes, inusualment escassos en aquest cron. A més, la dificultat de localitzar amb precisió el límit K-Pg a la regió dificulta l'estudi d'aquesta extinció.

ANTECEDENTS, OBJECTIUS I ESTRUCTURA DE LA TESI DOCTORAL

2

2.1. Antecedents, motivació i objectius de la tesi doctoral

A inicis de la dècada dels 90 es van iniciar els primers estudis sistemàtics del registre fòssil de dinosaures de la zona sud dels Pirineus, principalment en els dipòsits Maastrichtians dels Sinclinals de Tremp i Àger. L'Institut de Paleontologia de Sabadell (actualment Institut Català de Paleontologia Miquel Crusafont, ICP) va liderar aquesta primera recerca, de la qual destaquen els primers estudis taxonòmics que donaren lloc a la definicó de *Pararhabdodon isonensis* (Casanovas-Cladellas et al., 1993), el primer (i de moment l'únic) dinosaure definit a Catalunya. En aquest primer període destaca l'estudi magnetostratigràfic dels dipòsits Maastrichtians del Sinclinal d'Àger per part de Galbrun et al. (1993), que va posar les bases per al posterior estudi del registre de dinosaures des d'un punt de vista de successió faunística. Una de les primeres propostes en aquest sentit és el treball de Galbrun (1997).

L'interès per l'estudi del registre de dinosaures del Campanià-Maastrichtià a la zona sud dels Pirineus va rebre un gran impuls a les acaballes de la dècada dels 90 i la primera dècada del 2000, gràcies als treballs de la Dra. Nieves López Martínez, de la Universidad Complutense de Madrid. La seva recerca es va centrar en el ric registre geològic i paleontològic de les àrees de Tremp i Àger, donant especial èmfasi en la potencial aportació que les faunes de dinosaures sud-pirinenques podien aportar a l'estudi dels darrers milions d'anys d'evolució d'aquest grup i la seva extinció. A tall d'exemple, es poden destacar una sèrie d'articles centrats en l'establiment d'un marc cronostratigràfic pels diferents jaciments de dinosaures (López-Martínez et al., 1998; López-Martínez et al., 2001); d'altres sobre l'estudi de les postes d'ou i ambients de nidificació (Sanz et al., 1995; López-Martínez et al., 2000); i sobre la diversitat faunística just abans del límit Cretaci-Paleogen en el context pirinenc (López-Martínez et al., 1999; López-Martínez, 2003).

A partir de la segona meitat de la primera dècada del 2000 l'estudi del registre de dinosaures sud-Pirinenc adquireix novament un gran impuls amb la recerca conjunta de l'ICP i la Universitat Autònoma de Barcelona, i de la Universidad de Zaragoza, la qual dura fins l'actualitat. Així, la recerca geològica pel que fa a l'estratigrafia, la datació de successions sedimentàries, la sedimentologia i els paleoambients es va fer indestriable de l'estudi pròpiament paleontològic de les restes fòssils de dinosaure (per exemple veure Oms et al., 2007). En el marc de la col·laboració entre aquestes institucions es desenvolupen tres tesis doctorals per part dels doctors Bernat Vila, Violeta Riera i Albert G. Sellés. La primera d'elles (Vila, 2010) se centrava en l'estudi icnològic, els modes de nidificació i la diversitat dels sauròpodes titanosaures del sud dels Pirineus. Riera

(2010) realitzà una aportació significativa en el coneixement del marc estratigràfic del Maastrichtià sud-pirinenc, mentre que Sellés (2012) va dur a terme una revisió del registre oològic dels dinosaures de la regió i actualitzà i amplià l'ús de les oospècies com a potencials marcadors biostratigràfics (idea inicialment desenvolupada per les autores franceses Vianey-Liaud i Garcia, 2000 i Garcia i Vianey-Liaud, 2001). A més a més, a aquestes tesis doctorals cal afegir-hi les realitzades per estudiants de la Universidad de Zaragoza. Així, Penélope Cruzado Caballero va estudiar les formes d'hadrosaures presents en el sector occidental del Sinclinal de Tremp (jaciments de Blasi, a Areny de Noguera/Arén), mentre que Eduardo Puértolas Pascual va aprofundir en el coneixement de les diferents formes de cocodrilomorfs que acompanyaven a les faunes de dinosaures a la regió.

Partint de l'estat del coneixement sorgit de les tres primeres tesis doctorals esmentades es van dissenyar dos projectes coordinats, els quals van ser concedits pel Ministerio de Ciencia e Innovación (actualment el Ministerio de economía y Competitividad): "El fin de una era: La extinción de los dinosaurios: una prespectiva europea" i "El fin de una era: Registro geológico continental del Cretácico Superior pirenaico". Aquests projectes tenien com a principal objectiu, entre d'altres, l'obtenció d'un marc cronostratigràfic actualitzat del sud-oest europeu, que permetés millorar el coneixement sobre els canvis faunístics que es van produir en aquesta regió durant el Maastrichtià. Aquesta voluntat de millora del coneixement de la successió de dinosaures, per tant, esdevé la principal línea de recerca seguida en aquesta tesi doctoral.

Qualsevol estudi sobre successions de faunes en un temps determinat, on es contemplen primeres aparicions, reemplaçaments i extincions d'espècies o grups en el registre estratigràfic ha de tenir en compte la possible existència de factors tafonòmics i/o ambientals. Així, la desaparició d'un clade pot ser conseqüència d'una extinció real del grup o bé un producte d'un canvi ambiental en l'àrea considerada. En aquest sentit, Riera et al. (2009) i Riera (2010) van concloure que el reemplaçament de faunes proposat inicialment per Le Loeuff (1994), en el qual els hadrosaures esdevenien el grup de dinosaures dominant al sud-oest europeu, no era real, sinó el producte d'un biaix de fàcies o paleoambients disponibles en el registre geològic del Maastrichtià superior. Així, els sauròpodes, suposadament dominants en les fàcies costaneres i transicionals del Maastrichtià inferior, experimenten un aparent declivi a causa de la menor disponibilitat d'aquests ambients durant el Maastrichtià superior. En canvi, en aquest període les fàcies fluvials dominades per hadrosaures afloren més extensament a causa del context regressiu que es dóna a la regió, generant un aparent domini d'aquest grup respecte els sauròpodes. Aquesta idea partia amb una sèrie de problemes ja en el moment de ser plantejada. Tal com comenta Dalla Vecchia et al. (2014), el domini dels sauròpodes en el medi costaner i transicional no està clar, donat que alguns dels jaciments més importants d'hadrosaures dels Pirineus es donen precisament en aquest tipus d'ambient (per exemple els jaciments de Blasi, a la comarca de la Ribagorça, província d'Osca i els jaciments de Larcan i Tricouté de l'Alta Garona, a la vessant francesa (Pereda-Suberbiola et al., 2009a; Laurent et al., 2002). Per tant, es fa indispensable avaluar i estudiar en detall les ocurrències d'aquests dos grups de dinosaures (especialment aquelles restes *in situ*, com ara les petjades) pel que fa a la qüestió dels paleoambients que van habitar, per tal de confirmar o descartar possibles biaixos com el proposat per Riera (2010).

Referent al context geològic, en la present tesi doctoral es fa palesa la necessitat de millorar la datació dels dipòsits maastrichtians del sector est del Sinclinal de Tremp, és a dir, el sector d'Isona. Aquest indret presenta alguns dels millors afloraments de roques maastrichtianes de tot el registre dels Pirineus, alhora que conté un ric registre de jaciments de dinosaure (veure Riera et al., 2009 i Riera, 2010). Així, qualsevol proposta de successió faunística del Maastrichtià del sud-oest europeu requereix d'una bona datació de Cretaci terminal d'Isona. No obstant això, a diferència dels Sinclinals d'Àger i Vallcebre, l'estudi magnetostratigràfic realitzat a en aquest sector va donar com a resultat una datació ambígua, on molts dels jaciments (entre ells alguns dels més importants, com ara Basturs Poble) quedaven inclosos en zones de polaritat indeterminada (Riera, 2010; Vila et al., 2012). Aquesta situació dificulta la correcta datació dels jaciments de dinosaures d'Isona en el marc temporal del Maastrichtià. De manera similar, algunes de les localitats més importants del registre del sud de França, com ara Bellevue (la localitat tipus del sauròpode *Ampelosaurus atacis*), restaven datats de forma indeterminada entre el Campanià i el Maastrichtià.

En resum, aquesta tesi tracta de donar resposta a una sèrie de qüestions sobre els dinosaures del sud-oest Europeu que són objecte de debat en la literatura recent, com ara la influència dels paleoambients en els estudis de successió faunísitica, i en la validesa del marc cronostratigràfic emprat per a determinar les extincions i primeres aparicions dels diferents grups de dinosaures.

Els objectius concrets són:

- Estudiar els paleoambients on s'han trobat evidències (tant en forma d'acumulacions d'ossos com restes *in situ*) dels hadrosaures i dels sauròpodes en jaciments nous i d'altres de coneguts de la vessant sud i nord dels Pirineus, per tal de determinar l'existència o no de preferències de tipus ambiental entre els dos grups i avaluar la seva dominància (Capítols 5, 6, 7, 8).

- Calibrar temporalment mitjançant estudis bio- i magnetostratigràfics successions sedimentàries considerades clau respecte al contingut paleontològic de dinosaures que contenen, com ara el sector oriental del Sinclinal de Tremp (Isona) i el jaciment de Bellevue, a l'Alta Vall de l'Aude, al sud de França (Capítols 8 i 9).

- Integrar les dades pròpies i les existents per discutir escenaris proposats prèviament sobre la successió de dinosaures del sud-oest europeu i plantejar una millora actualitzada amb les aportacions derivades dels punts anteriors (Capítol 10 i Discussió).

2.2. Estructura de la tesi

La tesi doctoral s'estructura com a un compendi de publicacions en el qual els continguts es corresponen a articles, ja sigui publicats en revistes SCI (capítols 5, 6, 8 i 9), enviats a revisar (capítol 7) o en preparació (capítol 10), a excepció dels capítol introductoris (capítols 1, 2, 3 i 4) i els de discussió i conclusions (capítols 11 i 12).

Tots aquests articles tracten de donar resposta als objectius enunciats en l'apartat 2.1. Així, tots ells tenen com a fil conductor el refinament i millora del coneixement sobre la successió de dinosaures durant el Cretaci terminal del sud-oest europeu, abordant-la des de diferents perspectives. Pel que fa a la discussió, aquesta se centra en contrastar els resultats obtinguts amb dels objectius inicials.

A més a més, en els annexos hi apareixen dos articles més que, donada la menor implicació en ells per part d'un servidor, s'ha optat per no incloure'ls en el cos de la tesi doctoral. En aquest sentit, la major part de la recerca científica que contenen va ser realitzada per altres investigadors. No obstant això, aquests articles aporten dades importants pel que fa al context geològic de la zona dels Pirineus i són freqüentment citats en el cos de la tesi, de manera que s'ha considerat oportú incloure'ls per facilitar la seva consulta.

El fet que a l'hora de determinar l'ordre dels articles no s'hagi seguit la data de publicació de forma estricta, sinó la correspondència temàtica entre ells, dóna lloc a petites incoherències inevitables com ara que en un capítol aparegui citat un article del capítol següent. A més, l'evolució de l'estat del coneixement durant la mateixa tesi propicia que alguns continguts dels articles quedin esmenats o fins i tot refutats en els capítols posteriors, tal i com és habitual en el mètode científic.

Els articles inclosos com a capítols en la present tesi doctoral són:

- Vila, B., Oms, O., **Fondevilla, V**., Gaete, R., Galobart, À., Riera, V., Canudo, J.I. (2013) The Latest Succession of Dinosaur Tracksites in Europe: Hadrosaur Ichnology, Track Production and Palaeoenvironments. *PLoS ONE* **8**(9): e72579. doi:10.1371/journal.pone.0072579 (Capítol 5).

- **Fondevilla, V**., Vila, B., Galobart, À., Oms, O. (2016). Skin impressions of the last European dinosaurs. *Geological Magazine*, 1-6 (Capítol 6).

- **Fondevilla, V**., Vicente, A., Battista, F., Sellés, A. G., Dinarès-Turell, J., Martín-Closas, C., Anadón, P., Vila, B., Razzolini, N. L., Galobart, À., Oms, O. (en revisió). Genesis and taphonomy of the L'Espinau dinosaur bonebed, a singular lagoonal site from the Maastrichtian of South-Central Pyrenees. *Sedimentary Geology* (Capítol 7).

- **Fondevilla, V**., Dinarès-Turell, J., Vila, B., Le Loeuff, J., Estrada, R., Oms, O., Galobart, À. (2016). Magnetostratigraphy of the Maastrichtian continental record in the Upper Aude Valley (northern Pyrenees, France): Placing age constraints on the succession of dinosaur-bearing sites. *Cretaceous Research* **57**, 457-472 (Capítol 8).

- **Fondevilla, V**., Dinarès-Turell, J., Oms, O. (2016). The chronostratigraphic framework of the South-Pyrenean Maastrichtian succession reappraised: Implications for basin development and end-Cretaceous dinosaur faunal turnover. *Sedimentary Geology* **337**, 55-68 (Capítol 9).

- **Fondevilla, V**., et al. (en preparació). Dinosaur succession during the end-Cretaceous of southwestern Europe. A review (Capítol 10).

Els articles que apareixen com a annexos són els següents:

- Canudo, J.I., Oms, O., Vila, B., Galobart, À., **Fondevilla, V**., Puértolas-Pascual, E., Sellés, A. G., Cruzado-Caballero, P., Dinarès-Turell, J., Vicens, E., Castanera, D., Company, J., Burrel, L., Estrada, R., Marmi, J., & Blanco, A. (2016). The upper Maastrichtian dinosaur fossil record from the southern Pyrenees and its contribution to the topic of the Cretaceous–Palaeogene mass extinction event. *Cretaceous Research* **57**, 540-551 (Annex 1).

- Oms, O., **Fondevilla, V**., Riera, V., Marmi, J., Vicens, E., Estrada, R., Anadón, P., Vila, B., & Galobart, À. (2016). Transitional environments of the lower Maastrichtian South-Pyrenean Basin (Catalonia, Spain): The Fumanya Member tidal flat. *Cretaceous Research* **57**, 428-442 (Annex 2).

CONTEXT GEOLÒGIC

3

En aquest capítol es descriu el context geològic dels jaciments del Cretaci Superior de la Península Ibèrica i del sud de França. La tesi doctoral principalment se centra en l'àrea dels Pirineus (tant la vessant nord com la sud), de manera que en els capítols 5, 6, 7, 8 i 9 s'han descrit extensament les diferents zones d'estudi. En conseqüència, en el present capítol només se'n fa un resum.

La resta d'àrees que conformaven l'illa Ibero-Armoricana es tracten en major o menor mesura en el capítol 10. Per tant, a més de l'àrea dels Pirineus, a continuació s'esmenten les principals característiques de cadascun dels jaciments o àrees fossilíferes de la regió.

3.1. Els Pirineus

Els Pirineus constitueixen una serralada alpina amb una orientació d'est a oest, des de la Provença al Cantàbric, desenvolupada durant la col·lisió de les plaques Ibèrica i Europea entre el Cretaci Superior i el Miocè inferior. La serralada consisteix en un sòcol o basament paleozoic i cobertores sedimentàries (Fig. 3.1). Aquestes últimes inicialment es van formar durant la fase extensiva mesozoica que abastà fins el Cretaci Inferior, però a partir del Cretaci Superior les conques sedimentàries van esdevenir conques d'avantpaís en iniciar-se la fase compressiva.

La serralada pren la forma d'un ventall asimètric amb plecs i encavalcaments de doble vergència que defineixen les zones nord- i sud-pirinenques (Fig. 3.1B, C). L'asimetria ve donada pel fet que les làmines encavalcants que es van desenvolupar a la vesant sud van assolir majors desplaçaments (per exemple les làmines encavalcants del Montsec, Cadí, Serres Marginals i Pedraforca) que les de la banda nord (Muñoz, 1992; Teixell i Muñoz, 2000; Riera, 2010; Oms et al., 2014).

3.1.1. El Cretaci Superior continental a la vessant sud

La sedimentació continental a la vessant sud dels Pirineus s'inicià a partir del Maastrichtià inferior (Oms et al., 2016, Annex 2), desenvolupant les fàcies continentals tradicionalment anomenades com a Garumnianes. Aquestes van ser identificades per Leymerie (1868) a la zona de Coll de Nargó (Alt Urgell, Lleida). Més endavant, Vidal (1873, 1874, 1875, 1921) va extendre aquest terme a Vallcebre (Berguedà, Barcelona) i Isona (Pallars Jussà, Lleida; Fig. 3.2).

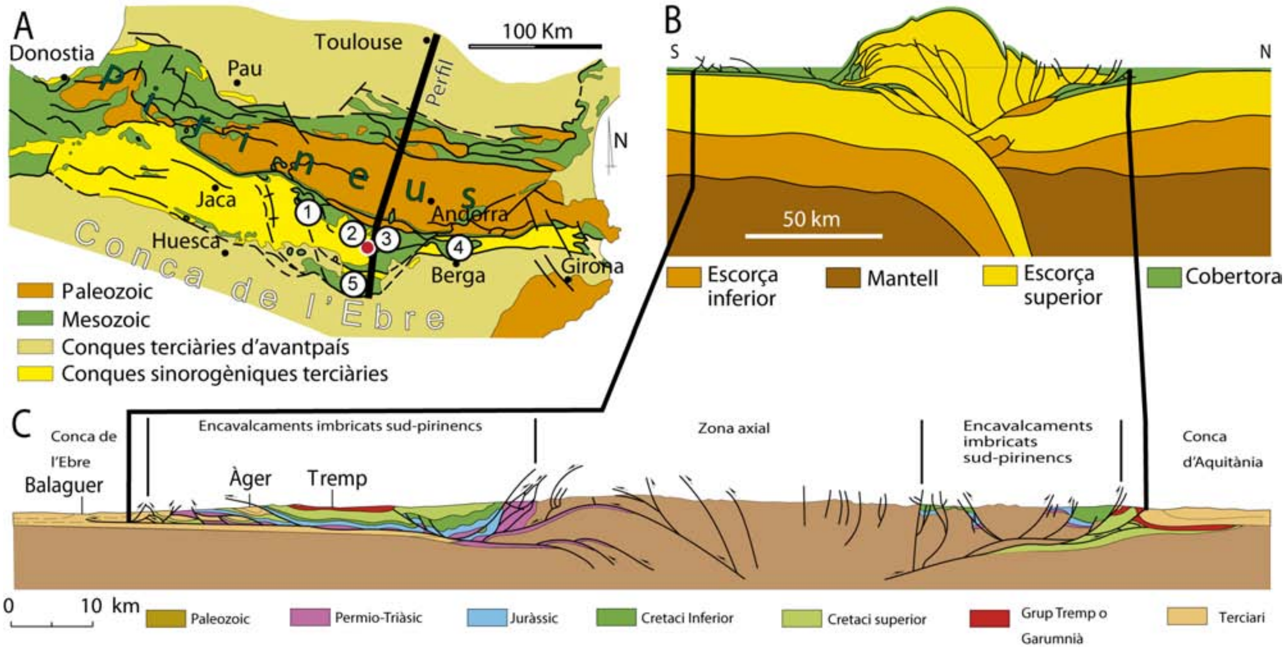

Figura 3.1. Estructura general dels Pirineus basada en el perfil sísmic ECORS (Muñoz, 1992; Berástegui et al., 1993). **A**, mapa geològic simplificat amb la localització del perfil i les zones de Campo (1), Areny/Arén (2), Tremp-Isona (3), Vallcebre (4), i Àger (5). **B**, estructura de l'escorça dels Pirineus. **C**, tall geològic dels Pirineus. Modificat d'Oms et al. (2014).

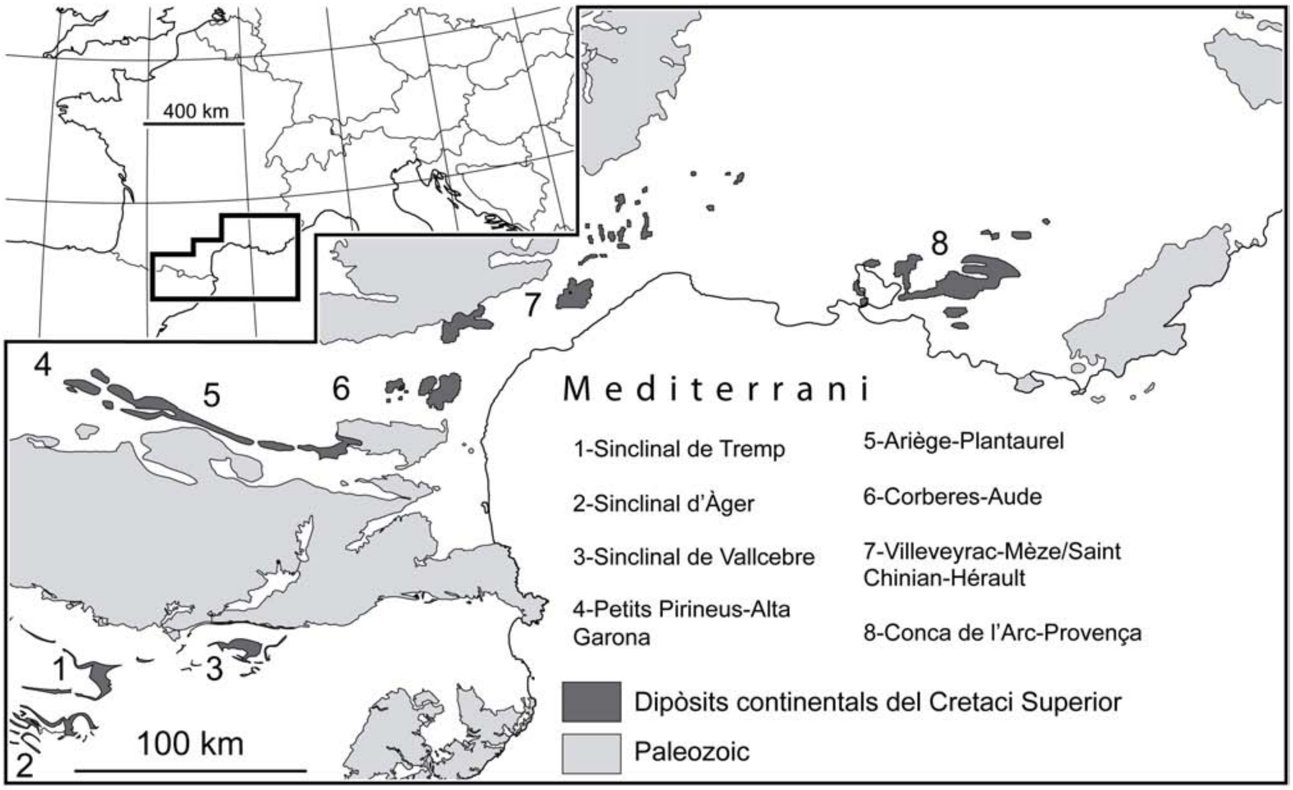

Figura 3.2. Situació dels dipòsits continentals del Cretaci Superior a la zona dels Pirineus i la Provença. S'hi indiquen les diferents àrees o sinclinals. Pel que fa a la vessant sud dels Pirineus, els dipòsits continentals fan referència a les fàcies Garumnianes. Modificat d'Oms et al. (2007).

El terme Garumnià, però, va ser objecte de debat en termes de cronostratigrafia i litostratigrafia (per exemple Bataller, 1958). Mey et al. (1968) va definir la Formació Tremp i la va adscriure completament al Garumnià. En temps més moderns, Cuevas (1992) va redefinir la formació i la va elevar a la categoria de Grup. Al Sinclinal d'Àger, Colombo i Cuevas (1993) van definir el Grup Fontllonga, equivalent al Grup Tremp i al Garumnià. Amb tot, el terme Garumnià, per la seva aplicabilitat a l'hora de fer estudis de camp, s'ha mantingut àmpliament utilitzat (per exemple veure Rosell et al., 2001 i Oms et al., 2007; Figs. 3.3 i 3.4).

Tradicionalment es divideix el Garumnià en les següents unitats (Rosell et al., 2001; Oms et al., 2014; Figs. 3.3 i 3.4):

- Garumnià gris: unitat formada per argiles i margues grises amb abundants restes d'invertebrats, amb intercalacions de carbons i calcàries amb caròfits i ostràcodes, i en menor mesura, gresos. S'interpreta com un dipòsit format en un ambient de *lagoon* amb aigües de variable salinitat que s'estenia des de l'àrea de Vallcebre fins a Tremp, connectat al sistema d'illes barrera representat per la Formació Gres d'Areny (o Arén, veure Mey et al., 1968). A la base d'aquesta unitat, en tota la conca (excepte en l'extrem occidental), s'ha identificat el membre Fumanya (Figs. 3.5 i 3.6). Aquest s'ha interpretat com una plana mareal fangosa que representa els primers ambients terrestres a la zona (amb els primers vestigis de dinosaures, veure Oms et al., 2016, Annex 2 i Gómez-Gras et al., 2016). El Garumnià gris també s'ha definit com a Formació Posa (Cuevas, 1992). Per contra, al Sinclinal d'Àger, després de la deposició del Membre Fumanya, s'hi desenvolupà un ambient lacustre (Formació Maçana, Puigdefàbregas et al., 1989) sense influència marina (Villalba-Breva i Martín-Closas, 2013).

- Garumnià vermell inferior: unitat formada per una successió de gresos i argiles i margues ocres, vermelles, violetes, taronges i marrons amb desenvolupament de paleosòls. Localment hi ha intercalacions de calcàries lacustres i palustres, com ara les representades pel Membre Basturs al Sinclinal de Tremp (Cuevas, 1992). S'interpreta com a dipòsits de plana costanera amb canals meandriformes amb influència mareal (veure Riera, 2010 i Díez Canseco et al., 2014, i referències allí incloses). La gran majoria de restes de vertebrats, incloent-hi dinosaures, s'han descobert en aquesta unitat. Equival a les formacions Conques i Talarn al Sinclinal de Tremp (Cuevas, 1992). Pujalte i Schmitz (2005) considera la Fm.

Talarn, en canvi, dins del Paleocè, però Gómez-Gras et al. (2016) situa la unitat dels conglomerats de Talarn en el Maastrichtià superior, de manera similar a la proposta de Cuevas (1992). Al Sinclinal d'Àger, el Garumnià vermell inferior s'ha definit com a Formació Figuerola (Colombo i Cuevas, 1993).

- Calcàries de Vallcebre i equivalents laterals, representades per calcàries amb *Microcodium* formades en un ambient lacustre proper al mar (López-Martínez et al., 2006). Al Sinclinal de Tremp es coneixen com a les formacions Calcàries de Suterranya i Calcàries de Sant Salvador de Toló (Cuevas, 1992), mentre que al d'Àger reben el nom de Calcàries de Millà (Colombo i Cuevas, 1993).

- Garumnià vermell superior, una unitat d'argiles i gresos vermells i conglomerats. Cap a la part superior de la unitat són freqüents els nivells de calcàries lacustres i de guixos. Mentre que al Sinclinal de Tremp s'identifica amb les formacions Esplugafreda i Claret (Pujalte i Schmitz, 2005), al d'Àger es reconeix com a Complex de Perauba (Colombo i Cuevas, 1993).

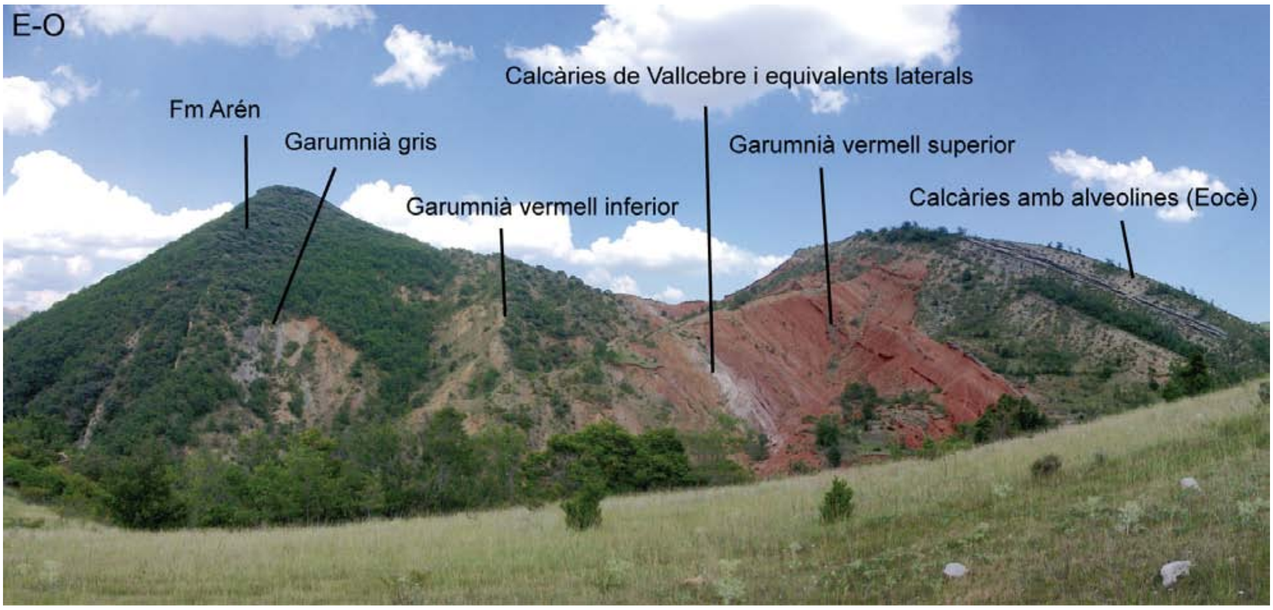

Figura 3.3. Panoràmica de la secció d'Iscles (Ribagorça, oest d'Areny de Noguera) amb indicació de les unitats litostrtigràfiques.

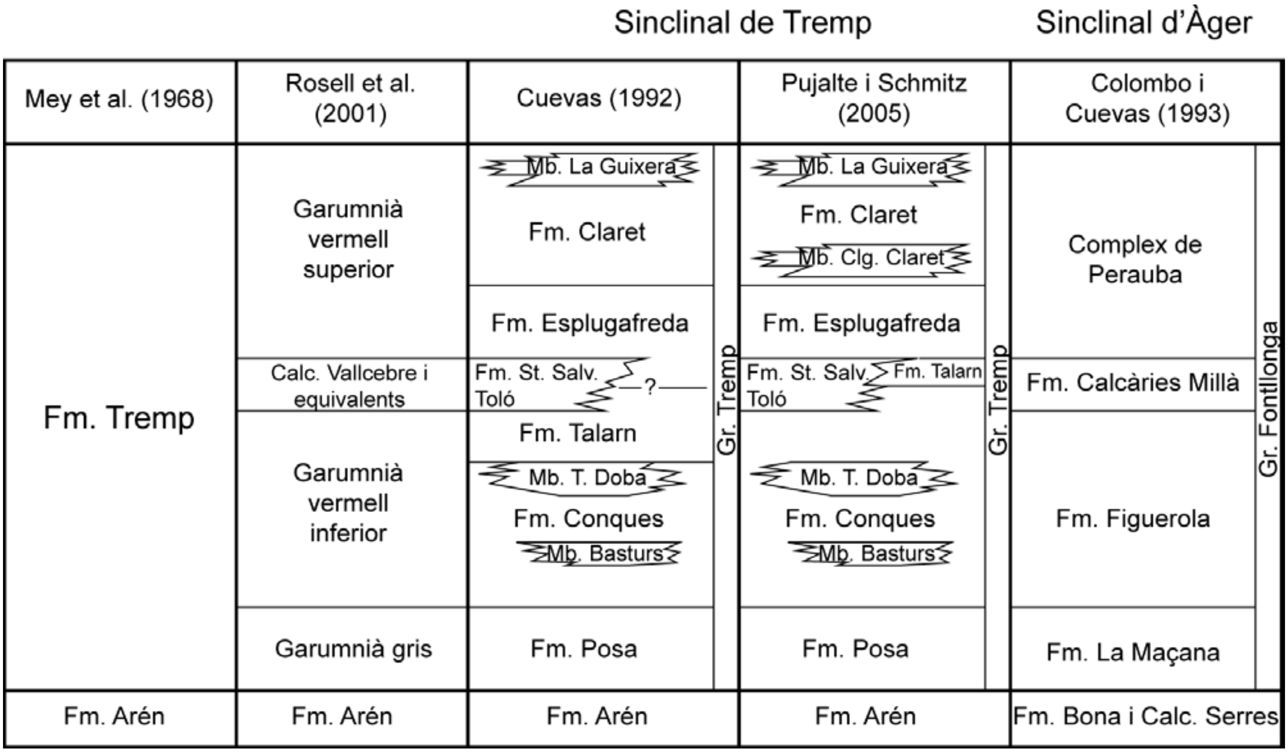

Figura 3.4. Divisions formals i informals dels dipòsits continentals del trànsit Cretaci-Paleogen al sud dels Pirineus. La proposta de Rosell et al. (2001) es pot aplicar a qualsevol sector (Àger, Tremp, Vallcebre…), mentre que les propostes de Cuevas (1992), Colombo i Cuevas (1993) i Pujalte i Schmitz (2005) tenen una aplicació més local. Modificat de Riera (2010).

L'edat maastrichtiana de les dues primeres unitats està ben establerta en base al seu contingut en caròfits (per exemple Feist i Colombo, 1983; Vicente et al., 2015) i especialment gràcies als estudis en magnetostratigrafia (Galbrun et al., 1993; Oms et al., 2007; Pereda-Suberbiola et al., 2009; Vila et al., 2012; Canudo et al., 2016, Annex 1). Amb tot, la resolució d'aquestes datacions difereix segons el sector estudiat, i és especialment ambigua en el Sinclinal de Tremp (veure Capítol 2 i Fig. 3.5). Les altres dues unitats es corresponen al Paleocè (Colombo i Cuevas, 1983; López-Martínez et al., 2006; Díez-Canseco et al., 2014; Vicente et al., 2015, 2016). La localització del límit K-Pg ha estat i és encara objecte de debat. Tradicionalment s'ha considerat que o bé es troba situat just a sota les Calcàries de Vallcebre (per exemple, Rosell et al., 2001), o bé no ha quedat enregistrat a causa d'un hiatus sedimentari (Baceta et al., 2004; Díez-Canseco et al., 2014). Amb tot, el cron C29r, que inclou els tres-cents mil anys abans de l'extinció, es troba ben representat en gairebé totes les seccions estratigràfiques del sud dels Pirineus (Fig. 3.5). López-Martínez et al. (1998) van constrènyer la transició entre el Cretaci i el Paleogen (K-Pg) en un intèrval de 3 metres al Sinclinal d'Àger en base a criteris faunístics i palinològics, però també geoquímics. En aquest sentit, van localitzar una excursió negativa de δ ^{13}C en aquest intèrval, dins el cron C29r.

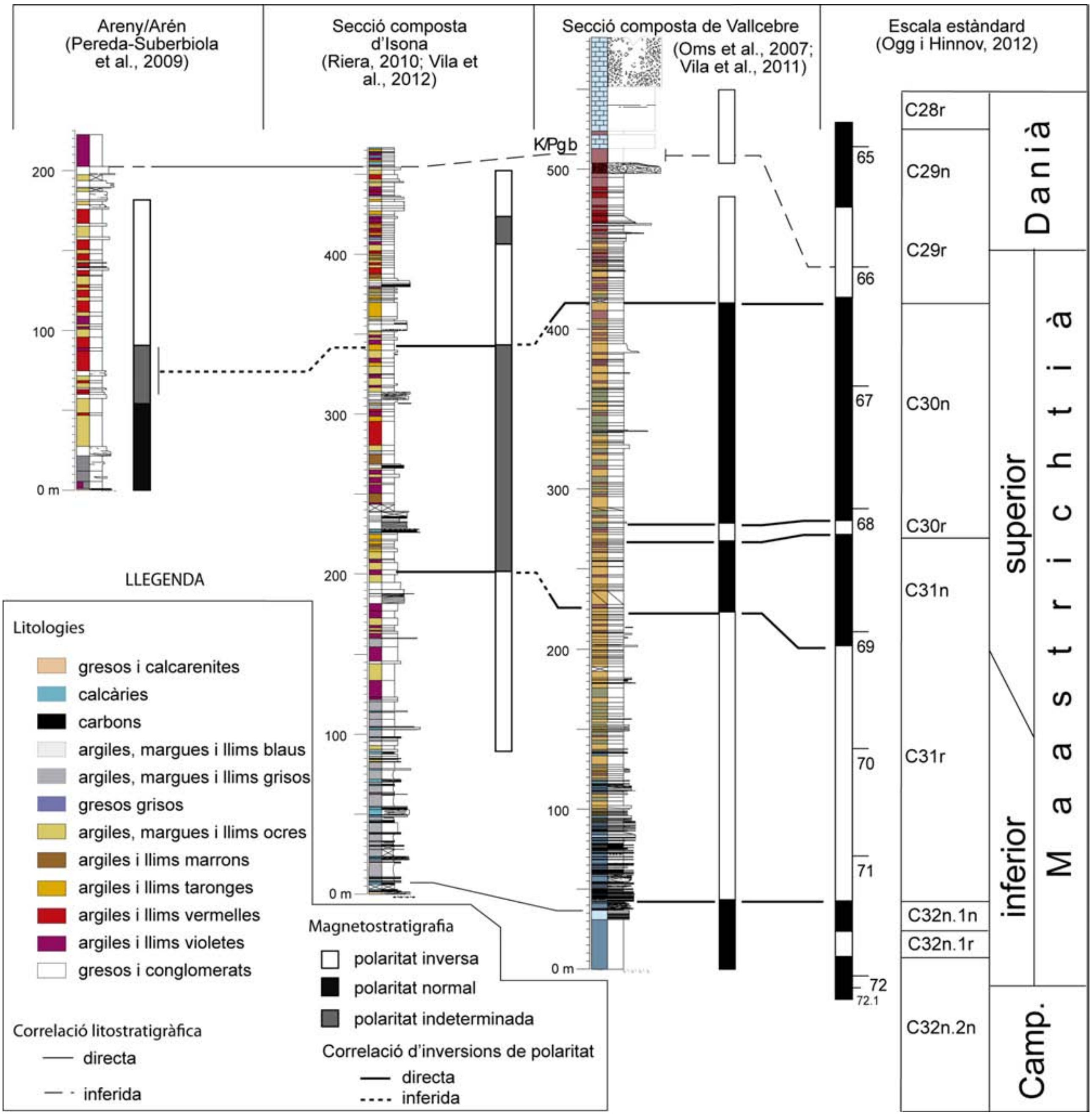

Figura 3.5. Marc cronostratigràfic de Riera (2010) i Vila et al. (2012) per als Sinclinals de Vallcebre i Tremp. La interpretació del paleomagnetisme, especialment l'intèrval de polaritat indeterminada d'Isona està basada en els resultats obtinguts a Vallcebre i Areny per part d'Oms et al. (2007) i Pereda-Suberbiola et al. (2009), assumint que la sedimentació és contínua en tots els punts de la conca.

La conca sud-pirinenca, oberta a l'Atlàntic (Fig. 3.7), estava envoltada per l'est i el sud per massissos com el de l'Ebre que actuaven com a àrees font (Oms et al., 2014; Gómez-Gras et al., 2016) durant el Cretaci Superior. Els dipòsits del Grup Tremp o Garumnià tenen un origen sintectònic (Souquet, 1967; Garrido-Megías i Ríos, 1972; Liebau, 1973; Simó i Puigdefàbregas, 1985; Simó, 1986; 1989; Díaz-Molina, 1987; Mutti i Sgavetti, 1987; Eichenseer, 1988; Sgavetti, 1992, 1994; Deramond et al., 1993; Mutti et al., 1994; Ardèvol et al., 2000). D'aquesta manera, el desenvolupament d'alts estructurals com ara el Montsec a causa de la compressió van dividir la conca en una sèrie de sectors que anirien quedant aïllats a partir del Maastrichtià. Aquests sectors s'individualitzarien en els sinclinals que reconeixem avui en dia: Tremp, Àger, Coll de Nargó i Vallcebre. Així, mentre que al Maastrichtià inferior s'hi troben unitats més o menys uniformes depositades arreu, com el Membre Fumanya (Oms et al., 2016, Annex 2), a partir d'un determinat moment la partició de la conca es veu reflectida en diferències a nivell petrogràfic (àrees font) i de fàcies entre els dipòsits continentals de cada sinclinal (Gómez-Gras et al., 2016; Fig. 3.6).

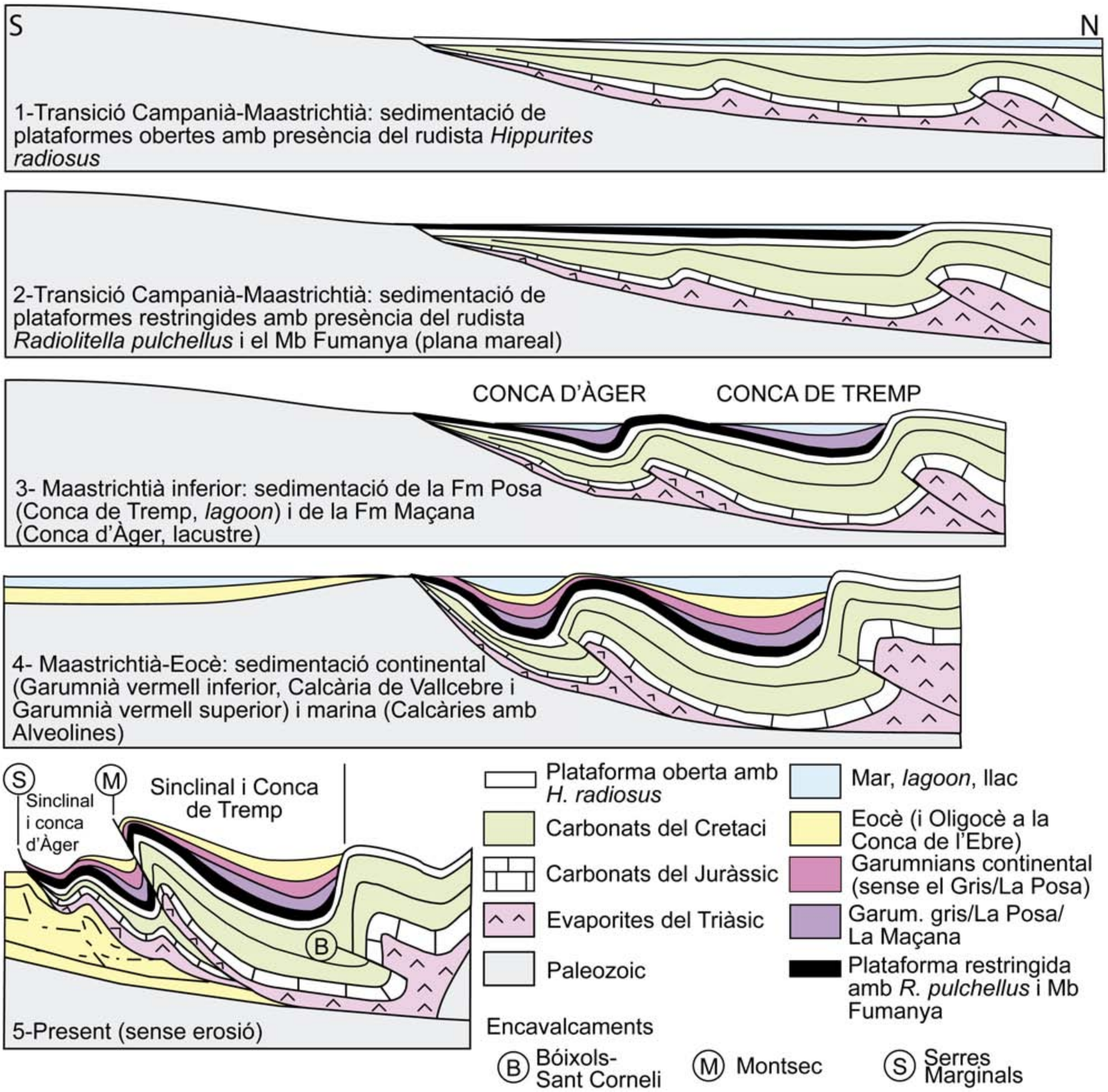

Figura 3.6. Evolució de la Conca sud-Pirinenca durant el Cretaci terminal fins l'Eocè. Veure Oms et al. (2016, Annex 2).

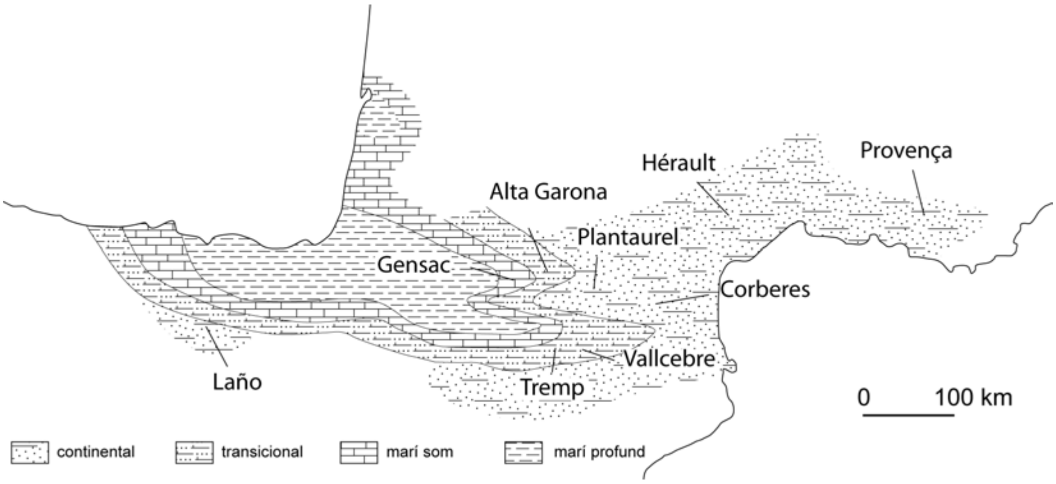

Figura 3.7. Esquema paleogeogràfic del Campanià-Maastrichtià de l'àrea de la Provença-Pirineus-País Basc. Modificat de Laurent et al. (2001).

Al sector occidental del Sinclinal de Tremp, a la Vall de l'Isàvena (Ribagorça, Huesca) Arostegi et al. (2011) van identificar un clima temperat perenne i subhumit durant el Maastrichtià superior, que canvià a un altre de càlid estacional durant el Paleocè. A més, Riera et al. (2013) van proposar unes condicions d'estabilitat climàtica al llarg del Maastrichtià al sud dels Pirineus.

3.1.2. El Cretaci Superior continental a la vessant nord

De manera similar al que ocorre a la vessant sud, a la vessant nord dels actuals Pirineus s'hi desenvolupà una conca sedimentària que abastava des de la zona de les Corberes a l'est, vorejant el massís pre-Mesozoic de Mouthoumet i extenent-se per l'Ariège fins la zona de l'Alta Garona i els Petits Pirineus, a l'oest (Figs. 3.2 i 3.7) (Bilotte, 1978, 1985; Bilotte et al., 1983). A diferència de la vessant sud, les conques sedimentàries mesozoiques de la vessant nord Pirineus no disposen d'acurades calibracions magnetostratigràfiques, amb l'excepció dels resultats de Galbrun (1997) a la secció d'Albas, a les Corberes.

En aquesta àrea dels Pirineus les fàcies continentals estan representades en la Formació Margues vermelles inferiors, les quals estan dividides en una sèrie de membres a la zona de l'Aude, al voltant dels pobles de Quillan i Espéraza (veure Bilotte et al., 1983 i Le Loeuff, 2005): i) Margues de Campagne, formades per gresos i margues i argiles vermelles. Contenen una associació palinològica atribuïda al Campanià (Bilotte, 1985); ii) Gres d'Estous, una unitat gresosa amb abundants restes de plantes, closques d'ous i ossos de vertebrats, incloent-hi dinosaures; iii)

Margues vermelles de la Maurine, una successió de margues vermelloses amb desenvolupament de paleosòls i nivells de gresos intercalats. Pel seu contingut en ous de dinosaure i caròfits s'ha considerat com a Maastrichtià (Bessière et al., 1989; Garcia i Vianey-Liaud, 2001). Contenen un els jaciments més importants dels Pirineus i de tot el sud-oest europeu, Bellevue (també conegut com a C3 en la literatura, veure Vila et al., 2012), i altres de clàssics com Rennes-le-Chateau; i iv) Conglomerat de Fleuri, un estrat molt continu format per gresos de gra groller i conglomerats que sovint s'ha relacionat amb unitats grolleres similars que apareixen al Sinclinal de Vallcebre i a la Provença (Gres amb rèptils i Conglomerat de la Galante, respectivament, veure Oms et al., 2007). La transició K-Pg es troba situada dins la Formació Calcàries i Argiles de Vignevieille, d'origen lacustre (Marty i Meier, 2006).

La Formació Margues vermelles inferiors esdevé progressivament més jove cap a l'oest a causa de la progradació de les fàcies continentals en el context regressiu del Maastrichtià (Bilotte, 1985; Fig. 3.7). A més de les Corberes i l'Aude, està representada a la zona del Plantaurel, al departament d'Ariège. En aquest indret hi destaquen jaciments com ara el Mas d'Azil.

Finalment, aquesta formació continental evoluciona lateralment a la Formació Margues d'Auzàs en els antinclinals de Plagne i Aurignac (Alta Garona), formada per margues argiloses grises amb intercalacions de nivells calcarenítics i gresosos amb abundant fauna d'invertebrats com poden ser gasteròpodes, bivalves, rudistes, ostràcodes i també foraminífers (Bilotte, 1980; 1985; Bilotte i Andreu, 2006). Aquests dipòsits mostren, de base a sostre, una transició d'ambients més marins a més continentals com ara llacunes, canals mareals, pantans litorals i paleosòls. A diferència de l'anterior formació, l'edat d'aquesta unitat s'ha pogut precisar millor gràcies a la major disponibilitat de marcadors biostratigràfics, com per exemple caròfits i foraminífers (Riera, 2010 i referències incloses). A més, les unitats marines infrajacents (Formació Margues de Plagne) s'han pogut datar com a Maastrichtià superior mitjançant nanoplàncton calcari (presència de *Arkhangelskiella cymbiformis, Cribocorona gallica* i *Lithraphidites quadratus*; Lepicard et al., 1985). Pel que fa a restes de vertebrats, la formació és rica en peixos osteictis, amfibis, quelonis, cocodrils i dinosaures (veure Laurent et al., 2002 i referències incloses).

Les plataformes, rampes carbonatades i planes mareals i de *lagoon* del Grup Ausseing, les quals estan situades estratigràficament per sota de les Margues d'Auzàs (veure a dalt), també han aportat alguns jaciments importants de dinosaures, com ara Lestaillats. La seva posició per sobre de les Margues de Plagne permeten datar-les com a la base del Maastrichtià superior (Bilotte et al., 1983;

Bilotte, 1985; Laurent et al., 2001, 2002).

Més cap a l'oest, en el Sinclinal de Latoue/Sepx s'hi troben les Margocalcàries de Gensac (Fig. 3.7), una formació marina equivalent de les Margues d'Auzàs. En aquesta unitat s'ha localitzat una discontinuïtat estratigràfica amb anomalia d'iridi atribuïda al límit K-Pg. Un metre per sota d'aquest nivell hi ha el jaciment de Larcan, important pel seu contingut en hadrosaures (Bilotte et al., 2010; Prieto-Márquez et al., 2013).

3.2. Llenguadoc i Provença

El registre continental del Llenguadoc es concentra sobretot en la conca de Villeveyrac-Mèze i l'àrea de Saint Chinian (departament de Hérault). A la Provença, aquest registre es concentra al Sinclinal o Conca de l'Arc i a Fox-Amphoux (departaments de Bouches-du-Rhône i Var) (Fig. 3.8A). Aquests dipòsits continentals s'han estudiat extensament tant pel que fa a la geologia com la paleontologia (tant vertebrats, com invertebrats, caròfits i pol·len). Clàssicament, la zona del Llenguadoc i Provença s'ha dividit en una sèrie d'unitats litostratigràfiques que s'han proposat com a estatges continentals regionals. Així, aquestes unitats prenen un valor cronostratigràfic aproximat, que de més antiga a més moderna són (veure Babinot i Durand 1980a–e, Westphal i Durand, 1990, Cojan i Moreau, 2006, i Riera, 2010 i referències incloses; Fig. 3.8C):

- Valdonià, format principalment per calcàries i margues blau-grises i gresos. S'ha correlacionat amb el Santonià.

- Fuvelià, una unitat lacustre formada per calcàries amb caròfits, bivalves i gasteròpodes i intercalacions de lignits. S'ha correlacionat amb el Campanià inferior.

- Begudià, una unitat fluvio-lacustre formada per successió de margues, calcàries amb caròfits, gresos i conglomerats. S'ha atribuït al Campanià mitjà i superior.

- Rognacià, una successió fluvial, lacustre i palustre formada per margues, argiles, gresos i calcàries. S'ha correlacionat amb el Campanià superior i el Maastrichtià.

- Vitrolià, una successió lacustre-palustre formada per argiles i margues vermelles i calcàries amb *Microcodium* calibrada amb el Paleocè.

Mentre que a la zona de Villeveyrac-Mèze només hi afloren roques atribuïdes al Fuvelià i el Begudià (és a dir, el Campanià inferior i mitjà), a Saint Chinian hi aflora fins el Rognacià (Campanià superior i Maastrichtià inferior); a la Provença, la sedimentació continental abasta des del Valdonià fins l'Eocè (Durand i Guieu, 1980; Durand, 1989; Benammi et al., 2005; Buffetaut, 2005).

Pel que fa a la zona de la Provença, la sedimentació continental del Cretaci terminal es va produir al llarg d'una conca orientada seguint un eix est-oest, limitada per paleorelleus al nord, sud i est (relleus carbonàtics mesozoics de Saint Victorie, Etoile i el relleu paleozoic i metamòrfic de Maure; Cojan, 1993; Fig. 3.8B). En aquest context, aquesta autora identifica una sedimentació principal d'origen fluvial amb àrees font situades en els relleus i zones veïnes que donà lloc a la formació de dipòsits de canals i de plana d'inundació. Prop dels paleorelleus, en canvi, la sedimentació va estar principalment causada per ventalls al·luvials. A la zona central de la conca, al voltant del sistema de falles d'Aix-en-Provence, s'hi desenvolupà un sistema lacustre representat per les Calcàries de Rognac durant el trànsit Campanià-Maastrichtià (Cojan, 1993; Cojan et al., 2003; Cojan and Moreau, 2006; Fig. 3.8B).

Cojan et al. (2000), mitjançant un estudi isotòpic del carbonat de nòduls edàfics en la zona oest del Sinclinal de l'Arc, van localitzar una excursió negativa en els valors del δ C^{13} entre els sediments de plana fluvial del Rognacià i les Calcàries de Vitrolles, d'edat Paleocena. Aquests autors van considerar aquest canvi isotòpic com l'evidència del límit K-Pg en una successió sedimentària continental. S'ha identificat un clima càlid estacional a la zona (Medus, 1972; Ashraf i Erben, 1986) amb ocurrència d'episodis semi-àrids (en forma de dipòsits de *playa-lake*, per exemple; Fig. 3.8B) que van deixar una empremta sedimentològica. Aquests nivells s'han utilitzat per correlacionar diferents seccions estratigràfiques (veure Cojan i Moreau, 2006).

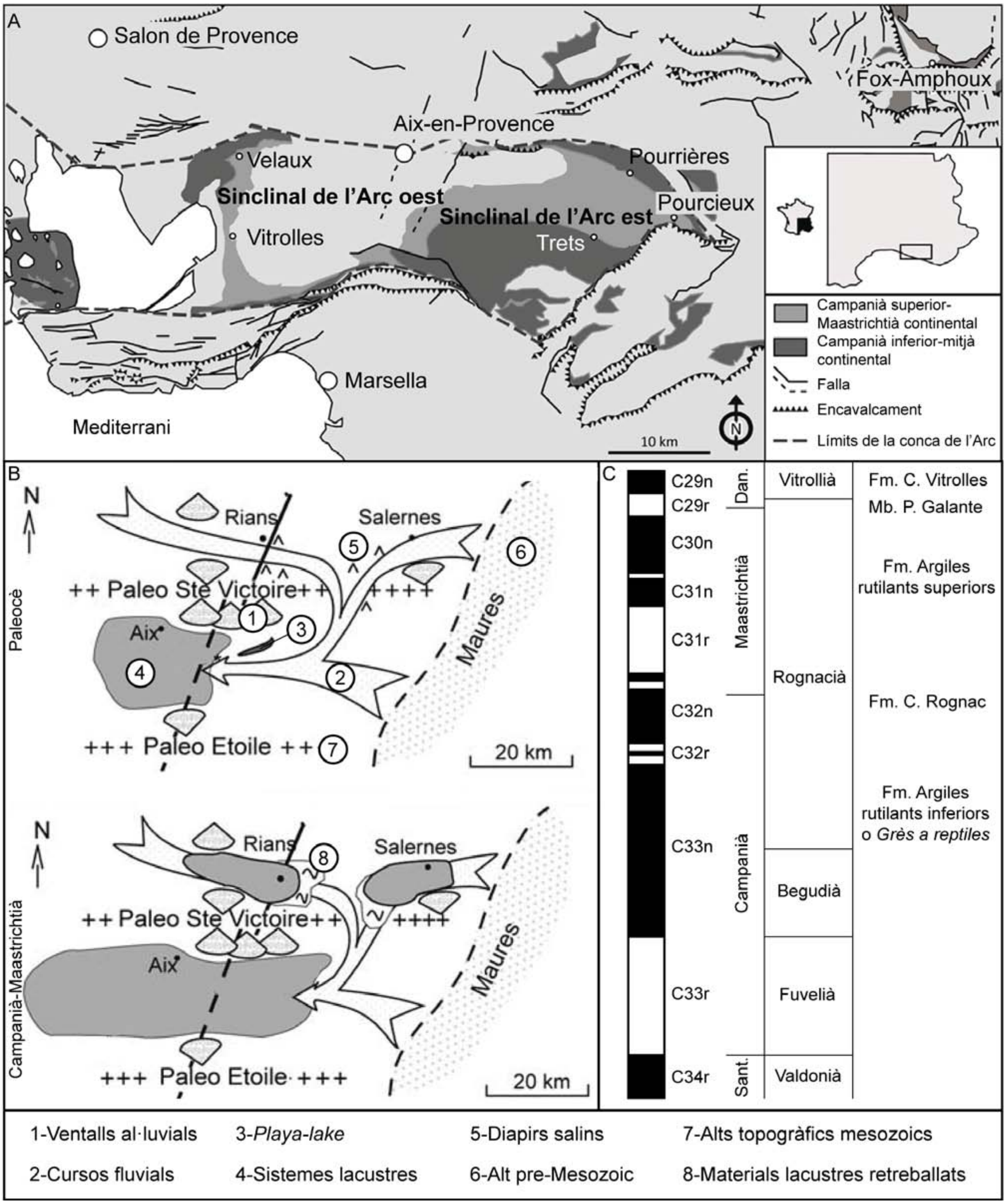

Figura 3.8. Geografia, paleogeografia i cronostratigrafia del Cretaci Superior del Sinclinal de l'Arc, a la Provença (sud de França). **A**, esquema geogràfic i geològic amb la localització dels dipòsits Campanians i Maastrichtians. Modificat de Tortosa et al. (2014). **B**, interpretació paleogeogràfica del Sinclinal de l'Arc, mostrant els principals paleorelleus, les àrees de procedència dels sediments i l'evolució del sistema lacustre representat per les Calcàries de Vitrolles (esquema superior), al Paleocè, i les de Rognac (esquema inferior), al Campanià-Maastrichtià. Modificat de Cojan et al. (2003). **C**, cronostratigrafia amb indicació dels estatges locals i les formacions que integren el Cretaci Superior del Sinclinal de l'Arc segons Cojan i Moreau (2006). Escala estàndard d'Ogg i Hinnov (2012).

La correlació entre les diferents parts del Sinclinal de l'Arc presenta una sèrie de dificultats donada la poca continuïtat que sovint presenten els afloraments de roques. Així, la Formació Calcàries de Rognac (dins del Rognacià), considerada isòcrona a banda i banda del sinclinal per Cojan i Moreau (2006), s'ha proposat com a diacrònica en base a la biostratigrafia d'ous de dinosaure plantejada per Garcia i Vianey-Liaud (2001). Aquests problemes de correlació afecten a la datació d'alguns jaciments de dinosaure (per exemple Vitrolles-La Plaine, veure Valentin et al., 2012), especialment en el sector occidental del Sinclinal de l'Arc.

La majoria de jaciments de vertebrats del Llenguadoc i de la Provença s'han trobat en successions fluvials formades per llims, argiles, gresos i conglomerats. En canvi, els dipòsits de carbonats lacustres i nivells de lignit han aportat moltes menys restes. Generalment, els fòssils de dinosaure presenten característiques tafonòmiques que evidencien transport. En aquest sentit, les restes articulades són infreqüents (Csiki-Sava et al., 2015). Pel que fa a les edats, principalment els jaciments s'han trobat en roques del Campanià mig, superior i del Maastrichtià inferior (Begudià i Rognacià, Formació Argiles rutilants inferiors al Sinclinal de l'Arc). Les localitats del Maastrichtià superior són, amb diferència, molt més escasses i majoritàriament es corresponen a jaciments de postes d'ous.

3.3. Ibèria

A diferència del registre dels Pirineus, el Cretaci Superior continental que es troba en la resta de la Península Ibèrica sovint abasta poca extensió d'aflorament o està representat per formacions d'escassa potència estratigràfica. Aquest fet dificulta les tasques de correlació estratigràfica i de datació precisa (amb l'excepció, fins ara, del jaciment de Laño). A continuació es descriuen les principals àrees fossilíferes o jaciments que han aportat fòssils de dinosaure d'aquesta època.

3.3.1. Jaciments del País Valencià

El registre del Cretaci Superior continental és important en dos jaciments situats en l'extrem sud-oriental de la Serralada Ibèrica. Es tracta de les localitats de Chera (comarca de la Plana d'Utiel-Requena) i La Solana (municipi de Tous, prop del poble de Carlet, comarca de la Ribera Alta), ambdós en la província de València.

El jaciment de Chera es troba situat en la Formació Sierra Perenchiza, en una successió de calcàries i margues de la interpretada com a un ambient de llacs i estanys d'aigua dolça efímers i proper a la línia de costa (Company, 2004). S'ha atribuït una edat de Campanià mitja-base del Campanià superior en base al contingut en caròfits (biozona de Peckichara pectinata, Company et al., 2005; veure calibració de la biozona a Riveline et al., 1996).

La localitat de La Solana es troba situada en la mateixa Formació Sierra Perenchiza, en una successió d'argiles, gresos vermells i margues ocres i grises, amb nòduls carbonàtics i d'òxids de ferro. L'ambient general s'ha interpretat com una plana d'inundació al·luvial distal (Company et al., 1997; Company, 2004). S'ha atribuït una edat de Maastrichtià superior per a aquesta successió.

3.3.2. Jaciments de Castella-La Manxa

També en el marge sud de la Serralada Ibèrica, a la província de Conca, s'hi troben jaciments de dinosaures del Cretaci Superior. El primer i més important és Lo Hueco, prop de la localitat de Fuentes. Es troba situat a la part superior de la Formació Margues, argiles i guixos de Villalba de la Sierra, la qual comprèn un ampli rang d'edat, des del Campanià mitjà fins l'Eocè. Per la seva posició estratigràfica i el seu contingut paleontològic, Ortega et al. (2008) situen el jaciment entre el Campanià superior i el Maastrichtià inferior. Aquest jaciment, molt ric en restes de macrovertebrats (s'ha considerat com un Konzentrat-Lagerstätten, amb més de 10000 ossos excavats d'ençà el seu descobriment l'any 2007), està format per una successió de guixos, argiles verdes, grises vermelles i marrons amb un canal gresós i conglomeràtic intercalat (Barroso-Barcenilla et al., 2010). Ortega et al. (2015) interpreten el jaciment com una zona de plana d'inundació associada a canals distributaris exposada de forma intermitent a una influència marina, així com a períodes de dessecació.

En la mateixa formació, prop de la població de Sacedón, hi ha un jaciment amb el mateix nom. Es troba en el mateix tram estratigràfic que Lo Hueco, en una successió de margues i argiles verdes i vermelles. Pel seu contingut en caròfits i la seva posició similar a Lo Hueco, s'ha datat com a Campanià superior-Maastrichtià inferior (Vilas et al., 1982; Ortega i Pérez-García, 2009).

3.3.3. Jaciments de Castella i Lleó

El nord-oest de la Serralada Ibèrica també presenta una sèrie d'afloraments del Cretaci Superior que contenen jaciments de dinosaures i altres vertebrats. A la zona de la conca de Cameros (Burgos) s'hi han trobat diversos jaciments en margocalcàries d'origen lacustre pertanyents al Maastrichtià de la Formació Santibañez del Val, atribuïdes a les fàcies Garumnianes. Conté jaciments com El Cogorro, prop d'Arauzo de Miel (Quintero Amador et al., 1982; Torcida, 1996; Bravo et al., 2006). El jaciment de Cubilla, (Sòria), situat en la mateixa unitat lacustre que els anteriors, ha aportat també restes de dinosaures (Lapparent et al., 1957; Quintero Amador et al., 1981; Pereda-Suberbiola i Ruiz-Omeñaca, 2001).

A la província de Segòvia, en la unitat coneguda com a Sistema Central del Massís Ibèric, també hi afloren dipòsits continentals del Cretaci Superior. Aquests es corresponen a la Formació Vegas Matute, representada per gresos intercalats amb argiles i llims. Els cossos de gres són lenticulars de gra mig a groller de composició arcòsica i subarcòsica, amb estratificació encreuada en solc i *mud drapes,* amb bases erosives i localment dipòsits residuals de graves. En alguns cossos de gres s'hi observen barres d'acreció lateral (Pérez-Garcia et al., 2016). Aquests autors interpreten la successió com a un ambient fluvial proper a la línia de costa. Malgrat no disposar de datacions precises, el jaciment d'Armuña s'ha situat en el Campanià superior en base a la seva posició estratigràfica.

3.3.4. Laño, País Basc-Condado de Treviño

El jaciment de Laño, localitzat en el Condado de Treviño (administrativament part de la província de Burgos però situat dins d'Àlava) és un dels jaciments del Cretaci Superior més rics del sud-oest europeu, amb milers d'ossos excavats des del seu descobriment l'any 1984. D'aquesta manera, el jaciment conté una de les associacions de vertebrats més riques de tot Europa, amb més de 40 espècies incloent dinosaures, cocodrils i altres rèptils, i mamífers (Pereda-Suberbiola et al., 2000, 2015).

Es troba situat en la part baixa de la Formació Sedano, situada en el Sinclinori sud-càntabre (regió Basco-Càntabra, nord d'Ibèria). Aquesta formació està formada per sorres i llims d'origen fluvio-deltaic. Aquesta deposició continental té el seu origen en una regressió marina que es va produir en la regió Basco-Càntabra a partir del Campanià superior (Gómez-Alday, 1999; Pereda-Suberbiola et al., 2000, 2015; Fig. 3.9). El jaciment ha estat datat mitjançant un estudi magnetostratigràfic com a Campanià superior per Corral et al. (2016), qui el va situar en la part baixa una zona de polaritat normal correlacionada amb el cron C32n.2n (Fig. 3.7). Els nivells fossilífers de Laño es troben en nivells de gresos i llims fins depositats en condicions de baixa energia (Pereda-Suberbiola et al., 2000).

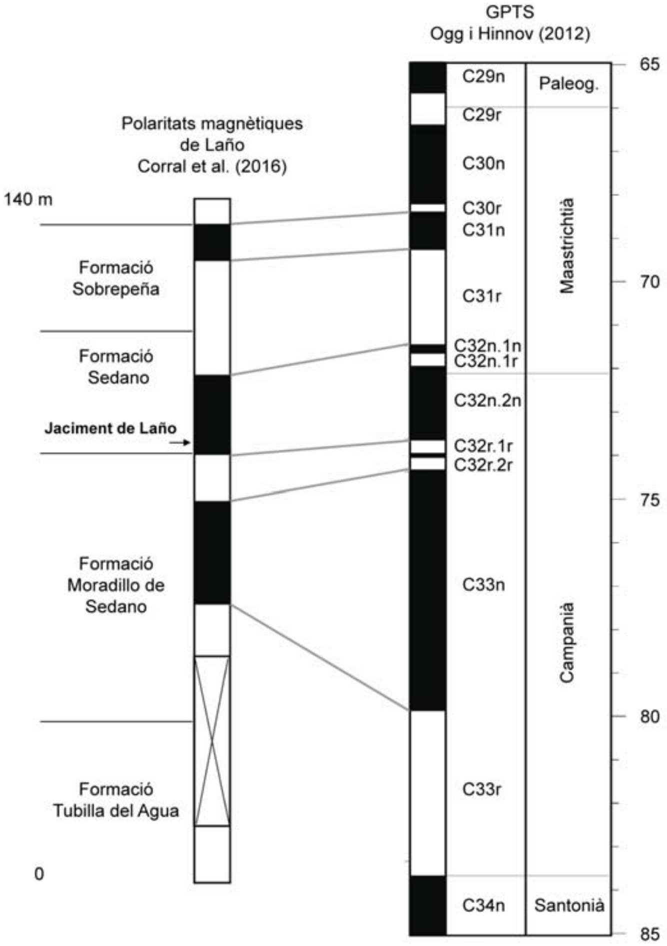

Figura 3.9. Posició cronostratigràfica del jaciment de Laño, en la part baixa de la Formació Sedano i en el Campanià superior. Adaptat de Corral et al. (2016).

3.3.5. Jaciments de Portugal

El registre del Cretaci Superior continental a l'extrem occidental de la Península Ibèrica es concentra en les localitats fossilíferes d'Aveiro, Taveiro i Viso, prop de Coimbra, a Portugal. En aquest cas, els estudis geològics disponibles no permeten precisar una edat més enllà del Campanià-Maastrichtià per a la successió d'argiles i gresos de la Formació Gresos i argiles d'Aveiro. Bernardes i Corrochano (1987) interpreten aquests dipòsits com a una plana costanera mareal (amb els seus canals o *tidal creeks*) protegida per una illa barrera. Inclou fàcies corresponents des del domini submareal al supramareal. Així, aquest ambient té moltes similituds amb el *lagoon* de la Fm. La Posa del sud dels Pirineus (veure apartat 3.1.1. i Oms et al., 2016, Annex 2).

MATERIAL I MÈTODES DE LA TESI DOCTORAL

4

La present tesi doctoral combina a parts iguals treball de caire geològic i l'estudi de material paleontològic. Així, la vessant geològica de la tesi inclou mètodes clàssics de l'estratigrafia i la sedimentologia, com ara l'aixecament de columnes estratigràfiques i descripció litològica, però també geoquímica d'isòtops estables en mostres de roca i magnetostratigrafia. Pel que fa a la part paleontològica, el material estudiat s'ha obtingut gràcies a campanyes de prospecció i excavació realitzades al llarg de la darrera dècada i durant la mateixa tesi per part de l'Institut Català de Paleontologia Miquel Crusafont, la Universitat Autònoma de Barcelona i la Universidad de Zaragoza.

En aquest capítol es descriuen de manera general els mètodes geològics emprats en la tesi, des del treball previ a les campanyes de camp fins a l'anàlisi de les mostres i estudi dels resultats. També es detalla la procedència del material paleontològic estudiat. En cadascun dels capítols següents, però, hi ha una secció específica on es detallen els materials i mètodes específics emprats en cada estudi.

4.1. Tasques de gabinet prèvies al treball de camp

El treball de gabinet previ a les campanyes de camp ha consistit en la recerca i consulta de bibliografia i cartografia per tal de localitzar i seleccionar afloraments idonis per a aixecar columnes estratigràfiques o realitzar mostratges de paleomagnetisme. Aquesta tasca ha resultat de gran utilitat per localitzar i resseguir possibles nivells de correlació física (fotohoritzons).

S'ha fet ús de visors web de cartografia geològica i ortofotomapes com ara *vissir3* de l'Institut Cartogràfic i Geològic de Catalunya (http://www.icc.cat/vissir3/), el *Géoportail* de *l'Institut national de l'information géographique et forestière* (https://www.geoportail.gouv.fr/le-projet-geoportail) i *Google Earth*. D'aquesta manera, s'ha pogut treballar amb cartografies generals de les zones estudiades (amb escala 1:50000), així com de detall (1:5000). També s'ha fet ús de la col·lecció Geotreballs (cartografia geològica a escala 1:25000 del territori català) de l'Institut Cartogràfic i Geològic de Catalunya.

4.2. Treball de camp

4.2.1. Litostratigrafia i sedimentologia

Per tal de contribuir a millorar el marc estratigràfic de la vessant sud dels Pirineus, s'han aixecat diverses columnes al llarg dels aflorament maastrichtians del Sinclinal de Tremp. D'aquesta manera, s'ha agafat com a punt de partida el panell estratigràfic de Riera et al. (2009) i Riera (2010) i s'ha anat completant amb la mesura de noves seccions que contenien jaciments inèdits, com per exemple la secció d'Iscles (veure Capítol 5). A més a més, també s'han afegit columnes i jaciments clàssics omesos en les referències anteriors, com ara el Coll de Faidella o Orcau-1. En algunes de les columnes realitzades en aquesta tesi doctoral s'hi han dut a terme mostratges de paleomagnetisme (veure per exemple la secció d'Orcau del Capítol 9). Les seccions s'han mesurat mitjançant la vara de Jacobs i cinta mètrica (Fig. 4.1).

Figura 4.1. Mesura de columnes estratigràfiques i recollida de mostres de paleomagnetisme a l'Alta Vall de l'Aude (Departament de l'Aude, França), amb la participació de la Dra. Rita Estrada i el Dr. Jaume Dinarès Turell. Fotografia d'Oriol Oms Llobet.

També s’han mesurat columnes en el marc de les campanyes d’excavació del jaciment de L’Espinau (veure a sota) en la zona sud de les Serres Marginals, per a situar la localitat en un context estratigràfic.

En la zona de l’Alta Vall de l’Aude (Departament de l’Aude, sud de França) es partia d’una situació de manca de treballs estratigràfics precisos més enllà de columnes esquemàtiques com ara les representades per Bilotte (1985) o Marty i Meyer (2006). D’aquesta manera, s’ha hagut de construir un nou panell de correlació que integra diversos jaciments ja publicats (veure Capítol 8).

Paral·lelament a la mesura dels estrats, cada litologia s’ha descrit en base a la composició, mida de gra, color, presència i descripció d’estructures sedimentàries, contingut paleontològic visible, variacions verticals i laterals i arquitectura dels cossos sedimentaris. S’ha seguit en la mesura del possible els patrons de color proposats per Riera et al. (2009) i Riera (2010), així com altres criteris descriptius similars. D’aquesta manera, la tasca d’integració de les columnes aixecades en aquesta tesi amb les publicades prèviament ha resultat més senzilla. La representació gràfica de les seccions s’ha realitzat mitjançant el programa Adobe Illustrator CS5.

4.2.2. Recollida de mostres per a làmines primes, estudis geoquímics i de paleomagnetisme

Paral·lelament a la meura d’algunes seccions estratigràfiques es van recollir mostres litològiques per tal d’obtenir làmines primes i mostres per realitzar estudis de paleomagnetisme i geoquímica.

Així, es van extreure petits blocs de roca en tall fresc de diferents litologies (calcàries i argiles) per tal de preparar làmines primes (veure Capítol 7). Aquestes làmines van ser elaborades pels operaris del Laboratori de làmines primes de la Universitat Autònoma de Barcelona.

Les mostres de paleomagnetisme es van extreure mitjançant mètodes manuals, atès que generalment les litologies disponibles en les àrees d’estudi eren suficientment toves com per poder-les treballar amb eines senzilles, sense necessitat de recórrer a maquinària de perforació per rotació. A més, generalment els materials argilosos disponibles es disgregaven amb facilitat, la qual cosa desaconsellava l’extracció de cilindres amb màquines perforadores que utilitzen aigua per refrigerar la broca i que haurien desfet les lutites. El mostratge es va realitzar individualitzant i extraient amb una navalla blocs prèviament orientats amb la brúixola. Aquests blocs es van extreure de roca fresca corresponent a litologies el màxim de fines possible (argiles i gresos de gra mig i fi). Per a cada nivell mostrejat es van extreure entre una i cinc mostres, depenent de la dificultat que presentés la litologia. Un cop extreta, cada mostra es va siglar i embolcallar amb paper d'alumini per tal de protegir-la.

Finalment, pel que fa a les mostres per estudis de geoquímica (difracció de raig X i isòtops estables de carboni i oxigen), aquestes es van obtenir a partir de mostres de mà recollides amb l'ajuda d'un martell o bé recollides directament en el cas d'oncoids o nòduls edàfics.

4.2.3. Prospecció paleontològica

Part del material que es presenta en el Capítol 5 es va obtenir gràcies a la prospecció realitzada durant l'estiu de 2012 entre les localitats d'Areny de Noguera i Serraduy, i dirigida per membres de la Universidad de Zaragoza. Es va participar en aquesta campanya, resseguint els afloraments mesozoics del Grup Tremp fins arribar al llogaret abandonat d'Iscles. Pels voltants del poble es van descobrir jaciments de petjades d'hadrosaure (Iscles-1,-2,-3,-4 i -5, veure Capítol 5). Les feines de camp de geologia també han portat a la descoberta de jaciments nous, com ara nivells de closques d'ous, petjades i impressions de pell de dinosaure (veure apartat 4.2.4).

4.2.4. Excavacions

El material paleontològic estudiat en el Capítol 7 es va recuperar gràcies a les intervencions paleontològiques dutes a terme al jaciment de L'Espinau (Àger, La Noguera, Lleida) per membres de L'Institut Català de Paleontologia Miquel Crusafont durant els anys 2010-2015. A partir de 2012 un servidor s'incorporà en les tasques de codirecció. D'aquesta manera, en el temps de duració de la tesi doctoral s'han codirigit 4 campanyes paleontològiques en el jaciment (Fig. 4.2) que han permès recuperar material directament utilitzat per a la tesi:

- Campanyes d'excavació al jaciment de L'Espinau:
  - 2012: Expedient 437 K121 N073-8586
  - 2013: Expedient 437 K121 N073-003 9796
  - 2014: Expedient 437 K121 N073, N003/11309
  - 2015: Expedient 437 K121 N0003-073/12362

Figura 4.2. Tasques de neteja del jaciment de L'Espinau (Àger, La Noguera, Lleida) durant l'inici de l'excavació del 2014. Fotografia d'Àngel Galobart Lorente.

La troballa fortuïta a finals de 2014 d'unes impressions de pell i petjades al jaciment del Mirador de Vallcebre (Vallcebre, Berguedà, Barcelona) va donar lloc a la codirecció de dues intervencions paleontològiques més que han permès desenvolupar el Capítol 6:

- Campanyes de documentació i excavació al jaciment del Mirador de Vallcebre:
  - 2015: Expedient 437 K121 N857/12338
  - 2016: Expedient 437 K121 N857 2016-1-17113

4.3. Treball de laboratori

4.3.1. Processament i anàlisi de mostres de paleomagnetisme

Els blocs orientats requereixen unes mides estàndards per a poder ser analitzats en el magnetòmetre. Cada mostra de paleomagnetisme recollida al camp es va rebaixar utilitzant paper de vidre fins a obtenir cubs de dos centímetres de costat. Alternativament, les mostres més dures es van tallar amb serres radials. Llevat de les litologies més cimentades, com ara els gresos, la resta de mostres formades per blocs d'argila sovint es disgregaven fàcilment durant el procés d'abrassió amb el paper de vidre. Per tal d'evitar la destrucció de moltes mostres, es va utilitzar silicat de sodi amb ciment aluminós per a unir les fractures quan aquestes apareixien. Aquest ciment no interfereix durant el procés de desmagnetització de les mostres.

La desmagnetització de totes les mostres recollides per aquesta tesi s'ha realitzat al 'Laboratorio di Magnetismo delle Rocce e dei Materiali' ('Istituto Nazionale di Geofisica e Vulcanologia INGV), a Roma. Una part d'elles va ser analitzada pel Dr. Jaume Dinarès Turell durant el 2013-2014, mentre que la resta es van analitzar durant l'estada breu feta en aquest centre entre l'abril i el juliol del 2015. La magnetització remanent natural (NRM) i la remanència a través de la desmagnetització de les mostres es van mesurar en un magnetòmetre criogènic tiaxial '2G Enterprises DC SQUID *high-resolution*', instal·lat en un recinte protegit del camp magnètic terrestre. Els passos de desmagnetització tèrmics es van realitzar mitjançant un forn 'Pyrox'. La desmagnetització per camps alternants (AF, *alternating fields*) es va dur a terme mitjançant tres bobines ortogonals instalades en línea amb el magnetòmetre. Així, després d'un primer pas d'escalfament de les mostres a 150º, es van aplicar 14 passos consecutius de desmagnetització per camps alternants (de 4, 8, 13, 17, 21, 25, 30, 35, 40, 45, 50, 60, 80, 100 mT). Després d'aquest procediment, es van aplicar successius passos de desmagnetització tèrmica assolint temperatures de fins a 660º. Les magnetitzacions romanents característiques (ChRM, *characteristic remanent magnetization*) van ser computades utilitzant el mètode dels mínims quadrats de Kirschvink (1980) en gràfics de desmagnetització ortogonal (Zijderveld, 1967). El programa utilitzat per aquesta tasca és Paldir, desenvolupat per la Universitat d'Utrecht. La mangetització romanent característica ha permés derivar la latitud del camp geomagnètic virtual (VGP, *virtual geomagnetic pole*), el qual s'ha utilitzat com a indicador de la polaritat original de les mostres.

4.3.2. Processament i anàlisi de mostres per a estudis geoquímics

Depenent de la naturalesa dels materials recollits durant les campanyes de camp, es va procedir a obtenir mostres en pols per a estudis geoquímics de dues maneres diferents:

- Quan els espècimens era fàcilment individualitzables, com ara els nòduls edàfics, es va optar per reduir-los a pols mitjançant un morter d'àgata manual. Prèviament però, la superfície dels nòduls es va polir amb paper de vidre per eliminar possibles alteracions en l'exterior de les mostres, i es van netejar amb etanol de 98º.

- En els casos en que la mostra es tractava de blocs massius, com ara calcàries, crostes o clastos, es va optar per obtenir pols en talls frescos mitjançant un micro-trepant elèctric.

Per determinar la composició mineralògica de les mostres seleccionades es va encarregar un estudi de difracció de raigs X en el difractòmetre 'D5005 BruckerTM' de l'Institut de Ciències de la Terra Jaume Almera, a Barcelona.

Per a conèixer les composicions isotòpiques, es va encarregar l'estudi als Centres Científics i Tecnològics de la Universitat de Barcelona. Cada mostra es va fer reaccionar amb àcid fosfòric a 70º durant tres minuts en un 'Carbonate Kiel Device III (Thermo Finnigan)'. El dispositiu d'extracció del CO_2 està acoblat a un espectròmetre de masses 'Thermo Finnigan MAT 252 triple collector', el qual determina la composició dels isòtops estables ($\delta^{13}C$, $\delta^{18}O$). Les dades s'indiquin en δ‰ en relació amb l'estàndard 'Vienna PeeDee Belemnite (V-PDB)'. La presició de les mesures és de 0.03‰ pel $\delta^{13}C$ i 0.06‰ pel $\delta^{18}O$.

Figura 4.3. Sala amb els magnetòmetres '2G Enterprises' a l'Istituto di Geofisica e Vulcanologia (INGV, Roma), durant el procés de desmagnetització de les mostres.

4.4. Treball de síntesi i preparació dels articles

A mesura que s'anaven adquirint les dades, aquestes es van discutir i comparar amb la bibliografia disponible per tal d'extreure'n el màxim d'informació. Donat que la tesi ja de bon principi estava planificada com a un compendi de publicacions, progressivament es van preparar articles que donarien resposta als objectius inicialment plantejats al Capítol 2.

The latest succession of dinosaur tracksites in Europe: hadrosaur ichnology, track production and palaeoenvironments

5

El capítol 5 correspon a l'article publicat online en la revista *PLoS ONE* el 15 de març de 2013:

Vila, B., Oms, O., **Fondevilla, V**., Gaete, R., Galobart, À., Riera, V., Canudo, J.I. (2013) The Latest Succession of Dinosaur Tracksites in Europe: Hadrosaur Ichnology, Track Production and Palaeoenvironments. *PLoS ONE* **8**(9): e72579. doi:10.1371/journal.pone.0072579

En aquest article l'autor V. F. ha contribuït en part en les tasques de prospecció de jaciments (Iscles-1, -2, -3, -4, -5, Sapeira-2, i revisió de la major part dels altres jaciments) i mesura de noves seccions estratigràfiques (Sapeira, Iscles, Barranc de Guixers Nord, Orcau Oest). També ha participat en l'estudi sedimentològic d'afloraments (Iscles-3, La Llau de la Costa, Masia de Ramon petjades), en la mesura de paràmetres del material estudiat i en la preparció del panell cronostratigràfic actualitzat de Riera (2010). També ha intervingut en la redacció del text (Ambients sedimentaris i cronostratigrafia), la preparació de la figura 1, 2 i 9 i la discussió dels resultats amb la resta de coautors.

Part dels continguts d'aquest treball es van desenvolupar en la tesi doctoral de V. R., els quals s'amplien en aquest article. Així, tal i com se cita en el treball, la major part de les seccions estratigràfiques provenen de Riera (2010). Els apartats C, F i G de la Figura 6 van aparèixer originalment a Riera (2010), així com algunes de les interpretacions sedimentològiques descrites en l'article.

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The Latest Succession of Dinosaur Tracksites in Europe: Hadrosaur Ichnology, Track Production and Palaeoenvironments

Bernat Vila[1,2*], **Oriol Oms**[3], **Víctor Fondevilla**[3], **Rodrigo Gaete**[4], **Àngel Galobart**[2], **Violeta Riera**[3], **José Ignacio Canudo**[1]

1 Grupo Aragosaurus–IUCA, Paleontología, Facultad de Ciencias Universidad de Zaragoza, Zaragoza, Spain, **2** Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona, Spain, **3** Departament de Geologia (Estratigrafia), Facultat de Ciències Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain, **4** Museu de la Conca Dellà, Isona i Conca Dellà, Lleida, Spain

Abstract

A comprehensive review and study of the rich dinosaur track record of the Tremp Formation in the southern Pyrenees of Spain (Southwestern Europe) shows a unique succession of footprint localities prior to the end-Cretaceous mass extinction event. A description of some 30 new tracksites and data on sedimentary environments, track occurrence and preservation, ichnology and chronostratigraphy are provided. These new track localities represent various facies types within a diverse set of fluvial environments. The footprint discoveries mostly represent hadrosaurian and, less abundantly, to sauropod dinosaurs. The hadrosaur tracks are significantly smaller in size than, but morphologically similar to, those of North America and Asia and are attributable to the ichnogenus *Hadrosauropodus*. The track succession, with more than 40 distinct track levels, indicates that hadrosaur footprints in the Ibero-Armorican region occur predominantly in the late Maaastrichtian (at least above the early Maastrichtian–late Maastrichtian boundary). The highest abundance is found noticeably found in the late Maastrichtian, with tracks occurring in the C29r magnetochron, within about the latest 300,000 years of the Cretaceous.

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* E-mail: bernat.vila@unizar.es

Introduction

The end-Cretaceous mass extinction was one of the major events in the history of life on Earth, resulting in the demise of multiple taxa [1]. On land, non-avian dinosaurs and many other vertebrates succumbed at the end of the Maastrichtian, the final stage of the Cretaceous. With the exception of data from the bolide impact zone and nearby areas (e.g. North America [2]), little is known about how the last dinosaur faunas reached the boundary in most parts of the planet [3–7]. Much of the current knowledge is from the fossil bone record recovered from the uppermost levels of many geologic formations around the world. In addition, the discovery of dinosaur tracks close to the Cretaceous–Palaeogene (K–Pg) boundary has shown their utility as chronostratigraphical markers [8]. The autochthonous character of fossil tracks means that they provide unmistakable proof of the presence of the track maker in a restricted temporal and spatial context, with no possibilities of reworking as is possible for bone remains. Tracks thus represent a valuable tool for analysing last occurrences and diversity patterns of dinosaurs before the K–Pg extinction event.

Geologic formations of Campanian and Maastrichtian age all over the world provide a rich track record of dinosaurs in the last 20 million of years of the Mesozoic [9]. Up until now the geologically uppermost known track record has been located in North America, more specifically within the Raton Formation of Colorado, where a diverse ichnofauna composed of ichnites from hadrosaurs, probable ceratopsians and large theropods has been identified very close to the K–Pg boundary [10]. Nevertheless, in the last decade new discoveries in other regions have brought to light an ichnological record comparable with that of North America in terms of age and stratigraphic position [11,12]. The Tremp Formation in the southern Pyrenees preserves one of the richest terrestrial track records yet identified in the latest Cretaceous of Europe. The dinosaur track record is composed of multiple footprint localities of Maastrichtian age with abundant tracks and trackways made by titanosaurian sauropods (Fumanya, Orcau-2, La Massana localities; [13–16]) as well as of hadrosaurian ornithopods (La Mata del Viudà, Moror B, Areny 1 localities; [17–19]) and theropods (Moror A locality; [18]). Other reports of purported dinosaur tracks are herein considered too poorly preserved to be of ichnotaxonomic significance (Mas Morull, Santa Maria de Meià, Coll de Jou localities; [20–22]) or of non-dinosaurian affinity (La Posa locality; [23]). Outside of the Pyrenees, Herrero-Santos [24] reported a hadrosaur trackway from the lower Maastrichtian deposits of Sierra de los Gavilanes (Murcia province, Spain), and Gierlinski et al. [25] reported hadrosaur and theropod tracks from an upper Maastrichtian locality in Poland.

The aim of the present paper is to provide the first comprehensive review and update of the latest Cretaceous dinosaur track record in Europe with the inclusion of 28 new localities, and to discuss their implications in terms of ichnotaxonomy, palaeoenvironments, chronostratigraphy, and the K–Pg boundary extinction event.

Geological setting

The study area is concentrated on several localities belonging to the Tremp Formation, along multiple sections distributed over various geographical areas of the southern Pyrenees (Tremp, Àger, and Vallcebre synclines in the provinces of Huesca, Lleida and Barcelona, Spain, SW Europe; Fig. 1). The Tremp Formation is a marginal marine and terrestrial unit, about 800 m thick, which is exposed in northern Catalonia and Aragón (Spain) and encompasses deposits of Late Cretaceous to Early Palaeogene age. The Cretaceous (Maastrichtian) part of the formation contains two lithologic units deposited as a result of a marine regression [27]: a basal lagoonal grey unit (coals, mudstones and sandstones) and a fluvial lower red unit (mudstones and sandstones) [28]. In the latter unit various lithostratigraphic subunits have been recognised such as the fluvial "Gres à reptiles" and the lacustrine "Tossal de la Doba limestones" (or "Tossal d'Obà" member), in the Vallcebre and Isona sectors, respectively [6,28–31]. The lacustrine Vallcebre limestones and laterally equivalent strata (the "Suterranya limestones" and "Sant Salvador de Toló limestones" subunits in the Isona sector) and overlying fluvial units represent the Palaeogene strata [28,29]. The transition from Cretaceous to Palaeogene strata is isochronous [32]. Even though no impact layer has ever been found in the Pyrenean continental sections, the Cretaceous–Palaeogene boundary is located at the contact between the lower red unit and the Vallcebre limestones and laterally equivalent strata or just below this contact, according to biostratigraphic and magnetostratigraphic determinations ([6,31] and references therein). In any case the boundary is found above the "Gres à reptiles" and "Tossal de la Doba limestones" members. With regard to the base of the Tremp Formation, this is not completely isochronous since laterally it evolves into the deltaic-marine Arén Sandstone Formation (Fig. 3 in [6]). This chronostratigraphical scheme can be expanded and correlated to other areas of the northern Pyrenees and Provence regions of France, within what is known as the Ibero-Armorican domain [33], though no dinosaur tracks have yet been reported there. Since the early 1920 s numerous fossil localities in the Arén Sandstone and Tremp formations of Spain have yielded multiple bones, tracks and eggs attributed to theropods, hadrosaurs, ankylosaurians, and sauropods [6,34].

Methods

Abbreviations

MCD: Museu de la Conca Dellà; MPZ: Museo Paleontológico de Zaragoza; IPS: Institut Català de Paleontologia Miquel Crusafont; TL: track length; TW: track width; SL: stride length; VcC: Vallcebre composite; IsC: Isona composite; SC: Serrat del Corb; TDS: Tossal de la Doba Sud; TDN: Tossal de la Doba Nord; LB: Lo Bas; LT: Les Torres; BP: Basturs Poble; BWB: Basturs West B; BWA: Basturs West A; BTN: Barranc de Torrebilles Nord; BTS: Barranc de Torrebilles Sud; OrE: Orcau Est; OrW: Orcau Oest; BGS: Barranc de Guixers Sud; CS: Costa de la Serra; BGN: Barranc de Guixers Nord; LTs: Lo Tossal; Mr: Moror; MR: Masia de Ramon; CR: Costa Roia; St: Suterranya; Sp: Sapeira; Ar: Areny; Bl: Blasi; Is: Iscles; Sr; Serraduy; SrW; Serraduy West; MS: Mas de Saurí.

Field data acquisition

All the localities and stratigraphic sections are indicated in Figure 1. They have been correlated with the lithostratigraphy and integrated in a chronostratigraphic frame. The western and eastern sectors of the Tremp Syncline (Isona and Isàvena-Ribagorçana areas) have been correlated and dated in accordance with data from the present study and the magnetostratigraphy of Oms and Canudo [35], Pereda-Suberbiola et al. [36], and Cruzado-Caballero et al. [37], and Riera et al. [6], Marmi et al. [38], and Vila et al. [39], respectively. The Vallcebre sector is dated on the basis of the magnetostratigraphy of Oms et al. [31] and Vila et al. [40]. The Àger sector is correlated and dated on the basis of López-Martínez et al. [20]. Their magnetostratigraphic succession for this area fits well in the standard time scale of Ogg and Hinnov [41] and Renne et al. [42], allowing correlation within the four sectors. Sections St, MR, LTs, BGS, CS, OrE, BWA, BP, LT, LB, TDN, TDS and SC correspond to sections I, V, VI, VII, IX, XIII, XIV, XVII, XVIII, XXII, XX, XXV and XXVII in Riera et al. [6], respectively. Sections Bl, CR, Mr and BWB correspond to sections H2, I1B, M1 and I15B in Riera [43], respectively. Sections BTS and BTN correspond to sections A and B in Marmi et al. [38]. Sections Ar, Sr, IsC and VcC have been redrawn from Vila et al. [39]. Sections MS and SrW have been redrawn from Llompart [17] and López-Martínez et al. [20], and Cruzado-Caballero et al. [37], respectively. The Areny 1, Tossal del Gassó, Camí de les Planes, Serrat de Santó, Orcau-4, Serrat de Sanguin, La Pleta Nord, La Pleta Resclosa, and Serraduy Norte sites are projected at the reference sections.

Detailed sedimentological analyses were conducted at Iscles-3, Masia de Ramon Petjades, Costa Roia, Serraduy Sur, La Llau de la Costa, Cingles del Boixader and La Mata del Viudà localities. High resolution, close-range photogrammetric models for MCD-5140 and MCD-5142 tracks in the La Llau de la Costa locality were generated using the methods described by Falkingham [44] in order to produce higher fidelity models (Appendix S1). Measurements of tracks and trackways refer to the parameters TL, TW and SL, taken after Thulborn [45], in cm. All necessary permits were obtained for the described study, which complied with all relevant regulations. The Departament de Cultura de la Generalitat de Catalunya and Gobierno de Aragón issued the permission for the studied localities.

Repositories

Thirty-five track casts and replicas have been collected and housed in repositories of the Museu d'Isona i Conca Dellà, Lleida, Spain (MCD-5140, MCD-5141, MCD-5142, MCD-5143, MCD-5144, MCD-5145, MCD-5146, MCD-5147, MCD-5148, MCD-5149, MCD-5150, MCD-5151, MCD-5152, MCD-5153, MCD-5154, MCD-5155, MCD-5156, MCD-5157, MCD-5158, MCD-5159, MCD-5160, MCD-5161, MCD-5162, MCD-5163, MCD-5164, MCD-5166), the Museo Paleontológico de Zaragoza, Zaragoza, Spain (MPZ 2012/831, MPZ 2012/830, MPZ 2012/829, MPZ 2012/828, MPZ 2012/826, MPZ 2012/827, MPZ 2012/833), and the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain (IPS-63272, IPS-63661).

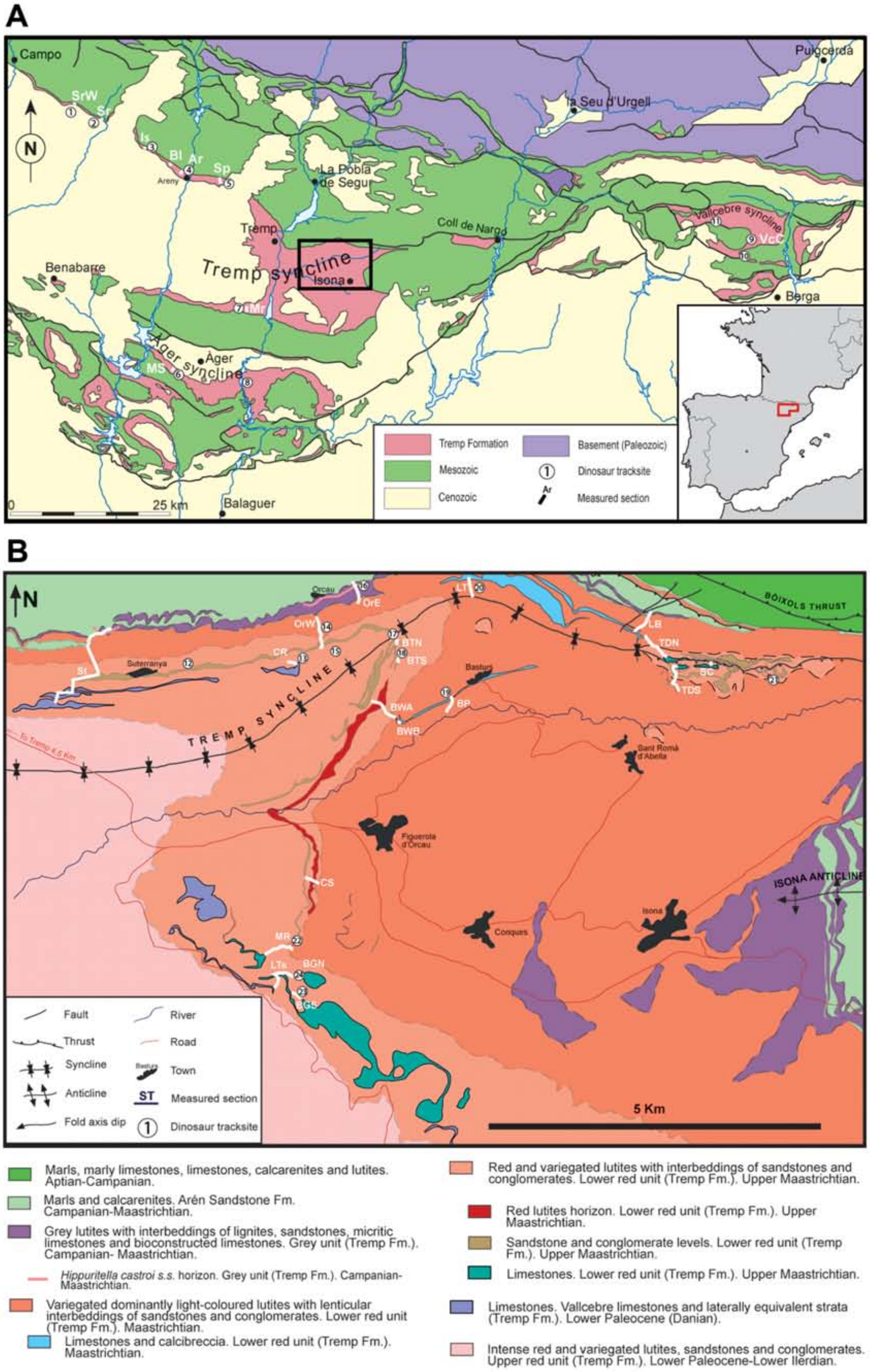
A
Campo
SrW
Sr
①
②
N
Is
③
Bl
Ar
Sp
Areny
④
⑤
La Pobla de Segur
Tremp
Coll de Nargó
Vallcebre syncline
⑪
⑨
VcC
⑩
Puigcerdà
la Seu d'Urgell
Benabarre
Tremp syncline
Isona
⑦
Mr
Àger
Àger syncline
MS
⑥
⑧
Berga
0
25 km
Balaguer
Tremp Formation
Mesozoic
Cenozoic
Basement (Paleozoic)
Dinosaur tracksite
Measured section
B
N
Orcau
⑯
OrE
LT
⑳
BÒIXOLS THRUST
OrW
⑭
⑰
BTN
⑱
BTS
LB
TDN
St
Suterranya
⑫
CR
⑬
⑮
TREMP SYNCLINE
Basturs
⑲
BP
BWA
BWB
SC
TDS
㉑
To Tremp 4.5 Km
Sant Romà d'Abella
Figuerola d'Orcau
CS
ISONA ANTICLINE
Isona
Conques
MR
㉒
LTs
BGN
㉔
㉓
BGS
Fault
Thrust
Syncline
Anticline
Fold axis dip
River
Road
Town
ST
Measured section
Dinosaur tracksite
5 Km
Marls, marly limestones, limestones, calcarenites and lutites. Aptian-Campanian.
Marls and calcarenites. Arén Sandstone Fm. Campanian-Maastrichtian.
Grey lutites with interbeddings of lignites, sandstones, micritic limestones and bioconstructed limestones. Grey unit (Tremp Fm.). Campanian- Maastrichtian.
Hippuritella castroi s.s. horizon. Grey unit (Tremp Fm.). Campanian-Maastrichtian.
Variegated dominantly light-coloured lutites with lenticular interbeddings of sandstones and conglomerates. Lower red unit (Tremp Fm.). Maastrichtian.
Limestones and calcibreccia. Lower red unit (Tremp Fm.). Maastrichtian.
Red and variegated lutites with interbeddings of sandstones and conglomerates. Lower red unit (Tremp Fm.). Upper Maastrichtian.
Red lutites horizon. Lower red unit (Tremp Fm.). Upper Maastrichtian.
Sandstone and conglomerate levels. Lower red unit (Tremp Fm.). Upper Maastrichtian.
Limestones. Lower red unit (Tremp Fm.). Upper Maastrichtian.
Limestones. Vallcebre limestones and laterally equivalent strata (Tremp Fm.). Lower Paleocene (Danian).
Intense red and variegated lutites, sandstones and conglomerates. Upper red unit (Tremp Fm.). Lower Paleocene-Lower Ilerdian.

Figure 1. Geographic and geological setting of the study area. (A) Geological map of the southern Pyrenees with Tremp Formation outcrops and location of tracksites and measured sections (modified from López-Martínez and Vicens [26]). (B) Geological map of the Isona sector (enlarged area in A) and location of tracksites and measured sections (modified from Riera et al. [6]). Numbers (tracksites): 1, Fornons 3 and Dolor 2; 2, Serraduy Norte and Serraduy Sur; 3, Iscles-1, Iscles-2, Iscles-3, Iscles-4, and Iscles-5; 4, Areny 1; 5, Sapeira-1 and Sapeira-2; 6, La Mata del Viudà; 7, Moror A and Moror B; 8, La Massana; 9, Fumanya; 10, Cingles del Boixader; 11, La Pleta Resclosa and La Pleta Nord; 12, Camí de les Planes and Serrat de Santó; 13, Costa Roia; 14, Torrent de Carant; 15, Serrat de Sanguin; 16, Orcau-2; 17, Orcau-4; 18, Barranc de Torrebilles-5; 19, Basturs Poble; 20, La Llau de la Costa; 21, Tossal del Gassó; 22, Masia de Ramon Petjades; 23, Barranc de Guixers-1 and Barranc de Guixers-2; 24, Barranc de Guixers-3. See abbreviations for measured sections in "Methodology" section.
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Results

The following descriptions (see also Text S1) refer to the 28 newly discovered localities (Table 1), some of which have been briefly referred by previous authors [6,21,37,46], and to two already known sites (La Mata del Viudà, Areny 1; [17,19]). The descriptions are complemented with data from other localities (Fumanya, Orcau-2, and La Massana, Moror A and B; [13,15,16,18]). This work further integrates data on the stratigraphic succession of sites, the sedimentary environments, track occurrence and preservation, ichnology and chronostratigraphy. The resulting dataset shows a unique succession of track localities prior to the terminal Cretaceous extinction event.

Sedimentary environments

Dinosaur tracks occur in various depositional settings in the grey and lower red units of the Tremp Formation. The new sites correspond to track horizons that represent various facies types within a diverse set of fluvial environments belonging to the lower red unit (Fig. 2). The remaining localities exemplify tracks produced in lagoonal environments (Table 1).

Meandering streams (channel facies) are identified at 27 localities in the Tremp and Vallcebre synclines (Table 1) on the basis of the following characteristics (Fig. 2A–D): (a) dominant texture composed of very fine- to medium-grained sands and mudstones; (b) mudstone layers commonly covering sandstones where footprint casts are found; (c) vertical trend arranged in fining-up cycles; (d) multiple and very well-defined lateral accretions; (e) occasional conglomerate lag at the base of each accretion surface or thalweg; (f) sedimentary structures restricted to the middle and lower part of the sequence and absent in the upper part due to plant bioturbation; (g) these sedimentary structures comprise planar lamination or small-scale cross-bedding mainly visible at the top of beds; and (h) sequence thickness varying from 2 to almost 6 metres. The characteristics of the sandstone bodies correspond to lithofacies F12B of Riera et al. [6]. The channel-shape of these sandstones and the presence of the lateral accretions or point bars are typical in alluvial systems with high sinuosity rivers [47].

A crevasse splay setting can be identified at the La Llau de la Costa locality (Fig. 2E and Table 1) on the basis of the following characters: (a) poorly sorted sandstone; with (b) a tabular-shaped morphology; (c) surrounded by floodplain overbank mudstones but laterally connected to the abovementioned meandering channel bodies; and (d) an abundance of small plant remains. At the La Llau de la Costa site the bed has an exposed lateral extension of about 30 metres and a maximum thickness of 1 metre. It consists of grey, poorly sorted, fine-grained sandstones with mud and scattered coarser elements, and abundant vegetal remains, a typical feature of crevasse splay deposits [48]. Dinosaur tracks occur at the bottom of, on top of, and within the tabular lens. Hence, the multiple track levels at the La Llau de la Costa site indicate different episodes of crevasse splay development and trampling.

Braided streams (channel facies) are recognized at the localities of Cingles del Boixader and La Mata del Viudà (Vallcebre and Àger synclines, respectively; Fig. 2F and G and Table 1) on the basis of the following features: (a) general texture composed of gravels; (b) mud-free horizons except for the occasional mud drapes interbedded with sandstone layers that preserve tracks; (c) absence of a vertical trend in texture or thickness; (d) unidirectional cross-bedding in gravels; and (e) well-rounded and mineralogically mature sediment. These characteristics correspond to lithofacies 12C of Riera et al. [6].

Associated with meandering and braided streams, the fine overbank deposits consist of massive red, ochre and purple mudstones (lithofacies F10, F7 and F11 of Riera et al. [6], respectively). Invertebrate activity may also be extensive and corresponds to burrows of the continental ichnogenera *Naktodemasis* and *Spirographites* [6], which obliterate the original sedimentary structures. Grey mudstones may be present, representing oxbow-lake deposits in abandoned meanders (lithofacies F5B of Riera et al. [6]). Of particular interest in the context of dinosaur track production and preservation is the absence of mud cracking in the mudstone layers of the floodplain or within channels. When the latter are not bioturbated, they are grey-coloured and are found in the lower parts of the cycles (lithofacies F5B of Riera et al. [6]).

Lagoon settings are identified exclusively in the grey unit (Table 1) as indicated by regional works [28]. At Moror A and B, they occur in a succession of grey mudstones, marls and limestones with charophytes, root bioturbation, bivalves and ostracods [18]. The Moror A site is located in a bioturbated and bioclastic limestone bed showing evidence of desiccation, and the Moror B outcrop occurs in a micritic limestone, which is also bioturbated. Other sites in the Tremp Formation that contain sauropod footprints (Orcau-2, La Massana and Fumanya) have also been characterized as lagoonal [49,50] with tidal influence [51]. All these lagoonal localities are found in limestones (lithofacies F2B facies of Riera et al. [6]).

Track occurrence and preservation

Up to 28 new track localities have been identified in the Tremp Formation deposits of the southern Pyrenean basins. The track-bearing levels are very abundant and moderately extensive, especially in the Tremp syncline succession where sandstones are more abundant. It is very common to identify unmistakable footprints and track-like load structures in many levels of the lower red unit. They occur in views from below of overhanging ledges (Fig. 3A–D), in cross-sectional outcrop views (Fig. 3E, F), and more rarely in plan-view outcrops (Fig. 3G, H).

The dinosaur tracks in the new localities are preserved in two main distinct modes: a) as natural casts (convex hyporeliefs) at the base of the sandstone beds, within the sandstone beds (i.e. in accretion surfaces), or within the mudstone levels, and b) as concave hyporeliefs on top of sandstone lenses or limestone beds. The tracks preserved as natural casts commonly occur as discrete, well-preserved moulds of footprint impressions but also as undetermined sandstone moulds on irregular surfaces, which

Table 1. Track localities and sedimentary environments of dinosaur track localities in the Tremp Formation.

Track locality	Geographic location	Stratigraphic position and Age	Sedimentary environment	Dinosaur Ichnotaxa
Masia de Ramon Petjades; Barranc de Guixers-1; Barranc de Guixers-3; Tossal del Gassó; Serrat de Santó; Costa Roia; Sapeira-1; Sapeira-2; Barranc de Torrebilles-5	Eastern Tremp Syncline (Isona sector)	Lower red unit C29r (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
Barranc de Guixers-2; Serrat de Sanguin; Camí de les Planes	Eastern Tremp Syncline (Isona sector)	Lower red unit C29r (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*, sauropod tracks
La Pleta Nord; La Pleta Resclosa	Vallcebre Syncline sector	Lower red unit C29r (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
Cingles del Boixader	Vallcebre Syncline sector	Lower red unit C29r (late Maastrichtian)	Fluvial. Braided streams, channel facies	*Hadrosauropodus*
La Mata del Viudà	Àger Syncline sector	Lower red unit C29r (late Maastrichtian)	Fluvial. Braided streams, channel facies	*Hadrosauropodus*
Iscles-1, Iscles-2, Iscles-3, Iscles-4; Iscles-5; Serraduy Sur; Serraduy Norte; Dolor 2; Fornons 3	Western Tremp Syncline (Isàvena-Ribagorça sector)	Lower red unit C29r (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
Areny 1	Western Tremp Syncline (Isàvena-Ribagorça sector)	Grey unit C30n (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
La Llau de la Costa	Eastern Tremp Syncline (Isona sector)	Lower red unit C30n (late Maastrichtian)	Fluvial. Meandering streams, crevasse splay facies	*Hadrosauropodus*
Basturs Poble	Eastern Tremp Syncline (Isona sector)	Lower red unit C30r/C31n (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
Torrent de Carant; Orcau-4	Eastern Tremp Syncline (Isona sector)	Lower red unit C31r (late Maastrichtian)	Fluvial. Meandering streams, channel facies	*Hadrosauropodus*
Moror A	Eastern Tremp Syncline (Isona sector)	Grey unit C31r (early–late Maastrichtian)	Lagoon	*Hadrosauropodus*
Moror B	Eastern Tremp Syncline (Isona sector)	Grey unit C31r (early–late Maastrichtian)	Lagoon	theropod tracks
Orcau-2	Eastern Tremp Syncline (Isona sector)	Grey unit C31r (early Maastrichtian)	Lagoon	sauropod (titanosaur) tracks
Fumanya	Vallcebre Syncline sector	Grey unit C31r (early Maastrichtian)	Lagoon	sauropod (titanosaur) tracks
La Massana	Àger Syncline sector	Grey unit (late Campanian)	Lagoon	sauropod (titanosaur) tracks

Table includes new localities and data from sites previously reported in the literature. See Text S1 and Dataset S1 for further description of the localities and repositories.

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represent "dinoturbated" track levels. Undetermined footprint casts show a globular, dish-like, rounded or ball-like shape (Fig. 4A–C) and are about 10–30 cm deep in the substrate. Well recognizable footprints reveal tridactyl, rounded or oval morphologies (Fig. 5). Some of them preserve striae or scale scratch lines on the margins of their toe or heel prints and/or slippage marks in the rear margin of the track (Fig. 5F). Some casts are three-dimensionally preserved (Fig. 4D–F) and noticeably deep (27 cm in MPZ 2012/827), revealing the complete shape of the pes or manus (MCD-5163). The sediment that fills the tracks is massive sandstone and occasionally displays burrows.

Tracks preserved as convex hyporeliefs present three modes of preservation. In mode 1 the tracks occur at the base of the sandstone bed indicating the infilling of footprints produced on the floodplain mud (Fig. 4B–E). In mode 2 the tracks occur within the sandstone bed (accretion surface) in immediate contact with the interbedded mudstones, thus reflecting infilling of tracks produced within the channel (Fig. 4F–I). In mode 3 the dinosaur tracks occur as isolated casts within the mudstone levels (Fig. 4J), revealing the infilling of the footprints produced in the floodplain by passing sands and the later deposition of mudstone.

Tracks preserved as concave hyporeliefs or natural impressions have been described on top of fluvial sandstones (Areny 1, La Llau de la Costa; Fig. 3G and H) and lagoonal limestones (Moror A and B; [18]). In the crevasse splay outcrop of La Llau de la Costa, the footprint preservation depends on the contrast in grain size between successive sedimentation episodes. Thus, track morphology is highly variable throughout the outcrop, probably reflecting trampling at different times.

Ichnology

The new findings in the southern Pyrenees refer to three track types that have been attributed to sauropods (pes) and hadrosaurs (pes and manus) (Fig. 5). The most abundant track types in fluvial settings are the pedal prints of hadrosaurs, which are of moderate sizes and share a similar morphology (Fig. 5, 6, 7 and

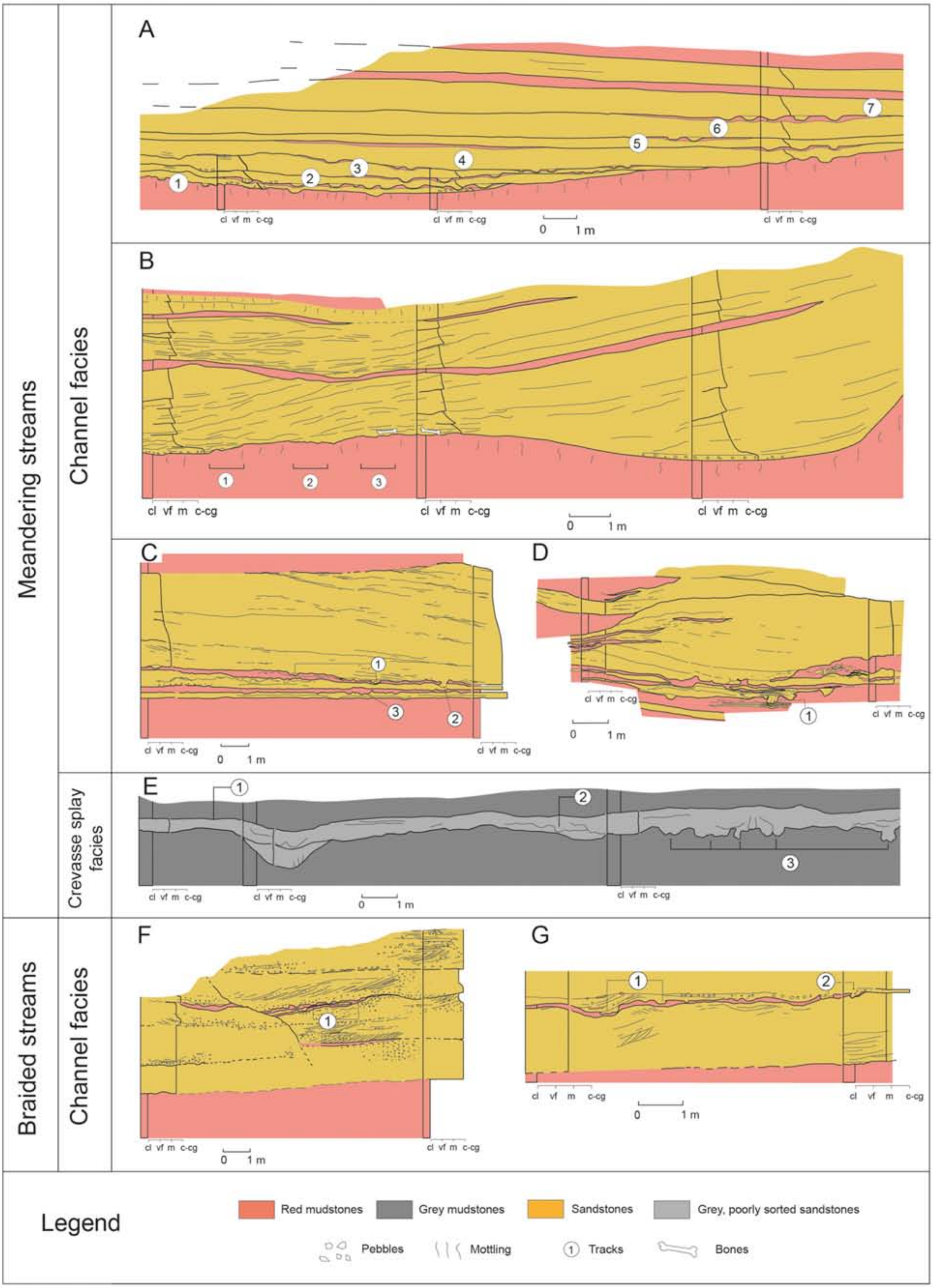
Meandering streams
Channel facies
Crevasse splay facies
Braided streams
Channel facies
A
B
C
D
E
F
G
1
2
3
4
5
6
7
cl vf m c-cg
0 1 m
Legend
Red mudstones
Grey mudstones
Sandstones
Grey, poorly sorted sandstones
Pebbles
Mottling
1 Tracks
Bones

Figure 2. Sedimentary architecture in outcrops of the main track localities of the Tremp Formation. (A–G) Iscles-3, Masia de Ramon Petjades, Costa Roia, Serraduy Sur, La Llau de la Costa, Cingles del Boixader and La Mata del Viudà sites, respectively.
doi:10.1371/journal.pone.0072579.g002

Appendix S1). These are tridactyl and mesaxonic, as wide as or wider than long (TL: TW ~1), and have blunt or rounded digits and a broad heel impression. The impression of digit III is thick and equal to or slightly shorter than digits II and IV but protrudes farther anteriorly than these (Fig. 7A, D, E; cf. [52]). The impressions of digits II and IV are sub-equal in length, usually oriented parallel to digit III and have an elliptical to tear-drop shape. Some of the digits preserve hoof-like impressions of unguals (Fig. 5D and 7J). The impression of the heel pad is wide and preserves a bilobed outline (Fig. 5C and E). Laterally, the heel pad displays symmetrical indentations or creases in relation to digits II and IV and constitutes a sub-rectangular morphology (Fig. 7A–P). Some tracks (MCD-5140, MCD-5141, MCD-5156, MRP-10) preserve the morphology of the plantar impression produced by the heel pad (Fig. 5E, 7D, E and Appendix S1), a triangular-shaped area that separates digit III from digits II and IV (i.e. the metatarsophalangeal pad). This is well featured in many other large ornithopod tracks [52–54]. Some of the pes casts (at the Serraduy Norte, Serraduy Sur, Serrat de Santó, and La Mata del Viudà localities) preserve slide marks or striae indicating a forward (horizontal and vertical) motion of the foot as it sank into the mud (Fig. 5F). These are vertical on the posterior margin of the heel area and slightly inclined on the lateral/medial sides of the digits. Similar structures have been reported in North American and Asian localities and they have been interpreted as the marks left by the skin tubercles of the foot when it sank into the substrate [11,53,55,56].

The manus tracks are less common in the European record. Those reported in the Pyrenees are smaller and show an oval to sub-rounded morphology without evidence of digital or hoof-like impressions. When associated with the pedal tracks (La Mata del Viudà and Masia de Ramon Petjades sites; Fig. 6B, C and 7L) they are situated anterior and lateral to digit III, between the impressions of digits III and IV, with their long axis oriented somewhat obliquely (about 45°) to the direction of progression. A three-dimensionally preserved manus cast (MCD-5163) from the Serrat de Sanguin locality confirms the ovoid morphology in plantar view and reveals a single, enhanced structure, similar to the mitten described in hadrosaur "mummies" [53]. It preserves vertical slide marks on the anterior margin of the cast.

Hadrosaur trackways are rare in Europe and mostly show bipedal locomotion (Fig. 8). In bipedal patterns (Fig. 8A, B and D) the pedal tracks are rotated inwards and exhibit a moderately high pace angulation (~144–166°) and a short stride (SL ~4.5TL). At the La Mata del Viudà locality, Llompart [17] and López-Martínez et al. [20] suggested that at least three of the pedal tracks were arranged in a trackway but no further measurements or maps were provided. The present study provides a detailed map of the whole surface and the relevant measurements of this trackway (Fig. 8C). The trackway consists of three pedal tracks with corresponding manus tracks, thus indicating a walking hadrosaur with a quadrupedal gait. Notably, the quadrupedal trackway from the La Mata del Viudà locality shows a high pace angulation value (174°) and a long stride (SL~8TL). Another example of a quadrupedal hadrosaur trackway in the Tremp Formation is at the La Pleta Nord locality, where a sequence of natural casts comprising three large pedes and one manus are aligned to form a trackway (Fig. 3E); the cross-sectional outcrop view prevents descriptions and measurements.

The morphological features of the Tremp Formation tracks (i.e. tridactyl and mesaxonic footprints with broad, blunt digits and a broad heel) are characteristic of large ornithopods

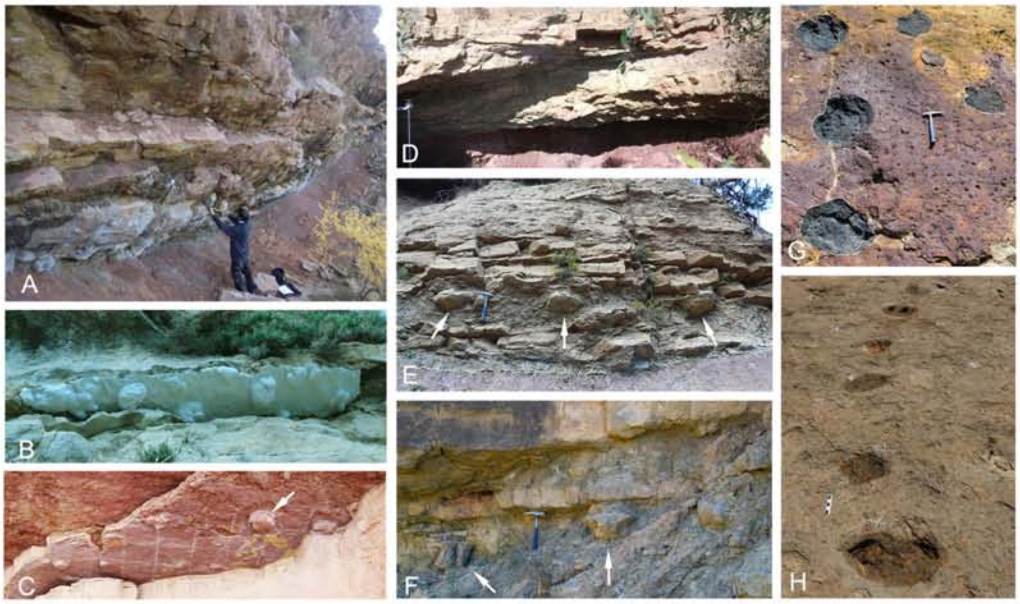

Figure 3. Track occurrence in the Tremp Formation. (A–D) Underneath views of overhanging ledges in the Iscles-3, Cingles del Boixader, La Mata del Viudà, and Masia de Ramon Petjades localities, respectively. (E and F) Cross-sectional outcrop views in the La Pleta Nord and Serraduy Sur localities, respectively. (G and H) Plan view outcrops in the Areny 1 and La Llau de la Costa localities, respectively. Scale bar: 15 cm; hammer length is about 33 cm. Arrows indicate the position of some tracks.
doi:10.1371/journal.pone.0072579.g003

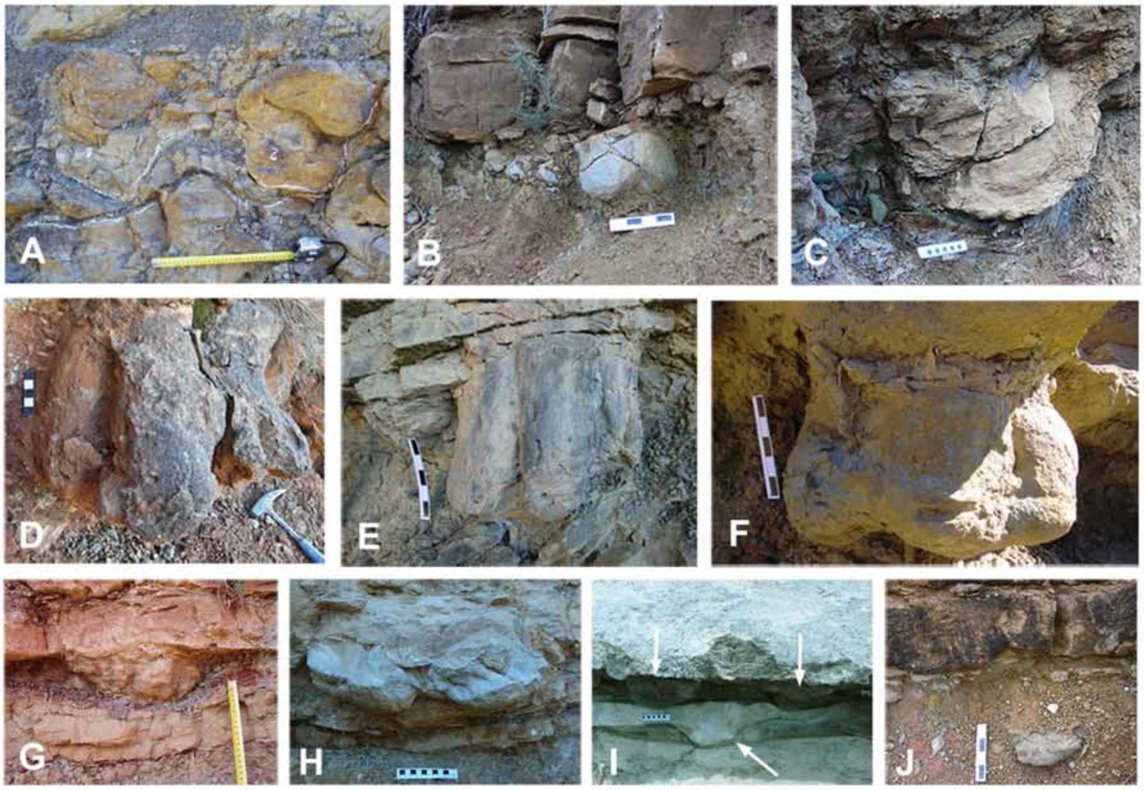

Figure 4. Track preservation in the Tremp Formation. (A) Footprints preserved as undetermined sandstone moulds on irregular surfaces, representing "dinoturbated" track levels. (B–E) Footprints impressed in the muddy floodplain and preserved as natural casts (convex hyporeliefs) at the base of the sandstone channel beds in the Serrat de Sanguin, La Pleta Nord, Sapeira-1, and Serraduy Sur localities, respectively. (F–I) Footprints impressed in accretion surfaces (mudstone) and preserved within the sandstone bed in the Serraduy Norte, La Pleta Nord, La Pleta Resclosa, and Cingles del Boixader localities, respectively. (J) Footprint preserved as an isolated sandstone cast within the mudstone of the floodplain in the Serrat de Sanguin locality. Numbers in A indicate tracks. Scale bars: 5 cm (in D), 10 cm (in C, H, and I), 15 cm (in E, and F), and 20 cm (in B and J); scale tape in A and G is in cm. Arrows indicate the position of some tracks.
doi:10.1371/journal.pone.0072579.g004

[45,53,54,57,58]. The hadrosaur pedal tracks described in the present study exhibit characteristics that are attributable to the ichnogenus *Hadrosauropodus* [54] on the basis of the following features: (a) tridactyl pes tracks wider than long; (b) blunt, oval digit prints with long axis parallel to track axis; (c) wide bilobed heel; and (d) symmetrical indentations or creases separating the posterior margin of the lateral digits and the heel pad (Fig. 7A–P). They show strong similarities with the hadrosaur tracks described from Maastrichtian deposits of North America and Asia (Fig. 7Q–T; [11,12,54]). Conversely, they clearly differ from *Hadrosauropodus nanxiongensis* [59] in the general pedal morphology. These latter tracks, however, are not well preserved [60]. As regards the manus tracks, they are ovoid to sub-rounded in shape and situated between the impressions of digits III and IV, oblique to the direction of progression. This morphology differs from that of *Hadrosauropodus langstoni* in that the latter are sub-triangular in shape but it resembles the morphology described by Currie et al. [53] in a hadrosaur trackway from the Dakota Group of Colorado. It is worth noting that these authors assigned the ichnites to the ichnospecies *Caririchnium leonardii* although the original diagnosis for this ichnospecies [61] included elliptical manus tracks but not a bilobed heel in the hindprints (typical of the ichnogenus *Hadrosauropodus*; [54]). With this in mind, we underscore the necessity of an ichnotaxonomic revision of the Late Cretaceous ornithopod ichnotaxa and propose that the hadrosaur ichnites of the Tremp Formation most probably represent a new *Hadrosauropodus* ichnospecies, different from *H. langstoni* and *H. nanxiongensis*, and with a manus morphology similar to the "*Caririchnium leonardii*" tracks described by Currie et al. [53].

Like other track records of the latest Cretaceous [11,12], sauropod tracks are less abundant than hadrosaur tracks in fluvial settings. In the Tremp Formation, they include pedal ichnites from Barranc de Guixers-2 and Camí de les Planes, and probably from the Serrat de Sanguin locality, where further excavation is required. In Camí de les Planes and Barranc de Guixers-2 the pedal casts (MCD-5152, MCD-5164 and an uncollected cast, respectively; Dataset S1) are longer than wide (26.5 to 38.5 cm in length) and oval in shape. One of the casts exhibits at least three digital impressions at the anterior margin (Fig. 5G). The sauropod track identified at the Serrat de Sanguin locality is a large and rounded natural cast (~32 cm across) that may correspond to the infilling of a pedal footprint (Fig. 4B). These all represent the uppermost track record of sauropods (presumably titanosaurs) in Europe, and their distribution is in accordance with the bone record [39].

Chronostratigraphy

The integration of the 28 new track localities with the previously known sites and their correlation with the magnetostratigraphic data show a rich succession of dinosaur tracks in the Tremp

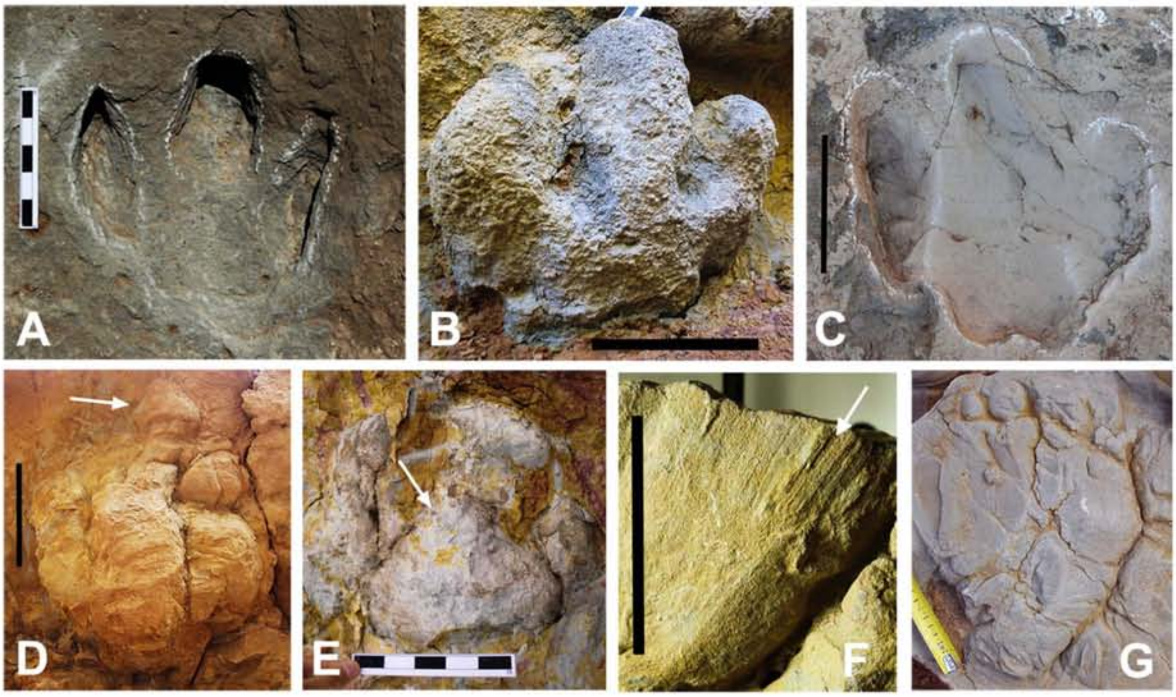

Figure 5. Footprint morphologies and characteristics. (A, C) Hadrosaur pedal tracks (MCD-5140 and MCD-5142, respectively) from the La Llau de la Costa locality. (B) Hadrosaur pedal track from the Iscles-3 locality. (D) Hadrosaur pedal track (uncollected) from the Barranc de Guixers-1 locality. Note the impression of the distal ungual phalanx (arrow). (E) Hadrosaur pedal track (uncollected) from the Masia de Ramon Petjades locality. Note the triangular-shaped plantar impression produced by the heel pad (arrow). (F) *Striae* or scale scratch lines (arrow) on the margins of a toe in the MPZ 2012/829 cast from the Serraduy Norte locality. (G) Sauropod pedal track (cast) from the Barranc de Guixers-2 locality. Scale bar: 15 cm (in A–E); 5 cm (in F); scale tape in G in cm.
doi:10.1371/journal.pone.0072579.g005

Formation (Fig. 9 and Table 1). The track succession indicates differences in the temporal distribution of the various dinosaur track types. Hadrosaurs are represented by tracks found noticeably in the late Maastrichtian. The track succession features: (a) an early occurrence of tracks (at the Moror B site) in the upper part of the C31r magnetochron, around the early Maastrichtian–late Maastrichtian boundary (~70 Ma); (b) a moderate abundance of tracks (at the localities of Areny 1, Basturs Poble, La Llau de la Costa, Torrent de Carant, and Orcau-4) in the C31n-C30r-C30n magnetochrons, in the middle–upper part of the late Maastrichtian (~69.1–66.3 Ma); (c) a high abundance of tracks in the lower part of the C29r chron (~66.3–66 Ma), in the latest Maastrichtian. The uppermost unequivocal evidence of hadrosaur tracks in the Tremp Formation occurs at the Cingles del Boixader site, 14 metres below the K-Pg boundary. Other localities with a similarly high chronostratigraphic position are those of Sapeira-2, Iscles-5 and unnamed levels in Blasi (Fig. 9). However, the magnetostratigraphic correlation is still tentative in these sites. Significantly, all the hadrosaur tracks occur in the late Maastrichtian (at least above the early Maastrichtian–late Maastrichtian boundary), and the highest abundance is found in approximately the last 300,000 years of this time stage. As regards sauropod tracks, they are found from the late Campanian to the latest Maastrichtian and do not show a particular time distribution along the succession. Theropod tracks are scarce in the Tremp Formation and have only been documented at one locality [18].

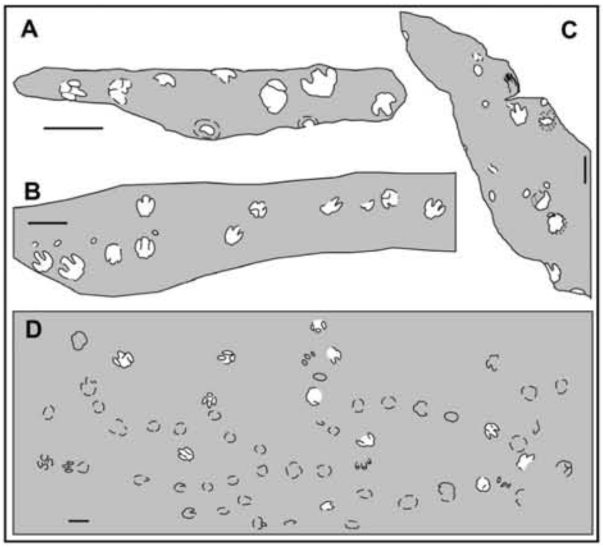

Figure 6. Mapping of some of the main hadrosaur track localities in the Tremp Formation. (A–D) Cingles del Boixader, Masia de Ramon Petjades, La Mata del Viudà, and La Llau de la Costa localities, respectively. Scale bar: 50 cm.
doi:10.1371/journal.pone.0072579.g006

Discussion

Footprint palaeoenvironments and production

The occurrence of dinosaur tracks (mainly and abundantly of hadrosaurs) in continental environments is well documented in various Late Cretaceous (Campanian–Maastrichtian) deposits in

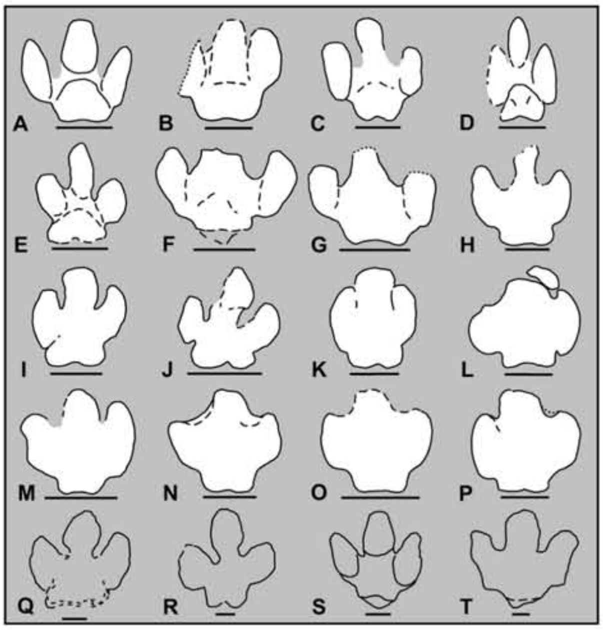

Figure 7. Hadrosaur pedal footprints from the Tremp Formation (white outlines) and other Maastrichtian formations (unfilled outlines) from North America and Asia. (A, C, D) Negative hyporeliefs from the La Llau de la Costa locality (MCD-5140, MCD-5141, MCD-5142, respectively). (B and O) Casts from the Serraduy Norte locality (MPZ 2012/829 and MPZ 2012/827, respectively). (E and F) Casts from the Cingles del Boixader locality (IPS-63661/CB1-CB3). (G) Cast from Serraduy Sur locality (MPZ 2012/828). (H) Cast from the Serrat de Sanguin locality (MCD-5159). (I and K) Casts from the Masia de Ramon Petjades locality (MRP-6, MRP-8). (J) Cast from the Iscles-3 locality (I3–5). (L) Manus-pes casts from the La Mata del Viudà locality (MV-3 and MV-2, respectively). (M and N) Casts from the Camí de les Planes locality (MCD-5149 and MCD-5150, respectively). (P) Cast from the Orcau-4 locality (MCD-5155). (Q) *Hadrosauropodus langstoni* cast (TMP 87.76.6) from the St. Mary River valley locality of the USA, after Lockley et al. [54]). (R) Cast (CU-MWC 224.1–224.11) from the Zerbst ranch locality of the USA, after Lockley et al. [54]. (S) Cast (MPD 100F/11) from the Nemegt locality of Mongolia, after Currie et al. [11]. (T) Cast from the Bugin Tsav locality of Mongolia, after Ishigaki et al. [12]. Scale bar: 15 cm. All drawings are in sole view, except A, C, and D which are in top view.

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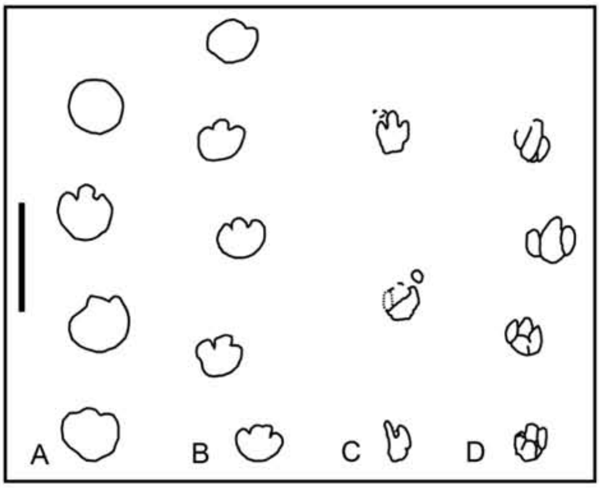

Figure 8. Hadrosaur trackways in southwestern Europe. (A, B, and D) Bipedal trackways from the Areny 1, Moror B, and Sierra de los Gavilanes tracksites (redrawn from Barco et al. [19], Llompart [18], and Herrero-Santos, [24], respectively). (C) Quadrupedal trackway from the La Mata del Viudà tracksite.

doi:10.1371/journal.pone.0072579.g008

North America and Asia [11,12,53–56]. Even though these do not strictly represent the same sedimentary settings (though most of them correspond to fluvial environments), some authors [53,55] have underscored their preservational similarities. The lower red unit of the Tremp Formation displays meandering and braided fluvial systems with equally favourable conditions for track production and preservation, similar to those of other fluvial (anastomosed) systems reported in North America and Asia [11,53,55,56]. Our sedimentological data from the Tremp Fm indicate that the braided systems exhibit features shared with the gravel-bed braided rivers of Miall [62]. The meandering systems (and associated crevasses) mainly belong to fine-grained meandering rivers, although some cases may display certain features of the sand-bed meandering rivers of Miall [62]. The close connection with entirely marine deposits through a lagoon is evidenced by regional geology [27–29] and by the fact that fine-grained meandering rivers are common in estuarine settings.

The preservation mode of footprints as natural casts has been well documented in many Late Cretaceous formations worldwide [11,12,52,55,56,63]. The general model for track formation and preservation in fluvial settings highlights that fluctuations in the water table are pivotal for facilitating a suitable substrate [64]. These fluctuations depend on flooding and subsequent emergence episodes, which are related with the hydraulic dynamics of the fluvial channel and probably with seasonal constraints [11,53]. In the lower red unit of the Tremp Formation the sedimentology of the footprint localities provides data for assessing the production and preservation of the tracks. As in other fluvial settings, the occurrence of tracks preserved as convex hyporeliefs is favoured by the alternating high and low water stages of the fluvial deposits. In the meandering and braided fluvial systems the successive high water stages provided suitable conditions for infilling (sandstone) the footprints produced in the floodplain or in the accretion surfaces within the channel (mudstone). Braided systems are generally less stable than meandering ones, so they have a lower preservation potential for footprints. The dinosaurs produced these tracks on mudstones in low water stage conditions (Fig. 10), and during the high water stage (stream reactivation) the footprints were infilled by sands. The track beds lack evidence of desiccation (e.g. mud-cracks) and this concurs with the hypothesis [11,56] that the dinosaurs left footprints in wet and muddy substrates in well-drained environments which never dried out and where the water table was close to or above the surface. Some deep casts preserving the three-dimensional shape of the foot (MPZ 2012/826, MPZ 2012/827, IPS 63272, MCD-5154; and Dataset S1) indicate that the water table was probably about 0.2–0.4 m above the surface. Interestingly, some casts (MPZ 2012/826 and MPZ 2012/827; Dataset S1) exhibit burrowing traces, suggesting that invertebrates inhabited the wet sand that infilled the footprint [56]. Extended root mottling and small plant remains in both mudstones and sandstones further indicate that vegetation probably colonized the floodplains, the abandoned channels and the braided and meandering bars, respectively (Fig. 10).

Currie et al. [53] and Nadon [55,63] pointed out that track formation requires a substrate that is soft enough to be deformed by the animal but firm, cohesive and dewatered enough to retain the shape of the foot until the sediment can infill the cavity. The best-preserved casts in the Tremp Formation reveal the foot shape,

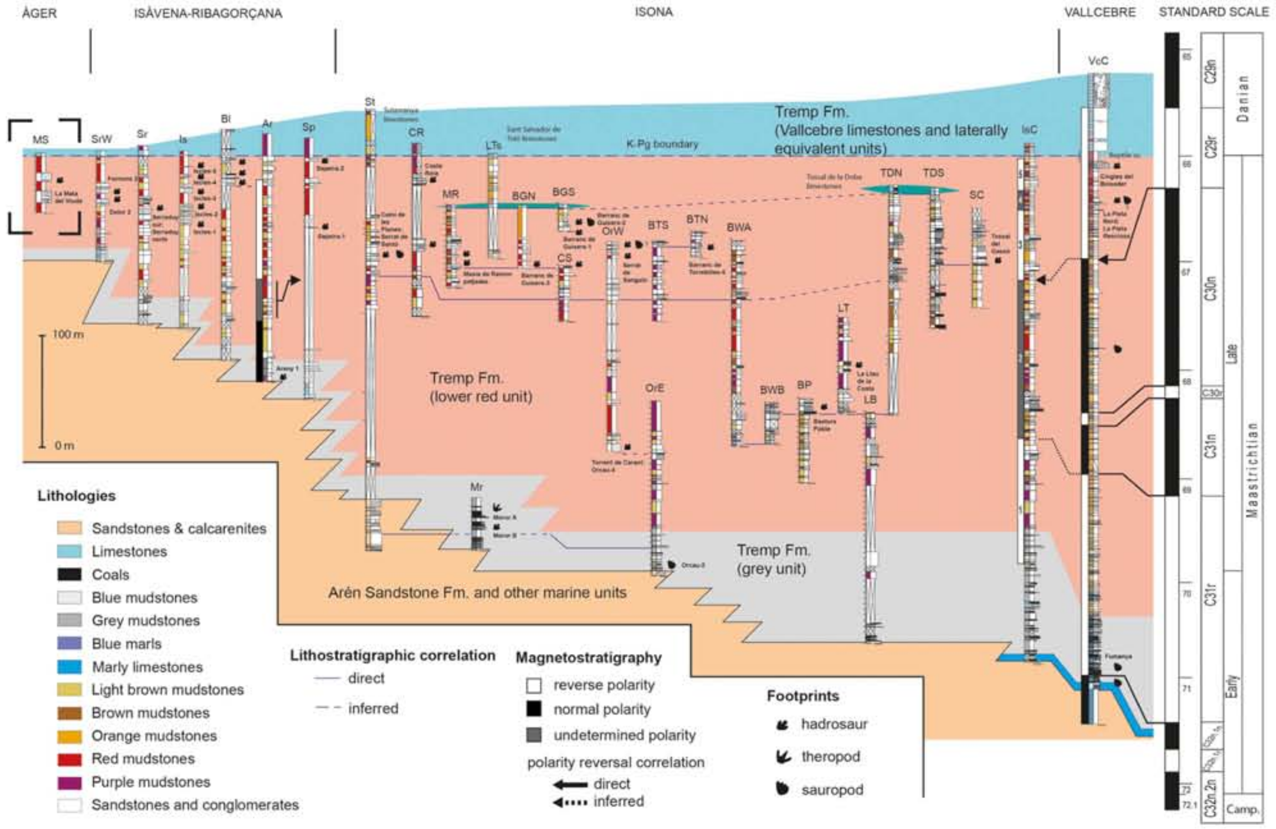

Figure 9. Chronostratigraphic correlation of uppermost Cretaceous deposits (Arén Sandstone and Tremp formations) in the southern Pyrenees (SW Europe). The standard geomagnetic polarity timescale is taken after Ogg and Hinnov [41]. See "Methods" section for further details on section abbreviations and magnetostratigraphical source data.
doi:10.1371/journal.pone.0072579.g009

thus indicating that the trampled muddy sediment was cohesive enough to resist erosion during the subsequent sheet flood. *Striae* or scratch marks in some of the tracks (Fig. 5F) demonstrate this cohesive feature. By contrast, some badly preserved and deformed casts indicate a less cohesive, softer, muddier substrate that prevented proper preservation of the foot shape (Fig. 4A). In all these cases, the tracks were produced in muddy substrates with the water table close to or above the surface. Conversely, substrates composed of poorly sorted sands with a low portion of cohesive mud (i.e. crevasse splay deposits; Fig. 10B) impede the homogeneous production of tracks, even though some of them are moderately well preserved (Fig. 5A, C).

Hadrosaur track size

In order to discern biometric and palaeobiogeographic differences and similarities between track makers during the Campanian and Maastrichtian we conducted a quantitative analysis of the size of the tracks attributed to hadrosaur dinosaurs available in the literature (Fig. 11). On the basis of the published data (see Dataset S1), the global record of individual (and measurable) hadrosaur tracks shows that the North American record is composed of individual tracks found in geologic formations of Campanian (57.1%), Campanian–Maastrichtian (14.3%), and Maastrichtian (28.6%) ages. In Asia and South America, the tracks occur in formations of Campanian–Maastrichtian and Maastrichtian age (Asia, Ca–Ma: 50%; Ma: 50%; South America, Ca–Ma: 33.3%; Ma: 66.6%; Fig. 11A). The European record is clearly biased (100% of the samples) in favour of geologic formations of Maastrichtian age, and more particularly, of stratigraphic levels that fall within the C30n and C29r magnetochrons. Southwestern Europe is thus potentially one of the most important areas in terms of yielding terminal Cretaceous track evidence of dinosaurs.

Within Europe, the track record from the Ibero-Armorican island (i.e., one of the ancient paleogeographic regions of the Late Cretaceous European archipelago) is composed of pes tracks that range from 11 to 51.5 cm in length (MCD 2012/831 being the smallest hadrosaur track yet discovered worldwide) and on average ($n = 94$; mean ± SD $= 29 \pm 8.9$ cm) these tracks are 45% and 65% of the size of those from North America ($n = 125$; mean ± SD $= 64.3 \pm 15.6$ cm) and Asia ($n = 41$; mean ± SD $= 44.3 \pm 20.8$ cm), respectively (Fig. 11B). The track record from South America still seems to be too scarce for further conclusions to be drawn but on average the tracks are the smallest in the sample ($n = 7$; mean ± SD $= 26.4 \pm 16.1$ cm). In the Ibero-Armorican island most of the hadrosauroid genera are of small to moderate size [36,65,66]. Thus, the track evidence agrees with data known from the bony record (cf. [46]). The studied sample describes a normal distribution that probably represents the size variability of the trackmakers within a population and this rules out the hypothesis that the Ibero-Armorican track sample may belong to immature juvenile individuals. In consequence, the ichnological data support the hypothesis of the likely influence of

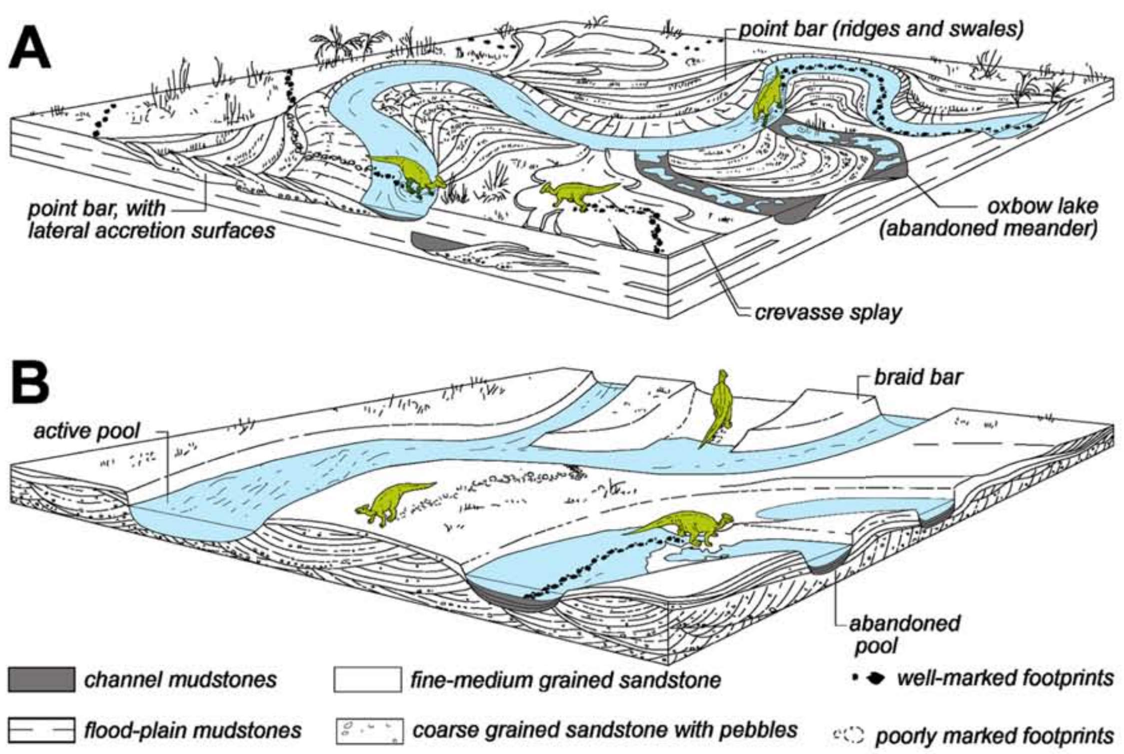

Figure 10. Sedimentary reconstruction of hadrosaur track production in fluvial settings of the Tremp Formation. (A) Sedimentary environments in meandering streams. (B) Sedimentary environments in braided streams.
doi:10.1371/journal.pone.0072579.g010

insularism on hadrosauroid body size (island rule) in the Ibero-Armorican island [67].

Biochronostratigraphy

Lockley et al. [9] reviewed the global record of Late Cretaceous dinosaur tracks and underscored the scarcity of the European record. With the new findings of dinosaur tracks in the upper levels of the Tremp Formation of the southern Pyrenees the number of footprint localities in southwestern Europe increases significantly. The track assemblage considered in the present study (with up to 40 track levels) represents the richest and youngest footprint succession in Europe and is among the most complete in the world. Thus, 25 localities have been reported in the C29r magnetochron, very close to the Cretaceous–Palaeogene boundary. The uppermost locality with unequivocal tracks is that of Cingles del Boixader, which is located 14 metres below the K–Pg boundary, in the C29r magnetochron (Fig. 9). This record represents the last dinosaur ichnological occurrence in Eurasia, and one of the latest pieces of evidence for non-avian dinosaurs anywhere in the world.

Furthermore, hadrosaur tracks are significant in terms of the biochronostratigraphy of the Cretaceous landmasses of southwestern Europe. Various authors [68,69] have hypothesized a faunal turnover within the Maastrichtian in the Ibero-Armorican island characterized by the disappearance of nodosaurids and *Rhabdodon* and the appearance and expansion of hadrosaurs. Currently, the fossil record in Spain and France seems to support this scenario ([70]; but see [71]). Indeed, recent updates of the fossil record and its chronostratigraphic framework in the Tremp basin [6,46] indicate that hadrosauroid remains are clearly dominant in the late Maastrichtian and yet have not been reported much below the upper part of the C31r, around the early Maastrichtian–late Maastrichtian boundary. Dalla Vecchia et al. [46] suggested that this faunal turnover was due to a time/event-related change rather than an ecological shift. The ichnological data studied here support this interpretation since hadrosaur tracks have been found both in lagoon (e.g. Moror B locality) and fully continental (fluvial) environments, all of late Maastrichtian age, though no hadrosaur tracks have been found in similar environments much below the early Maastrichtian–late Maastrichtian boundary. As most of them are found in a distinct temporal distribution within the late Maastrichtian, they show a specific time-span distribution. Therefore, the occurrence of hadrosaur tracks in the Ibero-Armorican island seems to be indicative of a late Maastrichtian age, and these tracks are thus important biochronostratigraphic markers in the faunal successions of the Late Cretaceous of southwestern Europe. As regards sauropods, the present data confirm that they were present at the very end of the Maastrichtian (Fig. 9), as indicated by the body fossils [39].

Conclusions

Recent findings in the Tremp Formation (southern Pyrenees, SW Europe) reveal that dinosaur tracks are much more abundant than previously thought. Sedimentological, ichnological, and chronostratigraphic analyses highlight the following conclusions:

a. The fluvial lower red unit of the Tremp Formation exhibits meandering and braided fluvial systems with favourable conditions for track production and preservation, like those of North America and Asia.

b. The dinosaurs mainly produced the tracks on the floodplain, within the channels, and on and within crevasse splay deposits

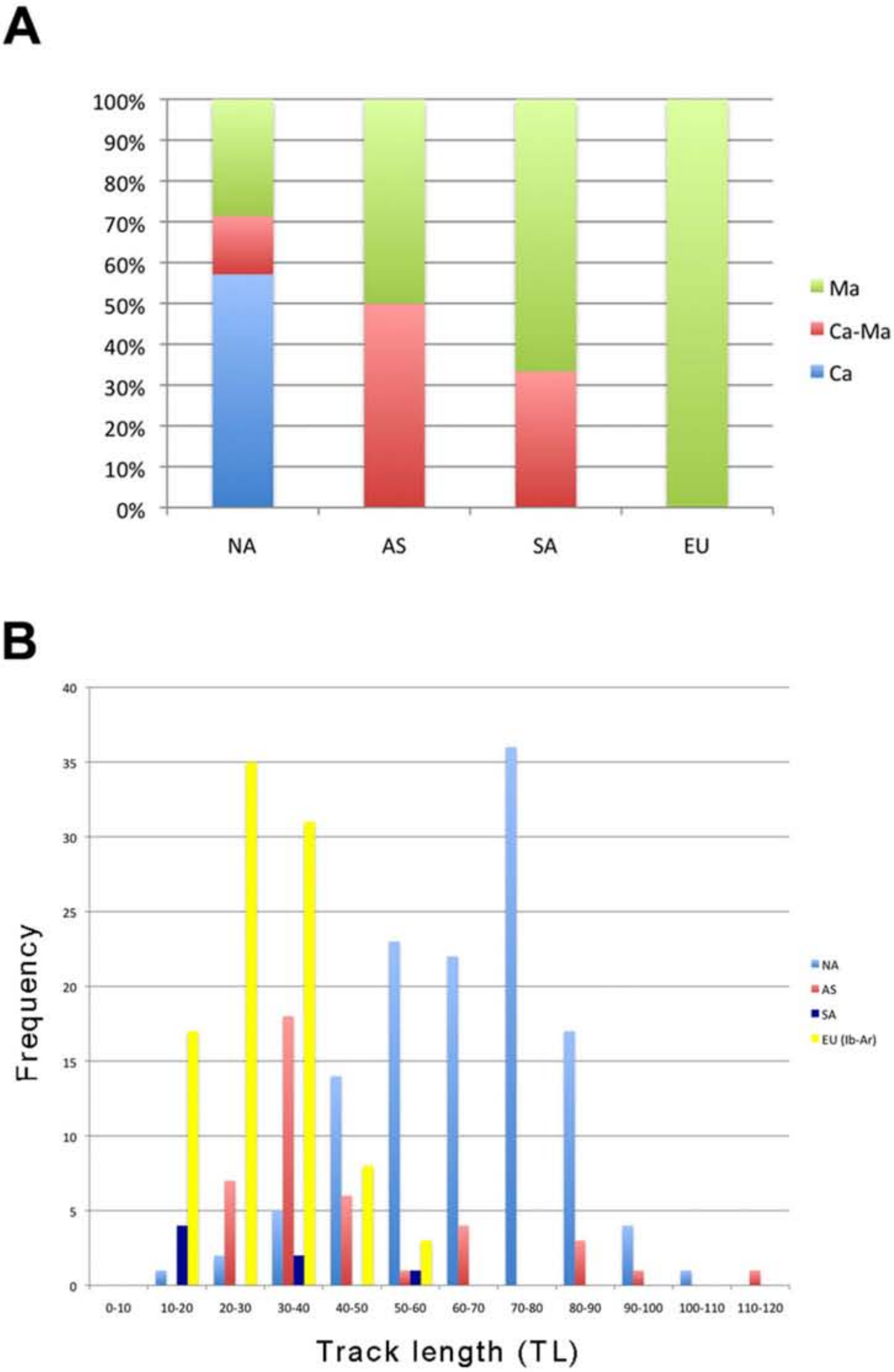

Figure 11. Age distribution and hadrosaur track size. (A) Graph showing the temporal abundance (%) of hadrosaur tracks in geologic formations of North America (NA), Asia (AS), South America (SA), and Europe (EU) through the Campanian, Campanian–Maastrichtian, and Maastrichtian time spans. (B) Size (track length, in cm) distribution of hadrosaur tracks through the abovementioned regions in the Campanian to Maastrichtian time span. Ib-Ar, Ibero-Armorican island. See source data in Dataset S1.
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in low water stage conditions, and the footprints were infilled by sands during high water stage (stream reactivation).

c. The track record is composed of abundant hadrosaur and scarce sauropod and theropod tracks. The hadrosaur tracks are significantly smaller in size but morphologically similar to comparable records in North America and Asia. They are attributable to the ichnogenus *Hadrosauropodus*.

d. A rich track succession composed of more than 40 distinct track levels indicates that hadrosaur footprints are found above the early Maastrichtian–late Maastrichtian boundary and most noticeably in the late Maaastrichtian, with tracks occurring abundantly in the Mesozoic part of the C29r magnetochron, in the latest 300,000 years of the Cretaceous.

e. The occurrence of hadrosaur tracks in the Ibero-Armorican island seems to be characteristic of the late Maastrichtian time interval and thus they are important biochronostratigraphic markers in the faunal successions of the Late Cretaceous in SW Europe.

Supporting Information

Text S1 Brief description of the main track localities found in the southern Pyrenees.
(DOCX)

Dataset S1 Measurements (in cm) taken for the latest Cretaceous (Campanian–Maastrichtian) hadrosaur pedal tracks reported in the literature. Abbreviations: NA: North America; AS: Asia, SA: South America; EU: Europe; Ca: Campanian; Ca–Ma: Campanian–Maastrichtian; Ma: Maastrichtian; TL: track length; TW: track width.
(XLSX)

Appendix S1 Photogrammetric models of the hadrosaur pes MCD-5140 and MCD-5142 from the La Llau de la Costa tracksite. Scale bar: 15 cm.
(ZIP)

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Author Contributions

Conceived and designed the experiments: BV OO VF RG AG VR JIC. Analyzed the data: BV OO VF RG AG VR JIC. Contributed reagents/materials/analysis tools: BV OO VF RG AG VR JIC. Wrote the paper: BV OO VF RG AG VR JIC.

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Text S1 Brief description of the main track localities found in the southern Pyrenees.

The following descriptions refer to the new track localities as well as other previously known sites reported in the literature. We use the stratigraphic distance between the localities and the base of the Vallcebre limestones and lateral equivalent strata as an indicator of site proximity with respect to the Cretaceous–Palaeogene boundary (see main text).

Vallcebre Syncline sector

Cingles del Boixader - The site is found in the upper part of the lower red unit ("Gres à reptiles" member) of the Tremp Formation, 14 meters below the Cretaceous–Palaeogene boundary (in the lower half of the C29r magnetochron). The site consists of a 5 meters-long overhanging ledge that contains nine tracks preserved as natural casts at the base of a sandstone level (Fig. 3B, 6A). Seven tracks are attributed to pedal (see measurements in Dataset S1) and two to manus footprints (TL=8 and 10 cm; TW= 13,5 and 13 cm, respectively) of hadrosaurs; two partial impressions of pedal digits are also distinguishable. All the tracks were replicated and catalogued (IPS-63661).

La Pleta Nord and **La Pleta Resclosa** - The two sites are found in the lower red unit, about 40 meters below the Cretaceous–Palaeogene boundary, within the C29r magnetochron. They are probably stratigraphically equivalent and are located some hundred meters apart from one another. The La Pleta Nord site contains several track casts and various track-like load structures exposed in cross-sectional outcrop views (Fig. 4C and G). Three casts probably correspond to pedal tracks of hadrosaurs and are aligned to form a short trackway (Fig. 3E). There is a manus cast in front of one of these tracks. A small hadrosaur pedal track was also documented at the site (see measurements in Dataset S1). The La Pleta Resclosa site contains two tracks preserved as natural casts (convex hyporeliefs) at the base of a thin sandstone level with multiple accretion surfaces. They are stacked vertically and are viewed in cross-section (Fig. 4H). One of the tracks may resemble a small sauropod pes as it presents various lateral indentations that may correspond to digital traces, but further excavation is required. The other track is of uncertain affinity.

Fumanya tracksites – The Fumanya localities are located in the lowermost levels of the grey unit of the Tremp Formation, in the early Maastrichtian (C32n.1n) [31]. They consist of extensive and vertical exposures of marly limestones bearing about 3,000 sauropod (titanosaur) tracks and 55 trackways [13, 49]. The tracks occur as concave hyporeliefs in at least four distinct stratigraphic levels, which record the transition from marine to lagoon environments [51].

Eastern Tremp Syncline (Isona sector)

La Llau de la Costa - The locality is located in the middle part of the lower red unit of the Tremp Formation, 185 meters below the Cretaceous–Palaeogene boundary, probably in the lower part of the C30n magnetochron (late Maastrichtian). The site consists of 140m^2 horizontal surface with about 50 tracks (concave hyporeliefs). Most of them are badly preserved (Fig. 3H) due to present erosion or most probably to original substrate conditions during track production; however, about ten tracks exhibit good morphological details and four have been replicated (MCD-5140, MCD-5141, MCD-5142, MCD-5143; Figure 5A, C, and Appendix S1) and measured (see measurements in Dataset S1). They all belong to hadrosaur pes and some of them may align in trackways. MCD-5140 is the best preserved, exhibiting exemplary features of the Tremp Formation hadrosaur pes prints (Fig. 5A, 7A); MCD-5142 displays a characteristic bilobed outline in the posterior heel margin (Fig. 5C, Appendix S1). The tracks are impressed on multiple trampling surfaces of poorly sorted grey sandstones representing the crevasse splay facies of a meandering stream.

Masia de Ramon Petjades - The site is found in the lower red unit, 100 meters below the Cretaceous–Palaeogene boundary, in the lower part of the C29r magnetochron. The outcrop contains 14 hadrosaur tracks preserved as natural casts (convex hyporeliefs) underneath an overhanging ledge of sandstone ledge. Most of the tracks correspond to pedal footprints (see measurements in Dataset S1) and only three tracks represent manus prints (TL=5.5 cm; TW=8.5 cm). The tracks are distributed randomly without a preferential direction and no trackway arrangement is distinguished (Fig. 6B). Two pedal cast tracks were collected as isolated blocks from the same channel body and catalogued in the Museu de la Conca Dellà collection (MCD-5156 and MCD-5157).

Barranc de Guixers-1, **Barranc de Guixers-2**, and **Barranc de Guixers-3** – These sites correspond to three close stratigraphic levels found close to one another in the lower red unit of the

Tremp Formation, 65, 60 and 98 meters below the K–Pg boundary (C29r magnetochron), respectively. Barranc de Guixers-1 used to contain at least two hadrosaur pes tracks preserved as natural casts at the bottom of a sandstone layer (recently the overhanging ledge collapsed and the tracks vanished). Barranc de Guixers-2 is a small outcrop containing a hadrosaur pes track (uncollected) and two likely sauropod pes casts (MCD-5164 and another uncollected sample), as well as multiple scratches attributed to other reptiles. The Barranc de Guixers-3 outcrops contain various hadrosaur tracks preserved as natural casts (MCD-5153) at the bottom of sandstone layers.

Camí de les Planes, and **Serrat de Santó** – These localities (also named "Suterranya") and other unnamed track levels west of the village of Suterranya are found in the upper part of the lower red unit of the Tremp Formation (104 meters below the K–Pg boundary, in the C29r magnetochron). They are equivalent stratigraphically equivalent to one another and contain abundant hadrosaur and (less abundantly) sauropod tracks preserved as natural casts (convex hyporeliefs). The tracks are usually found isolated as sandstone blocks that have come off the cross-sectional outcrop. MCD-5154 from the Serrat de Santó site is a three-dimensional cast of a hadrosaur pes, preserving striae and allowing inferences on the locomotor mechanics of the trackmaker. Ten tracks have been collected from both localities (see Dataset S1).

Serrat de Sanguin – The locality of Serrat de Sanguin is found in the upper part of the lower red unit of the Tremp Formation, 81 meters below the Cretaceous–Palaeogene boundary (C29r magnetochron). Dinosaur tracks, mostly hadrosaur footprints, occur as natural casts (convex hyporeliefs) at the base and within various levels of fluvial sandstone. Most of the tracks represent tridactyl pedal tracks of hadrosaurs (MCD-5159, MCD-5161, MCD-5162) though a three-dimensionally preserved manus cast was also collected (MCD-5163). A large, rounded cast was observed at the outcrop and this may belong to a sauropod footprint (Fig. 4B).

Tossal del Gassó, Costa de la Serra-4, Orcau-4 (=Barranc de Torrebilles-8), **Basturs Poble, Torrent de Carant**, **Barranc de Torrebilles-5, Costa Roia**, and other unnamed track levels – The localities are found in the middle and upper part of the lower red unit of the Tremp Formation, within the Maastrichtian part of the C29r magnetochron, a few dozen meters below the Cretaceous–Palaeogene boundary (except for Torrent de Carant and Orcau-4 (C31r), and Basturs Poble (C31n or C30r)). Most of the sites preserve several track-like load structures as well as well-defined hadrosaur pedal casts underneath overhanging sandstone ledges. Some of the collected tracks are good examples of the pedal morphology of Tremp Formation hadrosaurs (e.g. MCD-5155, MCD-5166; Fig. 7). An uncollected block near the Masia de Ramon petjades site preserves two pedal track casts of hadrosaurs (see measurements in Dataset S1).

Moror A and **Moror B** – The localities are found in the grey unit of the Tremp Formation around the early Maastrichtian–late Maastrichtian boundary (middle part of the C31r magnetochron). In Moror A a dozen of tracks are exposed in a small outcrop with a surface of about 35m^2. They are preserved as concave epireliefs, are tridactyl in shape, and have been attributed to theropods [18]. Moror B consists of 50-225m^2 surface of bioturbated grey limestone preserving several isolated tracks and one trackway attributed to hadrosaurs [18].

Orcau-2 – The locality is located in the grey unit of the Tremp Formation, around the early Maastrichtian–late Maastrichtian boundary (lower part of the C31r magnetochron), and has been characterized as lagoonal [6]. The tracks are preserved as concave hyporeliefs on a sub-vertical limestone exposure with abundant burrowing. Llompart et al. [14] first reported the locality with the description of the ichnogenera *Ornithopodichnites* and *Orcauichnites* (considered *nomina dubia* by Lockley and Meyer [22]) and sauropod footprints. A recent assessment of the site has provided evidence of titanosaur trackways [15].

Western Tremp Syncline (Isàvena-Ribagorça sector)

Sapeira-1 and **Sapeira-2** - The localities of Sapeira are found in the upper part of the lower red unit of the Tremp Formation, tentatively about 64 and 5 meters below the Cretaceous–Palaeogene boundary (C29r magnetochron), respectively. Each site preserves one hadrosaur pes track at the bottom of red, fine-grained sandstones. In Sapeira-1 the track (IPS-63272) is preserved three-dimensionally, with a tridactyl appearance (Fig. 4D).

Areny 1 - The site is found in the grey unit of the Tremp Formation, at the base of the C30n magnetochron [35]. It consists of a 55m^2 surface containing about 20 tracks preserved as concave epireliefs and attributable to hadrosaurs, some of them arranged in two (or probably three) trackways [19].

Iscles-1, Iscles-2, Iscles-3, **Iscles-4**, and **Iscles-5** – The Iscles localities are found in the lower red unit of the Tremp Formation, within the Maastrichtian part of the C29r magnetochron. Iscles-1 (60 meters below the K–Pg boundary) consists of a small, vertical exposure of sandstone that corresponds to an accretion surface of a meandering fluvial channel. The surface contains two casts (convex hyporeliefs) of circular shape that probably correspond to pedal footprints of hadrosaurs. An additional cast of a hadrosaur pes print was collected and catalogued in the Museo Paleontológico de Zaragoza (MPZ 2012/831). This is the smallest hadrosaur pes track reported worldwide. Iscles-2 is found 42 meters below the Cretaceous–Palaeogene boundary. It consists of a small outcrop, which bears various convex hyporeliefs at the bottom of a sandstone body. Iscles-3 (33 m below the K-Pg boundary) displays tracks preserved as natural casts (convex hyporeliefs) at the base of the successive accretion surfaces and exposed in vertical overhanging ledges (Fig. 4A). The four track surfaces contain a total of 40 tracks including manus and pes, attributable to hadrosaurs of various sizes (see measurements in Dataset S1); some of them may be aligned to form trackways. One track (MPZ 2012/830) was collected and catalogued in the Museo Paleontológico de Zaragoza. Iscles-4 and Iscles-5 are located 17 and 10 meters below the Cretaceous–Palaeogene boundary, respectively. The former site contains one single, vertically stacked and three-dimensionally preserved track; the latter preserves a single natural cast (convex hyporelief). Both footprints have been attributed to hadrosaur pes prints.

Serraduy Sur and **Serraduy Norte** – The Serraduy localities are found in the lower red unit of the Tremp Formation, 46 meters below the Cretaceous–Palaeogene boundary (C29r magnetochron). They are stratigraphically equivalent to one another and preserve similar tracks referable to hadrosaurs. The Serraduy Sur locality (172-J-04-A level; Fig. 3F) preserves various tracks, including various pes (see measurements in Dataset S1) and one manus cast (MPZ 2012/833; TL=12 cm; TW=10 cm). Well-preserved, three-dimensional casts of hadrosaur pes (MPZ 2012/826 and MPZ 2012/827) preserve *striae* and allow inferences on the locomotor mechanics of the trackmaker. The Serraduy Norte locality (172-I/12/H level) consists of three track horizons that constitute the architecture of a meandering fluvial channel. At least a ten of (pedal) tracks preserved as natural casts (convex hyporeliefs) occur at the base of each accretion level (Fig. 4F).

Dolor 2, **Fornons 3** and other unnamed track levels in the Blasi section – These outcrops are found in the upper part of the lower red unit of the Tremp Formation, about 10-40 meters below the

Cretaceous–Palaeogene boundary (C29r magnetochron). They exhibit various several track-like load structures, exposed underneath overhanging sandstone ledges or in cross-sectional outcrop views.

Àger Syncline sector

La Mata del Viudà – The locality (also named “Corçà”, “Mas de Saurí” or “Millà”) is located in the uppermost part of the lower red unit of the Tremp Formation, about 25 meters below the Cretaceous–Palaeogene boundary, at the base of the C29r magnetochron [72]. The tracks are preserved as natural casts (convex hyporeliefs) in a 5m^2-overhanging ledge at the bottom of a sandstone layer (Fig. 3C). Llompart [17] distinguished about 20 tracks, mostly attributed to ornithopod dinosaurs, and also noted the occurrence of traces referable to other reptiles. The present study provides a complete mapping of the site (Fig. 6C) and describes and measures a likely trackway (Fig. 8C) and the morphologies of particular pes and manus tracks (Fig. 7L). The pes (n=5; mean values TL=32 cm; TW=32.6 cm; see further measurements in Dataset S1) and manus tracks (n=6; TL=11 cm; TW=13 cm) have been attributed to hadrosaurs. In 2010 part of the overhanging surface collapsed and five of the tracks (MV10, MV11, MV12, MV13, MV14) vanished.

La Massana – The locality (also named “Camarasa”) is located in the lower levels of the grey unit of the Tremp Formation, in the late Campanian [50]. It consists of 1,200 m^2 of limestones exposures bearing an estimate of 900 tracks attributed to sauropods [16]. The tracks are rounded in shape and are preserved as concave hyporeliefs; no discrete trackways have been distinguished.

References

72. López-Martínez N, Fernández-Marrón MT, Valle MF (1999) The succession of vertebrates and plants across the Cretaceous-Tertiary boundary in the Tremp Formation, Àger valley (South-central Pyrenees, Spain). Geobios 32: 617–627.

Appendix S1 Photogrammetric models of the hadrosaur pes MCD-5140 (A) and MCD-5142 (B) from the La Llau de la Costa tracksite. Scale bar: 15 cm.

SKIN IMPRESSIONS OF THE LAST EUROPEAN DINOSAURS

6

El capítol 6 correspon a l'article aparegut online en la revista *Geological Magazine* el 26 de setembre de 2016:

Fondevilla, V., Vila, B., Galobart, À., Oms, O. (2016). Skin impressions of the last European dinosaurs. *Geological Magazine,* 1-6.

V. F. ha descobert el material i ha codirigit dues campanyes de documentació i excavació del material (veure Materials i Mètodes). A més, ha descrit el material que es presenta, ha elaborat totes les figures, ha redactat el text i discutit els resultats amb la resta de coautors.

Aquest capítol està protegit (pàgines 79 a 84). Pot consultar-se en el següent enllaç:

https://www.cambridge.org/core/journals/geological-magazine/article/div-classtitleskin-impressions-of-the-last-european-dinosaursdiv/ADBFD83B9A03F074571778CB44EE203E

DOI: https://doi.org/10.1017/S0016756816000868

GENESIS AND TAPHONOMY OF THE L'ESPINAU DINOSAUR BONEBED, A SINGULAR LAGOONAL SITE FROM THE MAASTRICHTIAN OF SOUTH-CENTRAL PYRENEES

7

El capítol 7 correspon a un manuscrit enviat a revisar el dia 7 de gener de 2017 a la revista *Sedimentary Geology:*

Fondevilla, V., Vicente, A., Battista, F., Sellés, A.G., Dinarès-Turell, J., Martín-Closas, C., Anadón, P., Vila, B., Razzolini, N.L., Galobart, À., Oms, O. (en revisió). Genesis and taphonomy of the L'Espinau dinosaur bonebed, a singular lagoonal site from the Maastrichtian of South-Central Pyrenees. *Sedimentary Geology.*

En aquest manuscrit, V. F. ha realitzat les tasques de camp (mesura de les seccions estratigràfiques, descripcions litològiques i recollida de mostres de paleomagnetisme i geoquímica) i l'estudi de les dades obtingudes. Ha codirigit l'excavació del material extret durant els anys 2012 i 2015. Ha participat en l'adaptació, actualització i interpretació de les dades tafonòmiques, les quals havien estat parcialment utilitzades en el treball de màster de F. B. També ha dut a terme gran part de les tasques de desmagnetització de les mostres de paleomagnetisme a l'Istituto Nazionale di Geofisica e Vulcanologia (INGV, Roma), durant l'estada breu. Ha coordinat les aportacions dels diferents autors. Ha redactat la major part del text, ha preparat les figures 1, 2, 3, 6, 7, 8, 9, 10, 11 i 12, i ha discutit els resultats amb la resta de participants.

Genesis and taphonomy of the L'Espinau dinosaur bonebed, a singular lagoonal site from the Maastrichtian of South-Central Pyrenees

Fondevilla, V.[a]*, Vicente, A.[b], Battista, F.[c], Sellés, A.G.[d, f], Dinarès-Turell, J.[g], Martín-Closas, C.[b], Anadón, P.[h], Vila, B.[d, f], Razzolini, N.L.[d], Galobart, À.[d, f], Oms, O.[a]

[a]Departament de Geologia (Estratigrafia), Facultat de Ciències, Universitat Autònoma de Barcelona, Carrer de l'Eix central, 08193, Cerdanyola del Vallès, Barcelona, Catalonia, Spain. vfondevilla@gmail.com; joseporiol.oms@uab.cat
[b]Departament de Dinàmica de la Terra i de l'Oceà, Universitat de Barcelona-UB, c/Martí i Franquès s/n, 08028, Barcelona, Catalonia, Spain. albavicenterodriguez@ub.edu; cmartinclosas@ub.edu
[c]Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le A. Moro 5 - 00185 Rome, Italy. francesco.battista87@gmail.com
[d]Institut Català de Paleontologia Miquel Crusafont, Carrer de l'Escola Industrial, 23, E- 08201, Sabadell, Catalonia, Spain. albertgarcia.selles@icp.cat; bernat.vila@icp.cat; novella.razzolini@icp.cat; angel.galobart@icp.cat
[f]Museu de la Conca Dellà, Carrer del Museu, 4, 25650, Isona, Lleida, Catalonia, Spain.
[g]Istituto Nazionale di Geofisica e Vulcanologia, Via di Vigna Murata, 605, I-00143 Rome, Italy. jaume.dinares@ingv.it
[h]Institut de Ciències de la Terra Jaume Almera-CSIC, 08028 Barcelona, Catalonia, Spain. panadon@ictja.csic.es
*Corresponding author: vfondevilla@gmail.com / victor.fondevilla@uab.cat

Abstract

The L'Espinau site is a rich dinosaur bonebed from the late Maastrichtian of the South-Central Pyrenees (North-eastern Spain) that have provided hundreds of bone remains attributed to hadrosauroids, together with a rich assemblage of herpetofauna, fish and microflora. The combined sedimentology, stable isotope geochemistry and palaeoecology show that this fossil site formed in a lagoon, in which a mixed freshwater-brackish palaeoenvironment was developed. This setting displays a charophyte zonation from freshwater (*Clavator brachycerus*-dominated assemblage) to brackish or eurihaline conditions (*Feistiella malladae*-dominated assemblage), revealing a facies shift towards the coast. Sedimentology and taphonomy (bidirectional arrangement of long bones, abrasion and disarticulation) indicate that the L'Espinau site is the result of a cohesive mass flow event originated very close to the sea, which entramped and mixed fauna from both the terrestrial and the brackish/marine environment. Mass flow-hosted bonebeds are commonly linked to fluvial palaeoenvironments, so L'Espinau becomes a rare example of fossil accumulations produced by this sedimentary process near the sea. In addition, it better documents the presence of hadrosauroids inhabiting coastal environments during the Maastrichtian in the southern Pyrenean area.

keywords mass flow, palaeoenvironmental reconstruction, palaeoecology, sedimentology, stable isotopes, coastal settings

1. Introduction

Our knowledge of the last Cretaceous terrestrial ecosystems of southwestern Europe has been largely improved during the last decade, especially thanks to the systematic palaeontological studies carried out in the Maastrichtian deposits of the southern Pyrenees. Of the more than two hundred vertebrate sites discovered to date in the region, there are some outstanding localities that have provided pivotal palaeontological data to understand end-Cretaceous faunal communities. Among them, it is worth mentioning the Basturs Poble site, the first hadrosaurid bonebed discovered in the southern Pyrenees (Dalla Vecchia et al., 2014); the Serrat del Rostiar-1 site, which has yielded a rich assemblage of microvertebrates such as amphibians and squamates (Blanco et al., 2016) and remains of the lambeosaurine hadrosaurid *Pararhabdodon isonensis* (Prieto-Márquez et al., 2013); Barranc de Torrebilles, a multi-site locality that has provided pterosaur remains (Dalla Vecchia et al., 2013), lambeosaurines (Prieto-Márquez et al., 2013) and the bothremydid turtle *Polysternon isonae* (Marmi et al., 2012); and the Molí del Baró-1, an exceptionally diverse locality with representation of dromaeosaurid theropods, lambeosaurine hadrosaurids, titanosaurian sauropods, crocodylomorphs, amphibians, fish, and a complete riparian plant community (Marmi et al., 2015, 2016). All these localities exemplify characteristic fossil assemblages of meandering channel deposits and their associated floodplains and palaeosoils.

On the contrary, vertebrate accumulations from coastal environments are much scarcer in the southern Pyrenees, although there are some valuable exceptions. Hence, in the swamp-like or lagoonal Blasi-1, -2 and -3 a rich amphibian and squamate association has been described (Blain et al., 2010), together with the lambeosaurines *Arenysaurus ardevoli* and *Blasisaurus canudoi* (Pereda-Suberbiola et al., 2009; Cruzado-Caballero et al., 2010). The Nerets locality is also a good example of a multitaxic fossil site, with remains of hadrosauroids, sauropods, ankylosaurs and crocodylomorphs accumulated in a lagoonal setting, closely connected to a barrier island system (Riera et al., 2009; Fondevilla et al., 2016a). Finally, a third noticeable example of coastal site is the L'Espinau site here studied.

The first fossil remains from L'Espinau site were discovered in 2004 by a neighbour of the village of Tartareu (La Noguera, Lleida, Catalonia, Spain) in grey marls of the Maastrichtian Figuerola Fm outcropping in the border of a wheat field. From that moment on, the site has been excavated for five years during which over 600 hadrosauroid bones and several microvertebrate remains have been recovered so far. Recent studies on that material indicate that the site contains fossils of several hadrosauroid individuals (Battista et al., 2014), as well as a significant taxonomic diversity of lissamphibians, squamates (Blanco et al., 2016), fish taxa (Blanco et al., 2017) and crocodylomorphs. Further, it is the type locality of the theropod oospecies *Prismatoolithus trempi* described by Sellés et al. (2014). Despite the relatively rich faunal content, very few is known about the age control, the local depositional context and the sedimentary processes that produced the bone accumulation.

Thus, combining sedimentology, geochemistry, taphonomy and palaeoecology we provide evidences about the genesis of a singular dinosaur bone accumulation in a mixed coastal lake and lagoon environments. In addition, we performed a magnetostratigraphic and biostratigraphic study in order to provide an age calibration for the site.

2. Geological setting

The South-Central Pyrenean unit (Fig. 1A) is composed by three main thrust units: Bóixols, Montsec and Serres Marginals (Vergés and Muñoz, 1990; Teixell and Muñoz, 2000). This study is focused in the latter unit, where the L'Espinau site is located. The general stratigraphic succession of the Serres Marginals is composed mainly of shallow marine rocks deposited in the southern margin of the Pyrenean basin during the latest Triassic, the Jurassic and the Late Cretaceous. From the Campanian to the Paleocene, a regressive trend resulted in sedimentation of lacustrine limestones and red beds (Rosell et al., 2001). A marine transgression took place in the Eocene, resulting in the sedimentation of the limestones of the Àger Group. From this moment, sedimentation was interrupted in the southern margin of the Serres Marginals, but in its northern sector it continued in form of fluvial deposits until the Cuisian. Hence, the total thickness of the

Serres Marginals units ranges from about 2000 m in the Àger syncline, to 300 m in areas located southwards. The unconformable Oligocene conglomerates represent the younger sediments of the Serres Marginals area (Fig. 1B) (Millán-Garrido et al., 2000).

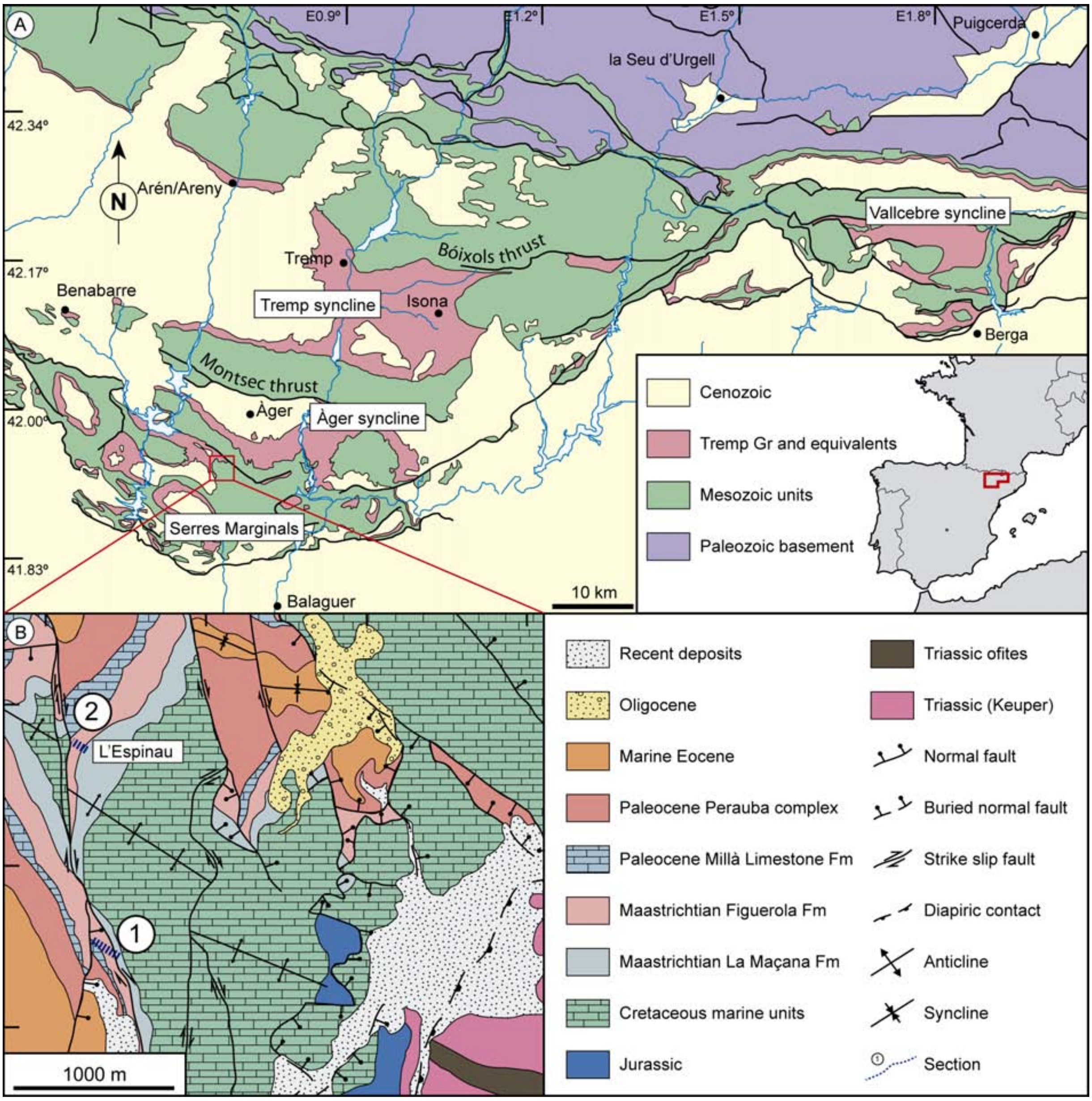


Figure 1. Geological context of the L'Espinau locality. **A**, general view of the South-Central Pyrenean Unit, which includes the Montsec and Serres Marginals thrust sheets. Modified from López-Martínez and Vicens (2012). **B**, enlarged geological map of the L'Espinau area, with the location of the two stratigraphic sections studied here. Modified from Cirés and Berástegui (2008).

The continental rocks of the South-Pyrenean area around the Cretaceous–Paleogene boundary (K–Pg) were originally referred as 'Garumnian' (Leymerie, 1862). In the Serres Marginals unit, this informal unit was defined as Fontllonga Group by Colombo and Cuevas (1993). This group is laterally uniform in terms of lithology, and it is subdivided from base to top in: i) La Maçana Fm, a limestone of shallow lacustrine environments that overlies the marine Bona Fm and the Les Serres Fm (Mey et al., 1968; López-Martínez et al., 1998); ii) Figuerola Fm, represented by channelized sandstone bodies and reddish mudstones with palaeosoils. Sandstone bodies increase in thickness towards the top of the succession. The Figuerola Fm has been interpreted as a fluvial environment with floodplains. Abandoned channels allowed accumulation of grey mudstones with abundant organic matter, plant and vertebrate remains. Further, shallow lakes and ponds are recorded in limestone layers. The L'Espinau site is placed at the base of this formation; iii) Millà Limestone Fm, featured by dolomicrites, bioclastic limestones with ostracods and charophytes, and brecciated limestones. They represent palustrine-lacustrine environments. *Microcodium* is extensively recorded in the upper meters of the succession; iv) the Perauba Complex, represented by red mudstones, fine grained tabular and lenticular sandstone bodies and gypsum levels. The unit is interpreted as a poorly drained mudflat and sabkha. The upper part of the succession passes gradually to limestone deposits with marine fauna. The thickness of these four subdivisions of the Fontllonga Group is variable through the Serres Marginals and the Àger syncline. In the study area we recognized and studied in detail the first two formations (La Maçana and Figuerola formations; Fig. 1B and Fig. 2).

The Figuerola Fm has been dated as Maastrichtian (Fig. 3) after the palaeomagnetic study of Galbrun et al. (1993) in the Fontllonga section (Àger syncline) (see also Vicente et al., in press). Charophyte biostratigraphy allocates the La Maçana Fm within the Peckichara cancellata biozone (Villalba-Breva and Martín-Closas, 2013), which is dated as late Campanian to early Maastrichtian (Oms et al., 2007; Vicente et al., 2015). This age is consistent with the strontium isotopic study of Caus et al. (2016), which dated the underlying marine levels as early Maastrichtian (around 72-71 Ma; Fig. 3). The presence of the Fumanya Mb at the base of the La Maçana Fm, regarded as early Maastrichtian (Oms et al., 2016), also supports this interpretation (Fig. 3).

3. Methods

The site of L'Espinau was first excavated in 2010 by members of the Institut Català de Paleontologia 'Miquel Crusafont' (ICP). Subsequent excavations were performed until 2015 also by members of the ICP, the Universitat Autònoma de Barcelona (UAB) and the Università di Roma 'La Sapienza'. During the successive excavations (Supp. Fig. 1), bones were recovered using conventional tools. Prior to extraction, bones were mapped using a TRIMBLE 5000 series topographic Total Station in order to preserve the spatial information and the relative position of the recovered elements. Geo-referenced data were exported to Adobe Illustrator CS5 using the Menu2000 software. The total excavated area measured 80 m^2, corresponding to about 30 m^3 of fossiliferous grey marl. Part of this sediment (around two tons) was collected and sieved using meshes with wire openings of 1.5, 0.8 and 0.5 mm in order to recover microvertebrate fossils. In addition, 3 samples of a normalized weight (3 kg each) of sediment from the same fossiliferous level and grey marls were disaggregated and screen-washed using sieves of mesh sizes of 1, 0.5 and 0.2 mm for a charophyte study. Charophyte fructifications (gyrogonites and utricles) where handpicked using a Wild M5A binocular microscope and were later photographed using a Quanta 200 scanning electron microscope at the 'Centres Científics i Tecnològics-CCiT' of the Universitat de Barcelona.

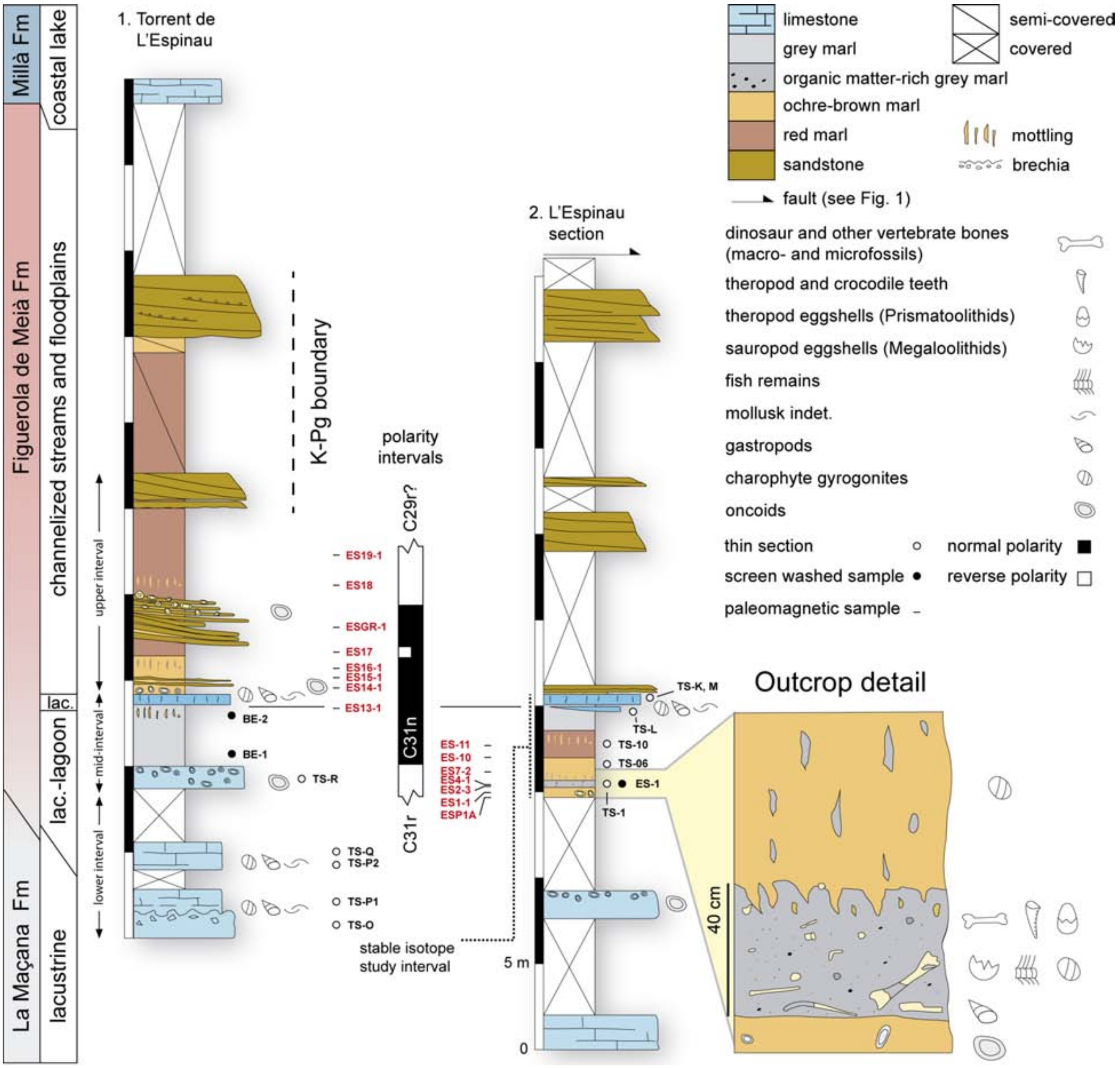


Figure 2. Stratigraphic sections of the L'Espinau area, with indication of the levels in which thin sections, samples for screen-washing, palaeomagnetism, X-ray diffraction and $\delta^{13}C$ and $\delta^{18}O$ stable isotope analyses have been collected. The results of the palaeomagnetism study are shown.

Stratigraphic and sedimentological works were performed together with the palaeontological excavation in order to integrate the L'Espinau locality in a geological framework and to study the sedimentary processes and palaeoenvironment that originated and preserved the bone accumulation. The geological fieldwork consisted in measuring a detailed log in the fossil site, but due to the limited outcrop conditions we searched for additional exposures. However, we only identified an equivalent section located 3 km towards the south (Fig. 2). Lithologies were described in terms of composition, colour, texture and palaeontological content. The field observations were complemented with the study of thin sections from selected specimens of each lithology.

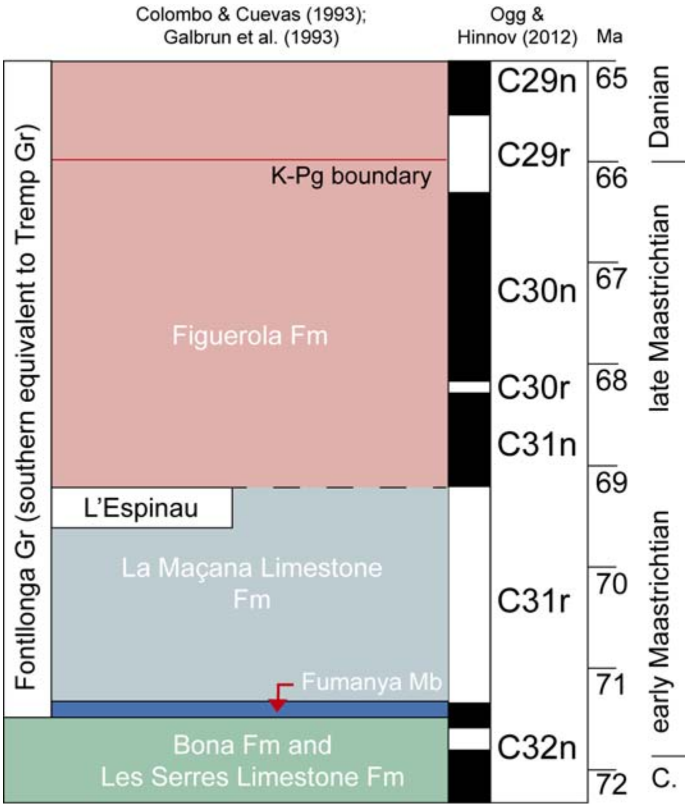


Figure 3. Chronostratigraphic scheme of the latest Cretaceous of the Serres Marginals unit and position of the L'Espinau locality according to the new data presented here.

In order to better determine the composition of the lithologies present in the L'Espinau locality, we carried out X-ray diffraction (XRD) and $\delta^{13}C$ and $\delta^{18}O$ stable isotope analyses on 24 carbonate samples of different origin collected from an interval of 2 m including the fossiliferous layer. Carbonate nodules were selected under a binocular microscope and powdered using a smasher, whereas powder of marls, oncolites, lacustrine limestones and carbonate crusts and clasts were collected using a micro-drill. Mineral composition was determined by XRD with a D5005 BruckerTM diffractometer at the Institute of Earth Sciences 'Jaume Almera' ('Consejo Superior de Investigaciones Científicas', CSIC, Barcelona, Spain). For the isotope analyses, each carbonate sample was reacted with phosphoric acid at 70 ºC for 3 min in a Carbonate Kiel Device III (Thermo Finnigan). The CO_2 extraction device is coupled to a Thermo Finnigan MAT 252 triple collector isotope ratio mass spectrometer ('Centres Científics i Tecnològics-CCiT', Universitat de Barcelona) for the determination of the stable isotope composition ($\delta^{13}C$, $\delta^{18}O$). Data are reported in δ‰ notation relative to the V-PDB standard. The instrumental precision of the isotopic measurements determined from deviations to simultaneous replicate analyses of certificated NSB-19 standards was 0.03‰ for $\delta^{13}C$ and 0.06‰ for $\delta^{18}O$. This methodology has taken from Canet et al. (2013).

For the magnetostratigraphic study, small blocks were collected from the available fine grained lithologies (grey, ochre, red mudstones and marls and fine-grained sandstones), excluding limestones due to their lower intensity values. These samples were oriented in situ using a magnetic compass. The palaeomagnetic analyses were performed in a shielded room at the laboratory of the 'Istituto Nazionale di Geofisica e Vulcanologia' in Rome, Italy. A 2G Enterprises DC SQUID high-resolution pass-through cryogenic magnetometer (manufacturer noise level of 10^{-12} Am^2) was used to measure the natural remanent magnetization (NRM) and remanence through demagnetization.

4. Results

4.1. Lithostratigraphy, sedimentology and charophyte content

The two lithostratigraphic sections at L'Espinau and Torrent de L'Espinau (northern and southern sections respectively; Fig. 1B, 2) display three distinctive intervals:

4.1.1. Lower interval (limestones)

This basal interval shows a succession of grey limestones, grey marls and oncolitic calcarenites and marls corresponding to the top of La Maçana Fm and the base of the Figuerola Fm (Fig. 2; Supp. Fig. 1A, B). The base of the interval (Torrent de L'Espinau section, Fig. 2) is represented by a tabular dark grey breccia with planar base and an upper karstified surface (pseudomicrokarst). The clasts of the breccia are limestone intraclasts with a micritic matrix, with rare fragments of gastropod shells and other undetermined bioclasts. Above this breccia a succession of 1.5–2 m thick grey tabular, wackestone beds and marl crops out. These limestones contain remains of charophyte thalli, mainly including *Charaxis,* and *Munieria grambastii* in minor proportions (Fig. 4). No charophyte utricles were found, however, some characean gyrogonites probably related to *Microchara* were recognized along with ostracod and gastropod shells. The abundance of the clavatoracean *Munieria grambastii* thalli and utricles increases to the top of the limestone beds, as was observed by Villalba-Breva and Martín-Closas (2013) in La Maçana Fm from the eastern Fontllonga section.

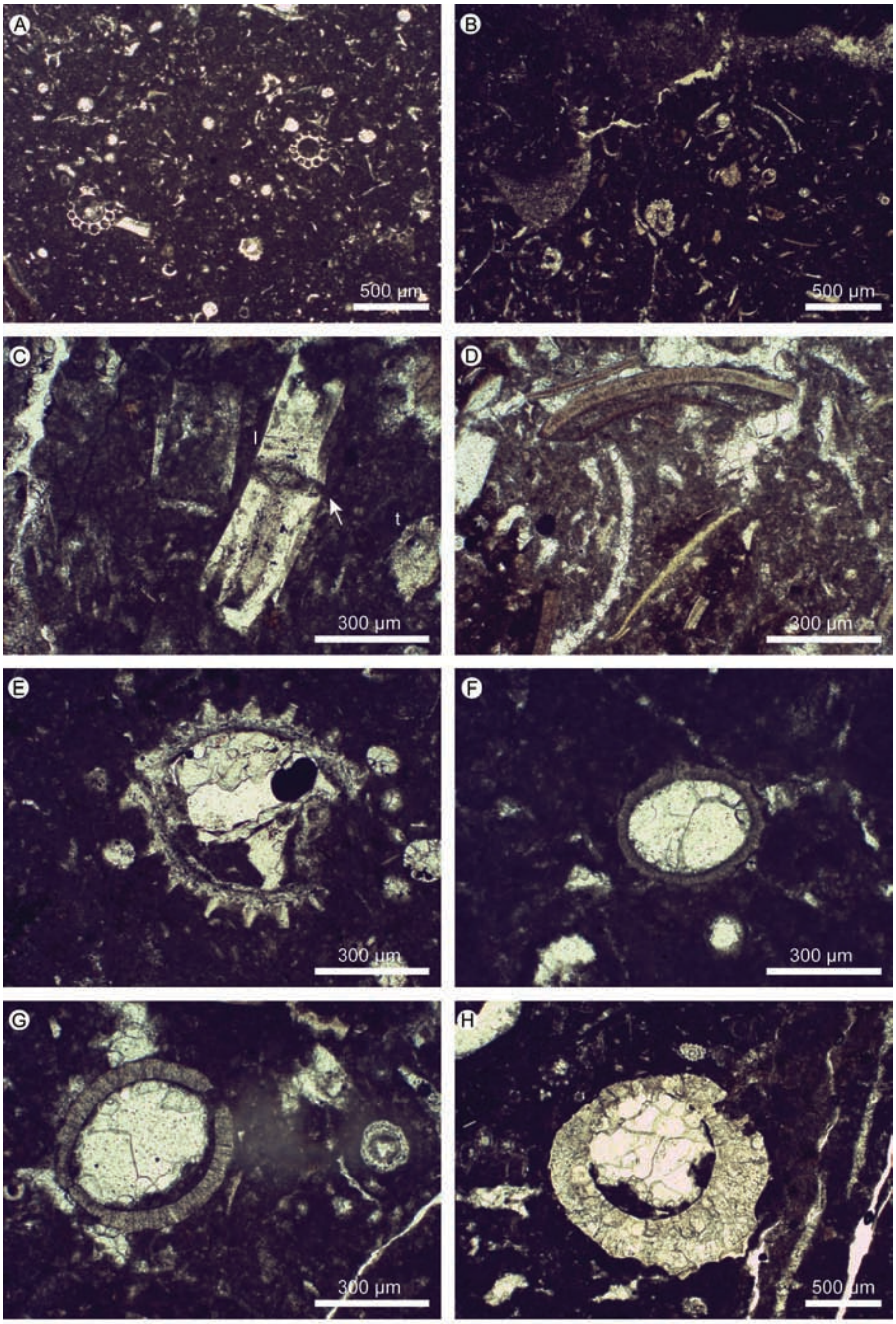


Figure 4. Bioclastic components found in the microfacies analyses. **A**, wackestone–packstone with *Charaxis* charophyte thalli and *Munieria grambastii* clavatoracean thalli. Thin section TS-P2. **B**, wakestone with triangular transversal section of *Munieria grambastii*. Thin section TS-K. **C**, transversal (t) and longitudinal (l) sections of an internode of *Munieria grambastii*. The longitudinal section (l) show the scars of nodal cells (arrow). Thin section TS-L. **D**, undetermined bioclast, possibly vertebrate eggshells. Thin section TS-M. **E**, longitudinal section of a gyrogonite showing a mid-cellular crest probably from *Microchara cristata*. Thin section TS-P2. **F**, longitudinal section of an oblate *Platychara* sp. gyrogonite. Thin section TS-L. **G**, longitudinal section of a *Feistiella* sp. gyrogonite showing thick cells and large apical pore. Thin section TS-K. **H**, transversal section of a clavatoracean utricle. Thin section TS-L.

Above this limestone sequence, there is a 1.5–2 m thick oncolite-rich bed, with fine-grained calcarenitic matrix. Oncolites are of milimetric to centimetric diameter and show lithoclastic or bioclastic (mainly bivalves or gastropod shells) nuclei. Grey marls above the oncolitic bed contain abundant charophyte remains (i.e. *Microchara nana*, *Platychara* sp. and eroded *Clavator ultimus;* Fig. 5), gastropod shells and opercula.

The aforementioned lower interval can be interpreted as a sedimentary deposition in freshwater lake. The breccia with intraclasts at the base of the interval may have been the result of the subaerial exposition and reworking of the lake margin deposits during periods of exposition of the lakeshores. In turn, the overlying succession of lacustrine marl and limestone represents shallowing upward sequences. However, the facies alternations between dark and grey limestones described in Villalba-Breva and Martín-Closas (2013) in the main part of the La Maçana Fm have not been found so far in this western locality. Charophyte limestones indicate deposition of autochthonous to parautochthonous remains of a charophyte meadow. Finally, the formation of oncolite-supported beds can be related to small fluvial channels similar to those described by Colombo and Cuevas (1993) at the base of the Figuerola Fm of the Fontllonga type section.

4.1.2. Middle interval. Lithology of the fossil site

The fossil site of L'Espinau is located at the middle part of the studied stratigraphic successions, which corresponds to the Figuerola Fm (Fig. 2). Laterally, the middle interval exhibits differences in thickness and lithology depending on the considered section. In the palaeontological-site (L'Espinau section), this interval starts with about 1 m of ochre mudstone with scattered oncoids. Neither sedimentary structures nor pedogenic features can be recognized in this layer. The size of the oncoids is between 5–10 cm in diameter, and they are ovoid in shape according to the nomenclature of Arenas et al. (2007), being very similar to other oncoids described in the Àger syncline (Astibia et al., 2012). Overlying the oncoid-bearing level, the vertebrate fossiliferous layer occurs as a massive grey marl stratum with no visible sedimentary structures other than some microscopic clay bands parallel to the stratification. The mean thickness of the bed is about 40 cm (Fig. 6A), being locally thicker (up to 60 cm) or thinner (20−30 cm). The lateral continuity is unknown, but the layer can be tracked up to 20 m to the South and West. The marl (45−50% of $CaCO_3$) contains a significant amount of quartz (~ 10%), and XRD of the rock also reveals that nontronite (ferric smectite) is the main clay component (Supp. Table 1).

Charcoal plant remains are abundant and at the base of the level appear as elongated structures that resemble palm leaf rachis, although their poor preservation prevents any definitive taxonomic identification. Dinosaur bones (from a few cm to 60+ cm) and subangular to rounded carbonate intraclasts (with mean diameters of 5 cm) represent the coarsest elements found in the layer. They appear scattered and floating in the marly matrix, instead of being accumulated in the base of the layer. However, an upward size-reduction trend can be observed in the dinosaur bones, with the larger ones preferentially accumulated in the first 10−20 cm of the layer. Bones are usually found subhorizontally, but some long bones have higher dips, up to 80 degrees. The orientation of long bones reveals an east-west bidirectionality (this point is further described below). Carbonate intraclasts are composed of micrite with a significant amount of quartz. Scarce undetermined mollusc and ostracod shells, as well as planktonic foraminifera are found within the micrite. It is important to note that the majority of the dinosaur bones display two different types of carbonate crusts (Fig. 7A-E). On the one hand, the smaller bony elements sometimes exhibit rounded grey, massive crusts that resemble the carbonate of the intraclasts described above (Fig. 7D). Hence, some ostracod shells can be observed within these crusts. On the other hand, most of the recovered bones are coated by a greyish-whitish crust that is usually harder closer to the bone. Sets of bones are often fused by these coatings. The fact that these second type of carbonates cover bones in anatomical connection (Fig. 7A) strongly suggest a post-depositional, diagenetic origin. However, few bones, show clean surfaces with no evidence of any crust. This is usually the case of bones found in the transition between the grey marl and the overlying layer. Microvertebrate remains recovered from screen-washing display no evidence of any crust.

Regarding the charophyte assemblage of the L'Espinau site and section, it is dominated by abundant and highly polymorphic gyrogonites of the porocharacean *Feistiella malladae* (Fig. 5).

However diverse species of characeans and clavatoraceans have been also found, like *Microchara cristata, M. nana, M. punctata, Peckichara sertulata, P. llobregatensis, Platychara compressa*, *Lamprothamnium* sp., *Clavator ultimus* and *C. brachycerus* (Fig. 5).

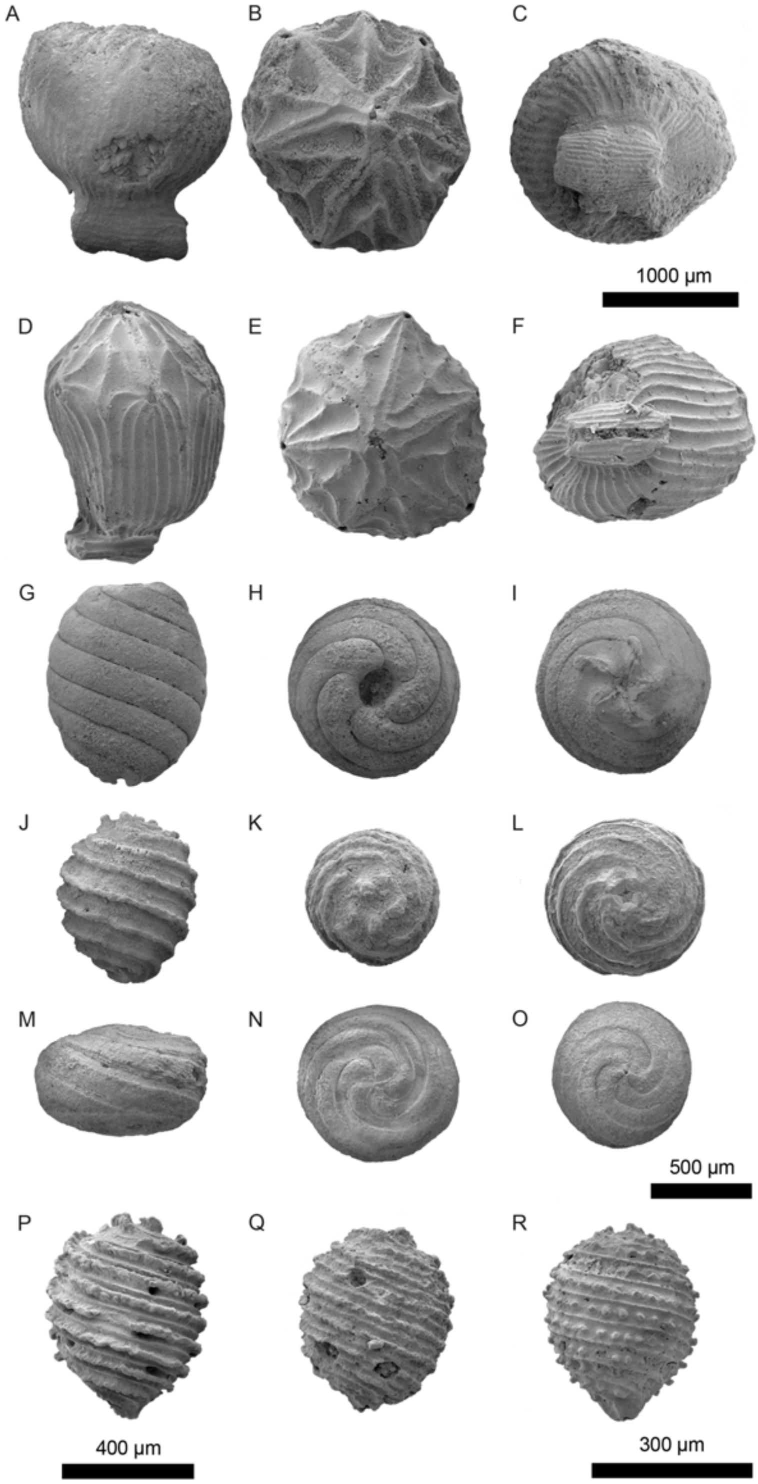


Figure 5. Most common charophyte fructifications of the studied sections. **A−C**. *Clavator ultimus*. A, lateral view. **B**, apical view. **C**, basal view. Samples from ES, L'Espinau section. **D−E**, *Clavator brachycerus*. **D**, lateral view. **E**, apical view. **F**, basal view. Samples from BE-2, Torrent de L'Espinau section. **G−I**, *Feistialla malladae*. **G**, lateral view. **H**,

apical view. **I**, basal view. Samples from ES-1, L'Espinau section. **J–L**, *Peckichara sertulata*. **J**, lateral view. **K**, apical view. **L**, basal view. Samples from BE-2, Torrent de L'Espinau section. M–O, *Platychara compressa*. **M**, lateral view. **N**, apical view. **O**, basal view. Samples from ES-1, L'Espinau section. **P**, *Microchara cristata.* Lateral view. Sample from ES-1, L'Espinau section. **Q**, *Microchara nana.* Lateral view. Sample from ES-1, L'Espinau section. **R**, *Microchara punctata.* Lateral view. Sample from ES-1, L'Espinau section.

Taphonomic analysis reveals that gyrogonites of *F. malladae*, *M. cristata* and *P. sertulata* are well-preserved; *P. llobregatensis*, *M. nana* and *Lamprothamnium* sp. are slightly eroded, while *P. compressa* is flattened. The gyrogonites do not show fracturation. However the superficial erosion of some specimens could result from lateral transport from the growth area, indicating parautochthony. Flattening of *P. compressa* is the result of a post-burial diagenetic process.

Charophytes assemblages dominated by *Feistiella malladae* indicate brackish or eurihaline waters from lagoons or coastal wetlands (Vilalba-Breva and Martín-Closas, 2011, 2013). Occurrence of *Lamprothamnium* sp. in these levels supports this interpretation since extant species of this genus (i.e. *Lamprothamnium papulosum*) is related to brackish environments (Soulié-Märsche, 1998).

The top of the fossiliferous layer passes gradually to 1.5 m of ochre marls (45% of $CaCO_3$) with grey mottling and scattered pedogenetic nodules and gyrogonites of *Feistiella malladae*. Above this pedogenized ochre marl, there is a bed of red lutite with ochre-yellowish mottling which contains reddish pedogenic nodules. In both cases, ochre marl and red lutite, the quartz content is around 10%. In the L'Espinau section, the top of this interval is featured by homogeneous grey marls and two dark grey limestone strata. The lower limestone (20 cm-thick) has a limited lateral continuity and wedges towards the south, while the upper limestone bed is thicker (1 m), highly bioturbated as in the southern Torrent de L'Espinau section, permitting the correlation of both successions (Fig. 1B, 2, 6C). These limestone beds show wackestone–packestone fabrics and are composed by abundant charophyte remains (thalli, gyrogonites and utricles), ostracods, gasteropod shells and other indeterminate molluscs. The charophyte remains of the first limestone bed of the L'Espinau section are mainly *Charaxis* thalli, characean gyrogonites probably belonging to *Microchara*, *Peckichara* and *Platychara* (Fig. 4), and a few clavatoracean remains such as *Munieria grambastii* thalli and *Clavator* utricles. The presence of characean remains decreases in the second limestone bed that contain portions of *M. grambastii* thalli, *Clavator* utricles, rare porocharacean gyrogonites, bivalves and gastropod shells. The abundance of clavatoracean remains in the second limestone suggests shallower conditions than those of the first limestone.

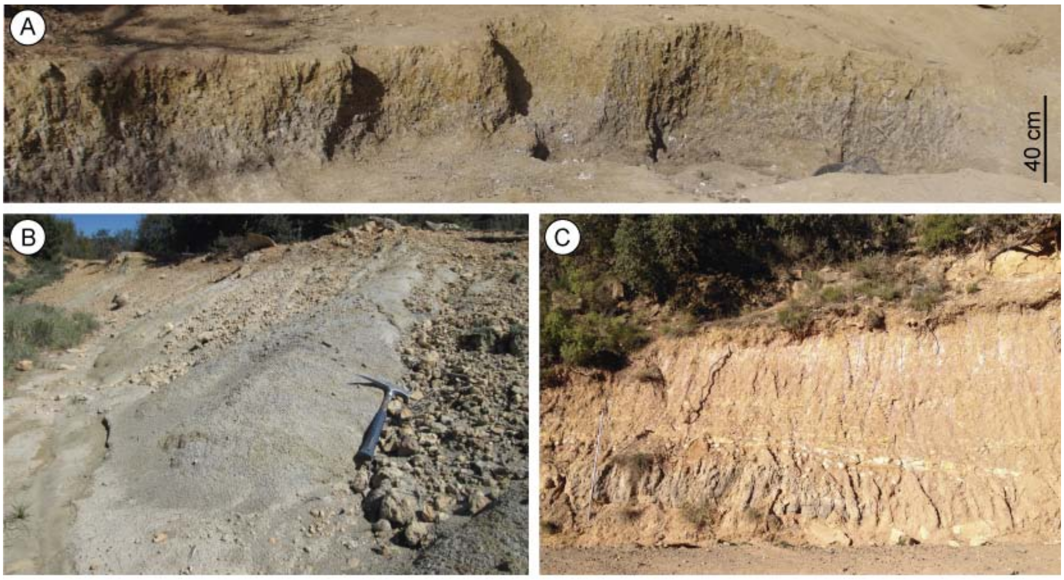


Figure 6. Photographs of the middle interval. **A**, the fossiliferous grey marl in the L'Espinau section. Note the transition towards the overlying ochre marl with grey mottling. **B**, grey marls in the Torrent de l'Espinau section, stratigraphically equivalent to **A**. **C**, transition from the top of middle interval represented by grey lacustrine limestones, to the upper interval represented by ochre and reddish lutites, and sandstones. Overlying the limestones, there is an oncolite level.

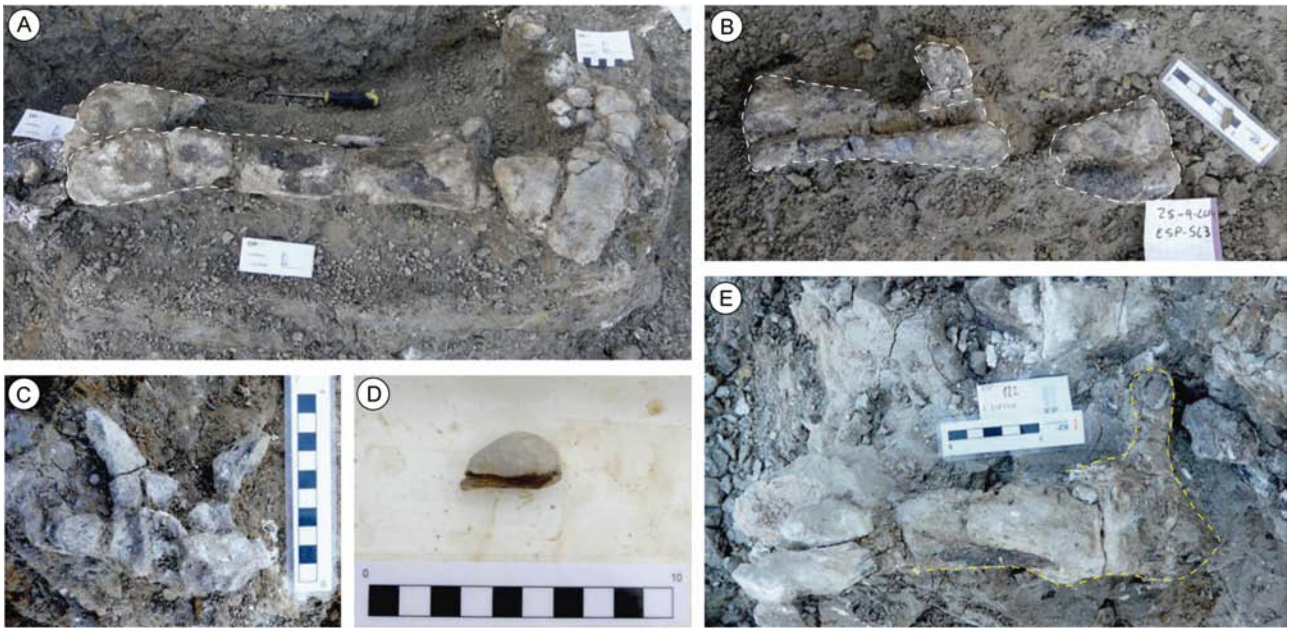


Figure 7. Examples of excavated bones with carbonate crusts. **A**, specimen ESP-62, composed of an articulated tibia and fibula. Note the contrast between the dark colour of the bone and the greyish-whitish carbonate crust. Scale bar: 5 cm. **B**, humerus ESP-563 exhibiting an oblique fracture below the deltopectoral crest. The missing portion of bone is found very close, displaced few cm. Scale bar: 5 cm. **C**, a well-preserved cervical vertebra displaying a fine greyish carbonate coating. Scale bar: 10 cm. **D**, small bone fragment covered by a massive carbonate crust. This coating appears rounded, suggesting a nucleation before a transport process. Scale bar: 10 cm. **E**, nearly complete right dentary (ESP-122) with a thick carbonate crust. The dental parapet is broken, so the alveoli are visible. Teeth are not preserved. Scale bar: 5 cm.

In the Torrent de L'Espinau section, the middle interval is much more monotonous, being characterized by homogeneous grey marls (Fig. 6B) with light ochre mottling towards the top of the layer. A rich charophyte assemblage has been described in the grey marls below the second, highly bioturbated limestone level. The assemblage is dominated by *Clavator brachycerus* along with gyrogonites of *Peckichara sertulata*, *P. llobregatensis*, *Microchara nana*, *Platychara caudata* and *Platychara* sp. and thalli *Munieria grambastii* (Fig. 5). The abundant, well-preserved utricles of *C. brachycerus* in the southern Torrent de l'Espinau section indicate freshwater conditions, contrasting with the brackish setting found in the fossil site.

4.1.3. Upper interval (reddish sandstones and claystones)

The last stratigraphic interval is almost fully covered in the L'Espinau section, and following observations were obtained from the Torrent de l'Espinau section. However, the combination of faults and present day colluvium also reduce the available rock exposures of this interval in this southern location. In general, the succession is characterised by alternations of massive reddish-purple and ochre lutites with channelized sandstones. Ochre mottling is present in the red lutite levels, but no other pedogenetic or bioturbation features have been identified. At the base of this interval, within red lutites, there is an oncoid-bearing bed of about 20 cm (Fig. 6C). Oncoids are large (around 10–20 cm) and ovoid in shape. Sandstones from the lower third of the interval are about 2 m thick and show general fining upward trends (from medium-grained sand to silt) and inclined heterolithic stratification (IHS; Supp. Fig. 2C, D). Sedimentary structures such as ripples and parallel lamination are clearly visible. Towards the top of the studied succession, sandstones become thicker (up to 3 m) and coarser, and lack the IHS arrangement described for the lower bodies. Sedimentary structures also increase their scale, being present in form of dunes.

The features found in this upper interval would correspond to the middle-upper part of the fluvial succession of the Figuerola Fm described by Colombo and Cuevas (1993) in the Fontllonga section.

4.2. Stable isotope analysis

Six different carbonate types with calcite as unique carbonate mineral have been analysed in terms of stable isotopic composition ($\delta^{13}C$, $\delta^{18}O$, PDB; Fig. 8 and Supp. Table 1): 1) wackestone limestones, 2) grey marls, 3) carbonate intraclasts, 4) carbonate crusts covering dinosaur bones, 5) oncoids, and 6) reddish pedogenic nodules.

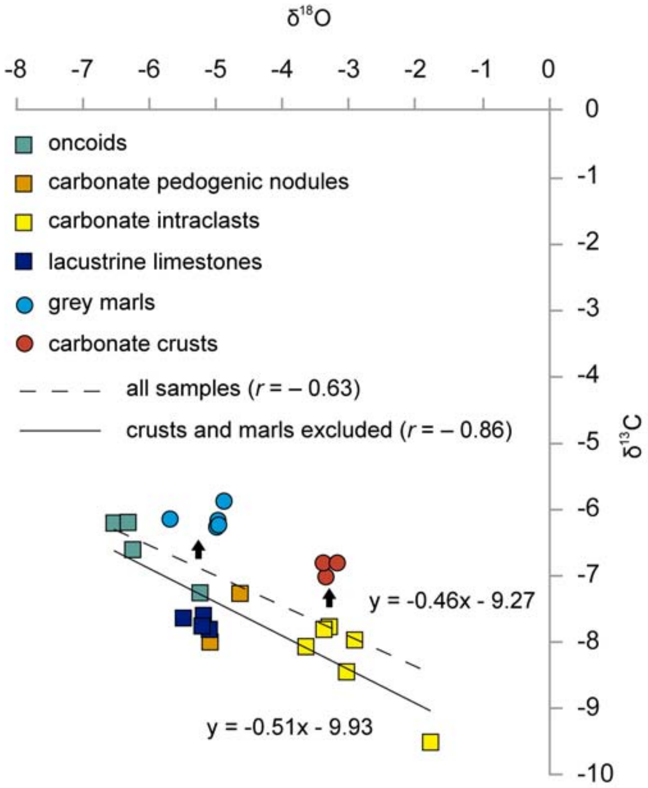


Figure 8. Isotopic signatures ($\delta^{13}C$, $\delta^{18}O$, PDB) of diverse carbonate samples. Note the general negative covariant trend and the enrichment in $\delta^{13}C$ of the marls and the carbonate crusts.

The oncoids show the most negative $\delta^{18}O$ values (between –6.53 and –5.24‰), whereas the carbonate intraclasts (–3.65to –1.78‰) and the bone crusts (–3.39 to –3.18‰) reach the less negative values. The rest of the samples display intermediate $\delta^{18}O$ values. Concerning to $\delta^{13}C$, oncoids, grey marls and carbonate crusts show the relatively less negative values (–5.87 to –7.01‰), and carbonate intraclasts exhibit the most negative ones (up to –9.50‰).

Considering the whole isotopic data, the $\delta^{13}C$ and $\delta^{18}O$ relationship displays a slight negative covariance (*r* = –0.63). The set formed by the oncoids, the pedogenetic nodules, lacustrine limestones and carbonate intraclasts, however, display a better (though still rough) negative covariance (*r* = –0.86). The values of the grey marl and the bone crusts, formed by carbonates in close contact with organic matter (such as bones and charcoal), appear as groups enriched in $\delta^{13}C$ outside the linear trend.

4.3. Vertebrate taphonomy

The L'Espinau fossil site occurs in a single fossil level of grey marls. It is a high diversity multitaxic bonebed (following Eberth et al., 2007) with a hadrosauroid-dominated macrofossil assemblage with representatives of several small microvertebrate groups. Hence, the excavations and the screen-washing of sediment have provided remains hadrosauroids and crocodylomorphs, as well as albanerpetontid allocaudatans, alytid, paleobatrachid, paleobatid and other indeterminated anurans, and iguanid squamates (Blanco et al., 2016). Further, the L'Espinau site is especially rich in ichthyofauna. In this respect, 16 different taxa have been identified, including chondrichthyans elasmobranchyians (anacoracids) and several groups of osteichthyans (chondrosteans, neopterigians and teleosteans) (Blanco et al., 2017). Dinosaurs are not only represented by skeletal remains, but also by eggshell material, which includes the oospecies *Megaloolithus baghensis*, which has been linked to titanosaurian sauropods (Sellés and Vila, 2015), and *Prismatoolithus trempi*, which has been linked to maniraptoran theropods (Sellés et al., 2014). Regarding invertebrate remains, hydrobiid and freshwater lymnaeid and planorbid gasteropods have been identified (Battista, 2014). The complete faunal list together with their habitats is presented in Table 1.

The macrovertebrate remains collected during excavations provide information about the spatial density, breakage frequencies and its typology, and bone orientations. Among a total of 617 excavated specimens, ≈ 70% (n = 424) have been ascribed to hadrosauroids. While skeletal elements recovered by screen-washing are just few millimetres in size, some excavated specimens, such as hadrosauroid hindlimb bones, reach 60 cm in length, although most of bones are less than 10 cm long. A significant 29% of the recovered bones represent small unidentified fragments with an average size of 3−5 cm. The mean spatial density of the fossil site is about 8 bones per square meter, but this distribution is not homogeneous through the outcrop (Fig. 9). A detailed analysis of the data also revealed that there are very low bone density areas (1-2 bones per square meter) adjacent to others with relatively higher values (about 30 bones per square meter).

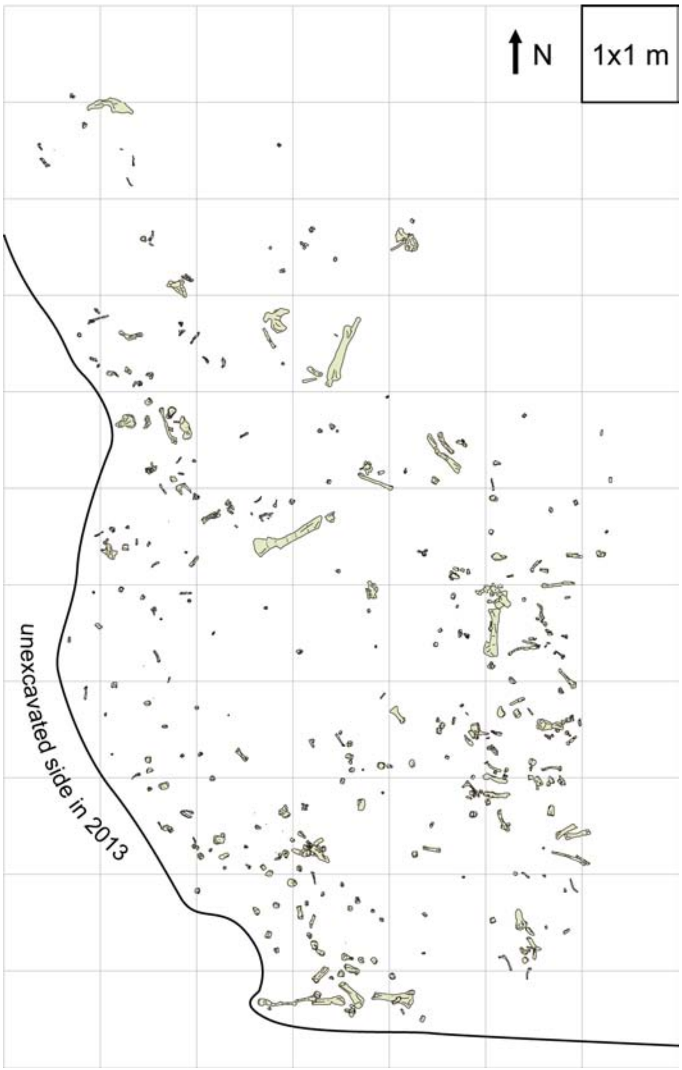


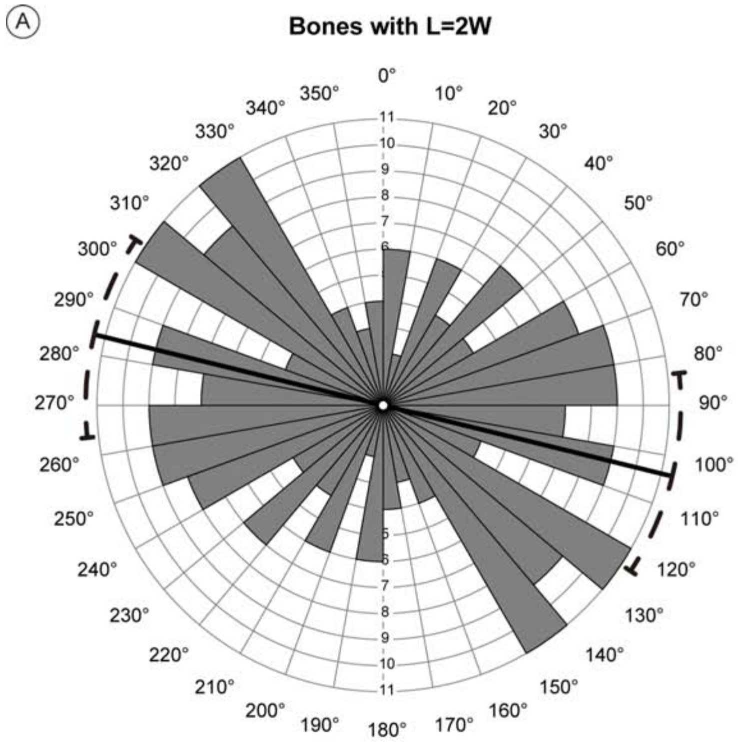
Figure 9. Mapping of the L'Espinau excavation in 2013. Modified from Battista (2014).

Bones with length ≥ 2 x width (n = 113) exhibit some sort of bidirectional arrangement. The rose diagram indicates an east-west bidirectional orientation with a mean vector of 104–284º, but its length (r-parameter) is only 0.182, indicating a low concentration of data around this vector. Four different statistic tests were performed in order to explore the randomness distribution of the bones in the site, following Eberth et al. (2006). Despite the Rayleigh, Watson U^2 and Kuiper's tests falsify the consideration of a uniformly distributed assemblage (α of 0.05), the Rao's Spacing test, however, supports the randomness ($0.90 > p > 0.50$) (Fig. 10A). Because the latter test is considered more powerful and better discriminator in bidirectional data, we cannot validate the east-west arrangement of the long bones at this level. Hence, we subsequently analysed the orientation the longest bones (length > 20 cm; n = 39). By splitting the data set at 20 cm length, we discard a large amount of small rounded bones that include fragments of apofisis and unrecognizable bone chips. This value (20 cm) corresponds to an inflection in the bone length histogram (Supp. Fig. 3). In this second case, the mean vector is quite similar (97-277º), but its length ($r = 0.428$) is higher than in the former analysis. The null hypothesis of random distribution is refuted in all the statistics, including the Rao's Spacing test ($p < 0.05$). Thus, a bidirectional distribution of the longest bones is now fully confirmed (Fig 10B). In summary, we can conclude that the largest bones were east-west oriented as a result of hydraulic transport, while the smaller ones were randomly deposited. The less resistance to the flow of the latter bones can explain this situation.

The analysis of the breakage frequencies of 603 considered bones reveal that most of them (specially the long ones) exhibit two or more fractures ($n = 420$, 70% of the recovered bones) being the complete elements much less profuse ($n = 47$, 7% of the sample; Fig. 11A). An important amount of elements ($n = 70$, 12% of the total sample) are bone fragments with less than five centimetres. The fractured elements can be subsequently classified according to the typology of breakage, following Galobart (2003) and Britt et al. (2009). Hence, transversal, longitudinal, oblique and mixed fractures have been considered (see Supp. Fig. 4). This classification reveals that the majority of the fractured bones exhibit one or more parallel transversal fractures ($n = 322$, 66% of the total observed bones excluding the small [< 5 cm] bone fragments; Fig. 11B), although a significant 30% ($n = 153$) also show mixed fractures (oblique, longitudinal and transversal). Approximately 2% ($n = 11$) of the broken bones only have oblique fractures.

Although carbonate crusts cover most of the bones, other taphonomic features can be observed. For instance, most of the vertebral centra and appendicular bones (i.e. tibiae, femora, metapods and phalanx) show abraded edges, especially in condyles and the more prominent areas. In some specimens, the bone have lost the outer compact bone tissue, exposing the inner trabecular bone structure. The broken edges of the transversally fractured bones are unabraded, as well as most of the oblique fractures. Weathering evidence such as cracking or flacking (following Behrensmeyer, 1978) is apparently absent.

In contrast to the variable preservation described for the hadrosauroid macrofossils, the microvertebrates recovered from the screen-washing exhibit no signs of abrasion. Instead, the bone edges are well preserved and show clean surfaces (see some examples in Blanco et al., 2016, 2017).



TREND DATA

n = 117

Mean vector = 104° - 284°

Length of Mean vector (r) = 0.182

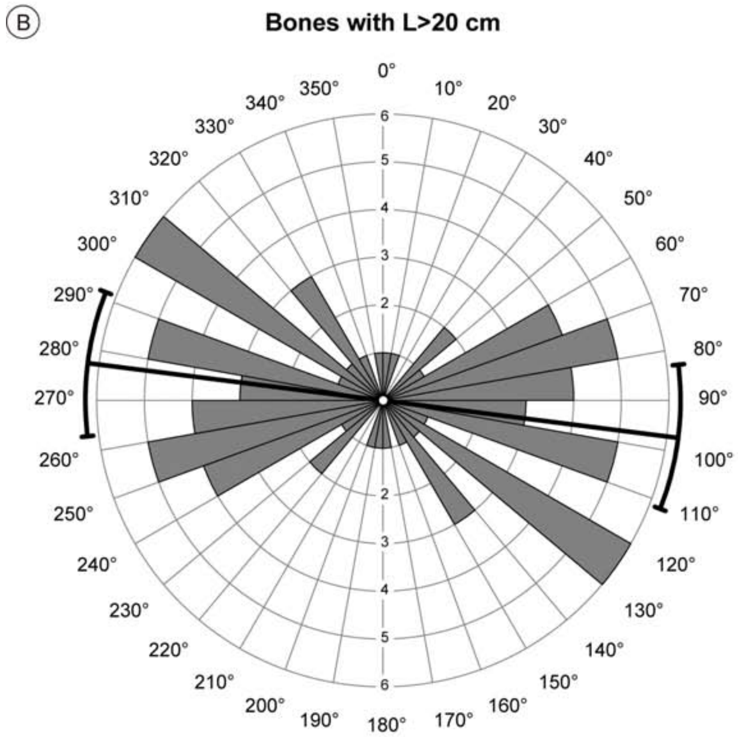
TESTS OF UNIFORMITY

Rao's Spacing Test (0.90>p>0.50): Supported

Rayleigh Test (p=0.021): Falsified

Watson U^2 Test (p<0.025): Falsified

Kuiper's Test (p<0.05): Falsified



TREND DATA

n = 39

Mean vector = 97° - 277°

Length of Mean vector (r) = 0.428

TESTS OF UNIFORMITY

Rao's Spacing Test (p<0.05): Falsified

Rayleigh Test (p=6.02E-04): Falsified

Watson U^2 Test (p<0.005): Falsified

Kuiper's Test (p<0.01): Falsified

Figure 10. Orientation of long bone elements in L'Espinau site and uniformity statistic analyses. All data are bidirectional. **A**, rose diagram of all bones with length more than twice the weight. In this case the Rao's Spacing Test cannot be falsified, so the random distribution cannot be completely discarded. Hence, the confidence interval (95%) of the mean vector appears as a dotted line. **B**, rose diagram of long bones with more than 20 cm. In this case, all uniformity tests are falsified, so a bidirectional distribution can be inferred for the largest long bones.

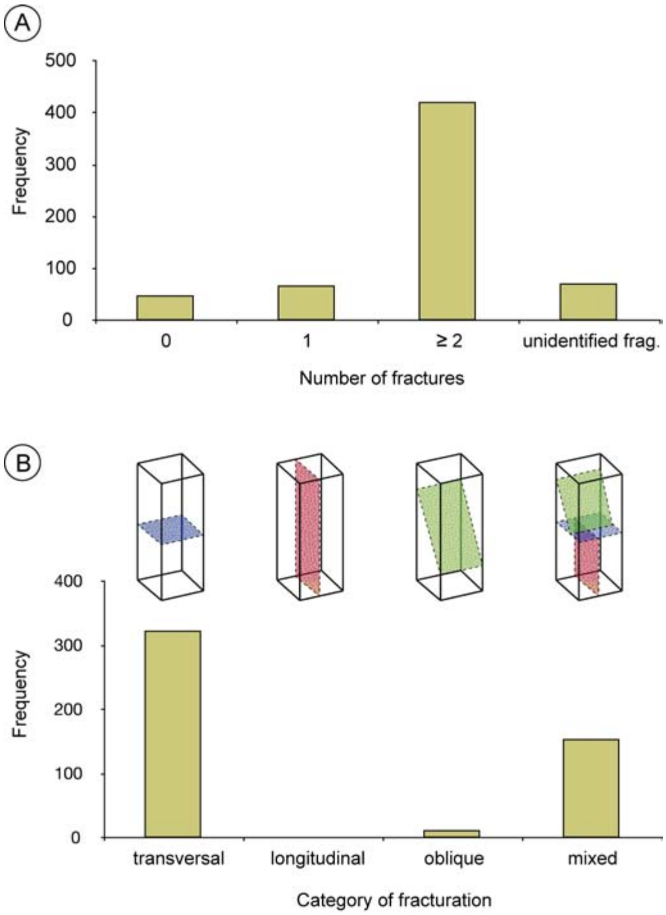


Figure 11. Breakage occurrence in the recovered bones from L'Espinau. **A**, classification according the number of fractures. The last category (unidentified fragments) corresponds to small chip bones. **B**, frequency of each tipology of fractures.

4.4. Magnetostratigraphy

Demagnetization of the studied samples indicates that a soft secondary component is demagnetized by 150ºC or up to 13 mT (Supp. Fig. 5). It can be assigned to a recent overprint probably representing the present geocentric axial magnetic field. A characteristic remanent magnetization (ChRM) component of both normal and reverse polarity is then defined upon demagnetization. The homogeneous subhorizontal dip of the strata along both nearby sections prevents any stability fold test to be carried out. However, the dual polarity of the ChRM in addition to the presence of the recent overprint suggests a primary origin. The studied samples have provided the succession of three polarity intervals (Fig. 2). The lower reverse magnetozone, where the bonebed is located, includes five samples (grey, ochre-brown lithologies) that fully demagnetize with the AF protocol indicating a magnetite-like mineral as the main magnetic carrier (Supp. Fig. 5A, B). The intermediate normal magnetozone is about 10 m long and is characterized by reddish and ochre-brown lithologies in which hematite dominates the magnetization (i.e. sample ES10-1, Supp. Fig. 5C) or appears together with a magnetite-like mineral phase (Supp. Fig. 5D, E) both carrying normal polarity. One single sample along this interval (ES17) display reverse polarity and is represented by a half-width bar in the polarity column (Fig. 2). The upper reverse magnetozone is determined by two sites in reddish lithology (3 demagnetized specimens) that are dominated by hematite (Supp. Fig. 5F).

5. Discussion

5.1. Age calibration of the fossil site

Charophyte biostratigraphy reveals that L'Espinau and Torrent de L'Espinau sections belong to the Microchara punctata biozone (lower Maastrichtian–basal Danian in age), based on the occurrence of the index species in the studied assemblage. Within this biozone, the presence of *Clavator ultimus* allows to relate the palaeontological site to the Clavator ultimus subzone (lower Maastrichtian in age) calibrated to chron C31r by Galbrun et al. (1993) and Vicente et al. (2016). Consequently, we correlate the lower reverse magnetozone to chron C31r (Fig. 2, 3). It follows that the 10 m long normal magnetozone represents most likely the interval comprising chrons C31n-C30n and the upper reverse interval represent then chron C29r. An alternative proposal implies correlating the upper reverse interval to the short chron C30r (see Fig. 3 for general chronostratigraphy). We disregard in any case the significance of the single reverse sample ES17. However, the relatively overall condensed nature of the Figuerola Fm along this section favours the former interpretation.

5.2. Genesis of the bonebed

Sedimentology and palaeontology show palaeoenvironmental differences between the two studied sections. The charophyte assemblage from the southern Torrent de L'Espinau section is dominated by *Clavator brachycerus*, which is indicative of very shallow and well-illuminated environments that usually occur in the lakeshores of freshwater lakes. On the other hand, the occurrence of *Feistiella malladae* in the L'Espinau bonebed indicates brackish conditions, thus revealing a south to north palaeoenvironmental shift along the studied outcrops. The latter marine-influenced environment likely represents a lagoonal setting, which is common in the Maastrichtian deposits of the studied area (Villalba-Breva and Martín-Closas, 2013; Oms et al., 2016).

In the southern Pyrenees, lagoonal deposits have been recognized in successions of freshwater limestones and grey marls with brackish taxa together with levels of palaeosoil development (see Villalba-Breva and Martín Closas, 2013; Oms et al., 2016). The L'Espinau site displays similar features. Therefore, the palaeoenvironment of the area is regarded as the landwards edge of a coastal lake/lagoon. Estuarine settings can be discarded since such environments have not been described in the Fontllonga and Tremp Groups, have a low preservation potential and should develop in transgressive contexts (e.g. Allen and Posamantier, 1993; Zaitlin et al., 1994). In this respect, a regression is well documented in the Pyrenean region during the Maastirchtian (Rosell et al., 2001).

The fossiliferous layer of the L'Espinau site has yielded terrestrial (dinosaurs) and freshwater faunal assemblages (e.g. osteoglossid fish) mixed with brackish and marine fish including phyllodontid teleostean morphotypes and anacoracid chondrichtian sharks (see Table 1). The mix between different groups of fauna and flora in the same layer can be related to short term (years) variations of the palaeoenvironment itself, such as alternations of freshwater, euryhaline and marine conditions (see Oms et al., 2016 and Blanco et al., 2017). In our case, the mixing mechanism is clearly the result of a mechanic accumulation (transport), although both mechanisms can be found together (transport of a mixed association). While the taphonomic features described for the recovered dinosaur bones concur with transport (e.g. bidirectional arrangement of long bones), other remains are non-reworked, indicating authochtony or parauthoctony (as occur in the charophyte assemblage and the microfossil remains, see above). Thus, we infer that a sedimentary process entramped or reworked previously deposited (and occasionally buried) macro- and microfossil remains such as dinosaur and freshwater fish remains, carbonate clasts and high amounts of marl from the coastal lake and the surroundings of the lagoon (Fig. 12A, B). Subsequently, the transported material was emplaced in a the lagoon as suggested by the presence of brackish, euryhaline and marine taxa in the final accumulation (e.g. the *Feistiella* charophyte assemblage and marine fish, see Table 1). An in situ accumulation (i.e., attritional) of the terrestrial remains found in the L'Espinau lagoonal bed is discarded since a tractive process oriented large and elongated bones. In this respect, a bone orientation due to tides within an estuary or a tidal mudflat is also unlikely, since the muddy matrix that comprise the macrofossil remains would have been washed.

The $\delta^{13}C$ - $\delta^{18}O$ stable isotope analyses of the inorganic and biogenic carbonates from L'Espinau section (marls, oncoids, pedogenic nodules, limestones, clasts and crusts) add further palaeoenvironmental information. The high variation of $\delta^{18}O$ and the relative low change in $\delta^{13}C$ (see Fig. 8) can be related with different environments. First, positive covariant trends are common in closed lakes (Talbot, 1990). Negative trends, however, have also been related to lakes with particular conditions (e.g. decomposition of organic matter that produces a depletion in ^{13}C or inputs of lighter C) that enrich the system in ^{12}C (see Utrilla et al., 1998). This last scenario is compatible with L'Espinau, but the presence of freshwater together with marine fauna in the site is against the consideration of a closed lake. Mixing of freshwater and brackish water can also produce carbonates with high variations in $d^{18}O$ (Hendry et al., 2001). This situation is found in transitional environments such as lagoons and estuaries (Hendry et al., 2001; Oms et al., 2016). Discarded the estuarine setting (see above), the isotopic signal found in the L'Espinau carbonates concurs with the lagoon, reinforcing the sedimentological and palaeoecological interpretation. Marine influence, represented by higher saline conditions, did not imprint a noticeable isotopic signature on the studied carbonates (e.g. values of $\delta^{18}O$ around 0‰). This fact suggests that the lagoonal conditions found in the L'Espinau site were ephemeral. In this respect, the development of a palaeosoil, with presence of mottling in the upper part of the fossil layer reveals a rapid shift back to palustrine facies after the mass flow was emplaced, also suggests a very short lagoonal development on the area.

The fossiliferous layer corresponds to a matrix-supported bed in which the following features have been identified: (i) presence of a non-lithified marly matrix that contains larger elements ranging from small bone fragments to complete long bones up to 60 cm in length, and 3−5 cm carbonate intraclasts, resulting in a poorly sorted deposit; (ii) normal size-grading, upward decreasing of bone density, and bidirectionally oriented long bones (E−W); (iii) presence of scattered organic matter, charcoal and plant remains; (iv) absence of any internal sedimentary structure other than some microscopic lineal structures in the muddy matrix. They could represent a primary feature or a lamination produced by compactation during the diagenesis. These characteristics concur with those reported for the debris flow-hosted Sun River Bonebed (Upper Cretaceous Two Medicine Fm, Montana, USA, Scherzer and Varricchio, 2010) and shares similarities with other fossil sites regarded as debris flow in origin (e.g. Fastovsky et al., 1995; Rogers, 2005; Van Itterbeeck et al., 2005; Eberth et al., 2006; Lauters et al., 2008; Schmitt et al., 2015). The high concentration of the clay size fraction (up to 40%) indicates that the original flow was rheologically plastic, a defining feature of high density cohesive flows (Mulder and Alexander, 2001; Dasgupta, 2003 and references therein). The apparent low density of the coarsest elements together with the predominance of the clay-sized particles are compatible with the term mud flow following Mulder and Alexander (2001). The unconfined nature of the muddy layer and the absence of a well-sorted and well-stratified deposit, without any visible sedimentary structure like cross-laminations or current ripples (see Sohn et al., 1999; Pierson, 2005; Hessel, 2006) permit to discard a streamflow origin for L'Espinau.

The fact that bones and clasts are matrix supported indicates that the flow did not undergo a prolonged subaquatic motion. Instead of being washed by water, the flow got 'frozen' earlier after entering the main lagoon. This is also supported by the bidirectional orientation of bones that keep the main transport direction following the basin axis (E−W; see Gómez-Gras et al., 2016). In this respect, freezing, or *en masse* deposition, is the common mechanism of deposition for cohesive flows (Mulder and Alexander, 2001).

Flaig et al. (2014) described three bonebeds from the lower Maastrichtian of Artic Alaska (Prince Creek Fm) deposited in a low-gradient coastal plain setting. In addition to the coastal environment, these sites exhibit some interesting sedimentological features shared with L'Espinau. The bonebeds exhibit two layers consisting on i) a basal silty bed with ripples where most of the bones were found, overlyied by ii) a sheared mudstone level with oriented plant remains and lesser amounts of bones. This last facies exhibits evidence of a frozen in flow deposition, with elongated elements arranged following the direction of the flow. The authors related both facies to the dual-phase hyperconcentrated flows that evolved from a streamflow (Fig. 12 C, D). In such flows, the largest particles are transported as bedload, while the finest sediments remain in suspension (Smith, 1986; Sohn et al., 1999; Lorenzini and Mazza, 2004; Pierson, 2005), conferring a stratified bed when the flow stops. If the clay content is high, a cohesive behaviour can be achieved in the suspended phase, resulting in a rigid debris flow-like mud plug as the flow dewaters (Pierson, 2005). Hence, the upper part of the hyperconcentrated flow can travel longer distances than the bedload sediments, as Flaig et al. (2014) described for the Alaska sites. The L'Espinau deposit has no dual layering, so we do not have evidence of this type of flow. However, it could be possible that the cohesive flow inferred for L'Espinau actually represents the segregated, suspended phase of an hyperconcentrated flow that traveled further than other frictional coarser sediments. Against this interpretation is the fact that the muddy layer of L'Espinau also contains very large elements (long bones with 60+ cm). Hence, it is difficult to accept that such bones could be transported in the suspended phase of the hyperconcentrated flow rather than settled as bedload. In this respect, Flaig et al. (2014) only found small bone remains in the upper mudstone. Hence, we reafirm that the sedimentary process that generated the bone accumulation was a cohesive flow in origin. The very low silt/sand component of the matrix of L'Espinau could not allowed a flow partition, preventing the evolution of the cohesive flow into an hyperconcentrated flow (Fig. 12; Hampton, 1972, 1975; Mulder and Alexander, 2001).

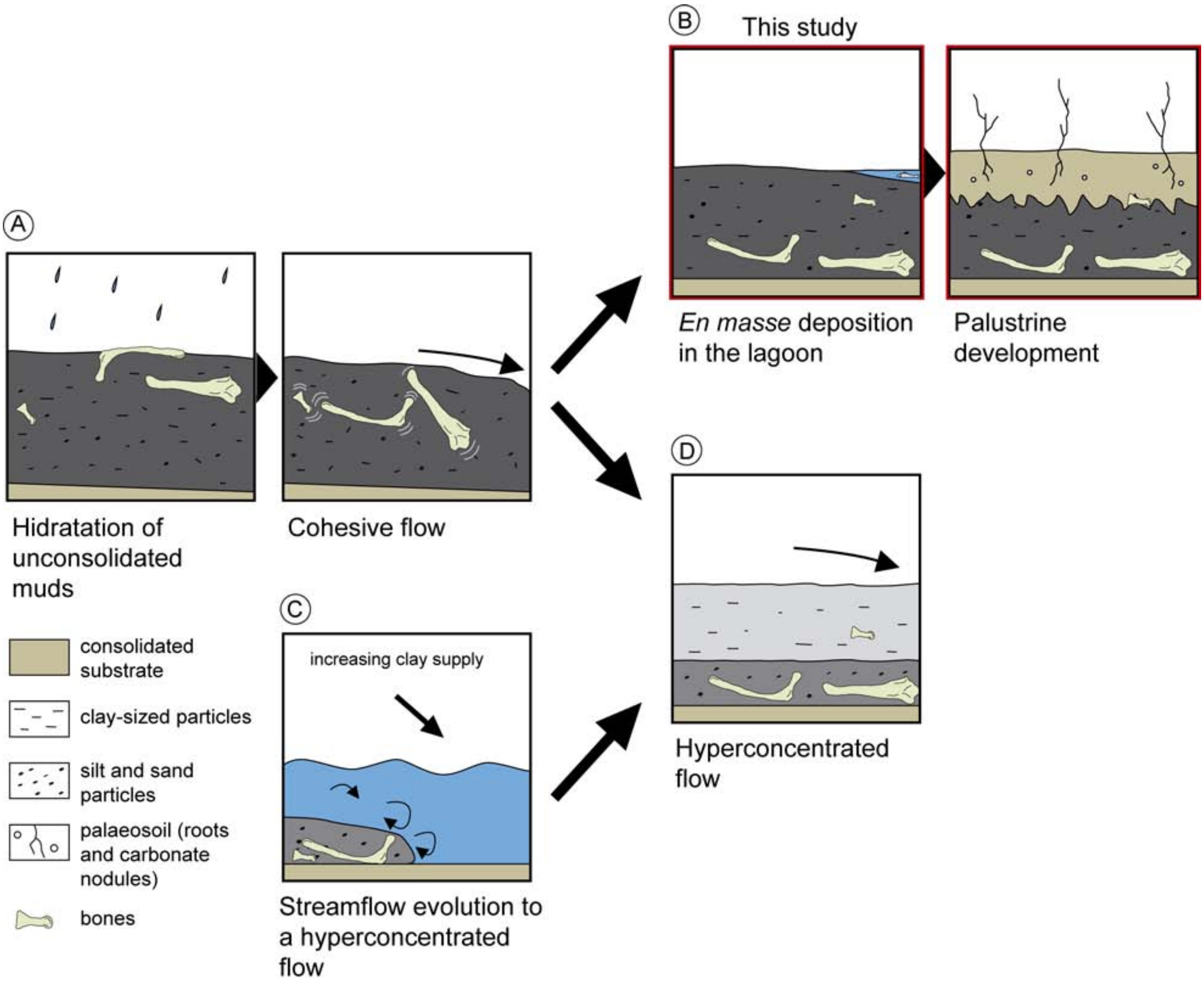


Figure 12. Schematic diagrams of the sedimentary processes discussed in the text. **A** and **B**, the preferred origin as a cohesive flow for the L'Espinau site. **C**, a streamflow process supplied by high amounts of clay material, that evolves to a hyperconcentrated flow (**D**). **D**, a hyperconcentrated flow, showing its bipartite nature, as Flaig et al. (2014) describe for bonebeds from Artic Alaska.

The normal grading trend and the higher density of coarse elements, like bones in the L'Espinau site, towards the base of the layer is described in some debris flow-hosted bonebeds (e.g. Eberth et al., 2006; Scherzer and Varricchio, 2010). This model, known as incremental deposition, occurs when a debris flow, instead of being emplaced as a single mass deposit, evolves and becomes longitudinally segregated during the course of the flow. In this scenario, the coarser components are progressively and preferentially located at the front of the flow, and subsequently emplaced first. The tail of the flow, enriched in smaller elements, overruns and overlaps the already deposited coarser front as the flow continues. As a result, this process develops a finning-upwards sequence (fig. 13 of Vallance and Scott, 1997). A similar process could took place in L'Espinau cohesive flow.

Because almost all the hadrosauroid bones display no signs of skeletal association, we consider that the pre-existing assemblage before the flow event already represented disarticulated elements or carcasses in a high degree of decomposition (thanatocoenose) that were reworked, transported and finally separated during the flow event. One exception of the aforementioned is the tibia and fibula specimens ESP-62, which still exhibit an anatomical connection (Fig. 7A). The hypothesis of corpses and/or living dinosaurs being trapped by the flow is unlikely, since we would expect higher degrees of skeletal articulation as occurs in the Dalton Wells bonebeds (Cedar Mountain Fm, Utah; Britt et al., 2009). According to other bone modification features, we can rule out at this point an extended subaerial exposure for the L'Espinau thanatocoenose due to the absence of weathering marks. In addition, the predatory and scavenging activity, which occurs early after the death of the individuals (Rogers, 1990), is unlikely given the fact scratches and tooth marks are apparently absent. Parallel fractures transverse to the major axis of the bones have been regarded as diagenetic (Galobart, 2003). Hence, most of the fractures observed in the L'Espinau bonebed (70% of the broken bones) have a post-depositional origin. The oblique fracturing, on the contrary, reveals that those bones were relatively fresh when they broke (Britt et al., 2009). Trampling, the breakage produced by large vertebrates roaming on the thanatocoenose, has been regarded as one of the main causes of post-mortem bone fracturing and skeletal disarticulation (Behrensmeyer, 1988; Britt et al., 2009). However, typical features of trampling like dominance of fresh, oblique fractures and presence of scratch marks in the bone surfaces (Behrensmeyer et al., 1986; Britt et al., 2009) are reduced or negligible in L'Espinau. In this respect, we discard this method as a the cause of bone disarticulation for L'Espinau. In addition, trampling does not explain the bidirectional arrangement of long bones. Instead, a sedimentary process that implies transport is the most likely cause for such features. In this respect, one possible cause of bone breakage is the flow itself. Cataclasis, the collision between bones and carbonate clasts during the mass flow event, has been proposed as one of the origins for the bone fractures (Eberth et al., 2006; Britt et al., 2009; Scherzer and Varrichio, 2010). Closely associated bone fragments of the same skeletal element supports this mechanism of breakage for the mixed and oblique fractures (Fig. 7B), as the muddy matrix prevented the scattering of the bone fragments. This process likely originated some breakage of small fragments or chipped bones (e.g. broken apophyses, which are particularly frequent in the site).

The presence of bones with rounded carbonate coatings suggests that at least some elements were already buried prior to being reworked by the debris flow, representing a primary taphocoenose. Further, the differences in the degree of abrasion also suggest that there is more than one taphonomic history (i.e. several events of mortality) in the original bone assemblage accumulated in the L'Espinau site.

Cohesive flows can be triggered by several mechanisms (see Eberth et al., 2006; Scherzer and Varricchio, 2010; Fastovsky et al., 1995; Rogers, 2005; Lauters et al., 2008) that generate a sudden runoff in poorly consolidated substrates rich in clay. So that, intense rainfall is the likely triggering mechanism for the mass flow forming the L'Espinau deposit. A main difference between the studied site and the aforementioned examples is that L'Espinau mass flow did not occurred in a fluvial-alluvial setting, but instead in a coastal setting, which is less common for bonebeds (see Eberth et al., 2007). (Fig. 13). The environmental changes identified by palaeoecological and sedimentological variations (e.g. development of lagoonal conditions in the middle interval of the L'Espinau section, adjacent to a coastal lake setting) suggest an alternating sea connection-disconnection for the coastal lake. Thus, a drop in the lagoon water level could easily generate a slope and trigger reworking of exposed areas of the unconsolidated muds of the lagoon margin (Fig. 13). A landwards transgression from the sea due to a storm, tsunami or tidal bores is discarded since no marine bioclasts are found at all, as well as no organized tempestite or rhythmite deposits are found (see Myrow, 1992). In addition, the muddy matrix would have been diluted and washed, instead of beeing freezed as we mentioned above. Other triggering mecanisms such as lake undamming (e.g. Martin and Turner, 1998; Capra and Macías, 2002) or volcanic-induced mass flows (e.g. Vallance and Scott, 1997) can be ruled out due to the lack of high reliefs and volcanic activity, respectively.

Geochemistry also sheds light on the origin of the carbonate crusts that cover most of the bones. The isotopic signal of these carbonates shows an enrichment in $\delta^{13}C$ from the primary trend (Fig. 8). According to Talbot and Kelts (1990), this enrichment can took place during an early diagenesis in sediments with high content of organic matter, as occurs in the L'Espinau fossiliferous marl, due to methanogenetic bacteria activity. Methanogenesis can increase alkalinity, inducing the precipitation of isotopically heavy carbonates as concretions (Martin, 1999).

The depositional model of the L'Espinau site is unusual compared to all other upper Cretaceous fossil sites in the Pyrenees, mainly consisting on accumulations linked to fluvial-deltaic channels (e.g. channel fill processes, oxbow lakes, deposition in meander margins). Examples of such sites are the localities of Molí del Baró-1 (Marmi et al., 2016), Sant Romà d'Abella (Prieto-Márquez et al., 2006) and Torrebilles (Marmi et al., 2012; Dalla Vecchia et al., 2013) from the uppermost Maastrichtian of the Tremp syncline (southern Pyrenees); the Laño site from the Upper Campanian of the Basque Country (Pereda-Suberbiola et al., 2000, 2015; Corral et al., 2016) and Bellevue, from the lowermost Maastrichtian of the northern Pyrenean area (Le Loeuff, 2005; Fondevilla et al., 2016b). Mass flow-hosted localities are scarce in this southwestern European context. In this concern, only the Basturs Poble bonebed from the Maastricthian of the Tremp syncline shares similar genesis and taphonomic features with L'Espinau (see Riera, 2010).

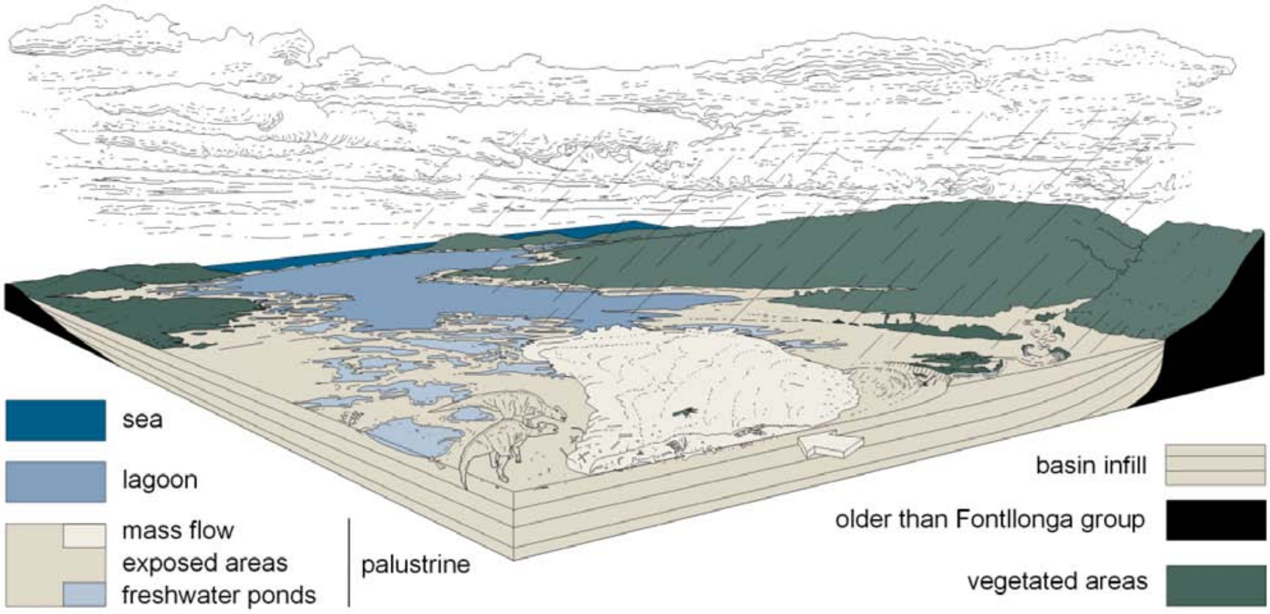


Figure 13. Palaeoenvironmental reconstruction of the coastal lake and lagoonal settings showing the mass flow event that produced the L'Espinau bonebed.

The South-Pyrenean record has provided multiple evidences of sauropod dinosaurs inhabiting near the sea. There are examples of nesting in tidal flats and barrier islands (Sanz et al., 1995; López-Martínez et al., 2000) and roaming and foraging in brackish lagoons (Marmi et al., 2014; Oms et al., 2016). Hitherto, the hadrosauroid record was mainly restricted to fluvial environment (channels and floodplains) of coastal plains (see Vila et al., 2013), with scarce examples of bone remains and tracks located in coastal settings (e.g. in the Els Nerets and Moror B sites; Riera et al., 2009 and Vila et al., 2013). In this respect, the L'Espinau site provides further evidence of hadrosauroids occupying environments connected to lagoonal conditions.

6. Conclusions

The integrated sedimentology, stable isotope geochemistry and charophyte and vertebrate palaeontology permit the accurate palaeoenvironmental reconstruction for the L'Espinau area and the sedimentary process that originated the fossil bonebed (see Fig. 13).

- A succession from lacustrine deposits (represented by the La Maçana Fm limestones) shifted to a coastal lake system (base of the Figuerola Fm) during the transition between the early and the late Maastrichtian as indicated by the magneto- and biostratigraphic study (upper part of the chron C31r, within the lower part of the charophyte Clavator ultimus subzone).

- The coastal lake deposits located in the mid-interval of the studied sections, represented by freshwater lacustrine limestones and grey marls, reveal a north-south facies shift from a freshwater lacustrine environment (presence of *Clavator brachycerus*) to a more brackish setting where the charophyte *Feistiella malladae* is dominant. This environmental change likely reflects periods of connection between the coastal lake and a lagoon, and appears to follow the general trend in the facies migration during the infilling of the Upper Cretaceous south Pyrenean basins as described in the literature, with a south to north component in the marine regression superimposed to the well-known east-west regression polarity.

- The tabular muddy layer that characterises the L'Espinau bonebed was produced by an exceptional mass flow (a cohesive flow) event that affected exposed sediments that were transported to the marine setting represented by a lagoon, probably during a drop in the water level. Further emersion intervals took place as evidenced by palustrine facies development (palaeosoils) on the debrite. The mass flow physically mixed both terrestrial fauna with freshwater, brackish and marine taxa.

- The taphonomical analyses indicate that the original macrovertebrate assemblage likely represented already disarticulated dinosaur bones, as reveals the profuse skeletal disarticulation.

- ^{13}C enrichment of the carbonate crusts suggests that early diagenetic processes like methanogenesis are the probable origin for the carbonate crusts observed in most of the bones.

The integrated sedimentological, geochemical, palaeocological and taphonomical data prove that hadrosauroids inhabited the coastal environment. This example from the southernmost Pyrenees adds evidence of dinosaurs exploiting the ecosystems connected to the sea during the Maastrichtian of southwestern Europe.

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Table 1. Faunal content and ootaxa from L'Espinau.

L'Espinau faunal content and habitat	
Dinosauria	
Ornithischia	
Ornithopoda	
Hadrosauroidea indet.	Fluvial, lacustrine, coastal wetlands
Crocodylomorpha	
Crocodylomorpha indet.	Fluvial, lacustrine, coastal wetlands
Lissamphibia	
Allocaudata	
Albanerpetontidae indet.	Fluvial, lacustrine, coastal wetlands
Anura	
Alytidae	
Alytinae indet.	Fluvial, lacustrine, coastal wetlands
Palaeobatrachidae indet.	Fluvial, lacustrine, coastal wetlands
Paleobatidae or Gobiatidae indet.	Coastal lake
Anura indet.	-
Lepidosauria	
Squamata	
Iguanidae indet.	Fluvial, lacustrine, coastal wetlands
Chondrichthyes	
Elasmobranchii	
Lamniformes	
Anacoracidae indet.	Marine
Osteichthyes	
Chondrostei	
Chondrostei indet.	Anadromous
Neopterygii (non teleosteans)	
Lepisosteiformes	
Atractosteus sp.	Freshwater-euryhaline
Semionotiformes	
Semionotiforme indet.	Euryhaline
Amiiformes	
Amiidae indet.	Marine-freshwater
cf. *Caturus* sp.	Marine
Pycnodontiformes	
Pycnodontiformes indet.	Marine-freshwater
Aspidorhynchiformes	
Belonostomus sp.	Marine
Teleostei	
Osteoglossiformes	
Osteoglossidae indet.	Freshwater
Phyllodontidae	
Phyllodontidae indet. 1	Marine
Phyllodontidae indet. 2	Marine
Phyllodontidae indet. 3	Marine
Phyllodontidae indet. 4	Marine
Cypriniformes	
Cypriniformes indet.	Freshwater
Acanthomorpha	
Percomorpha indet.	Marine-freshwater
Teleosteii indet.	-
Gastropoda	
Hydrobiidae indet.	Freshwater to brackish

Lymnaeidae indet.	Lacustrine
Planorbidae indet.	Lacustrine
Dinosaur oospecies content	
Dinosauroid	
Megaloolithidae	
Megaloolithus baghensis	
Prismatoolithidae	
Prismatoolithus trempi	

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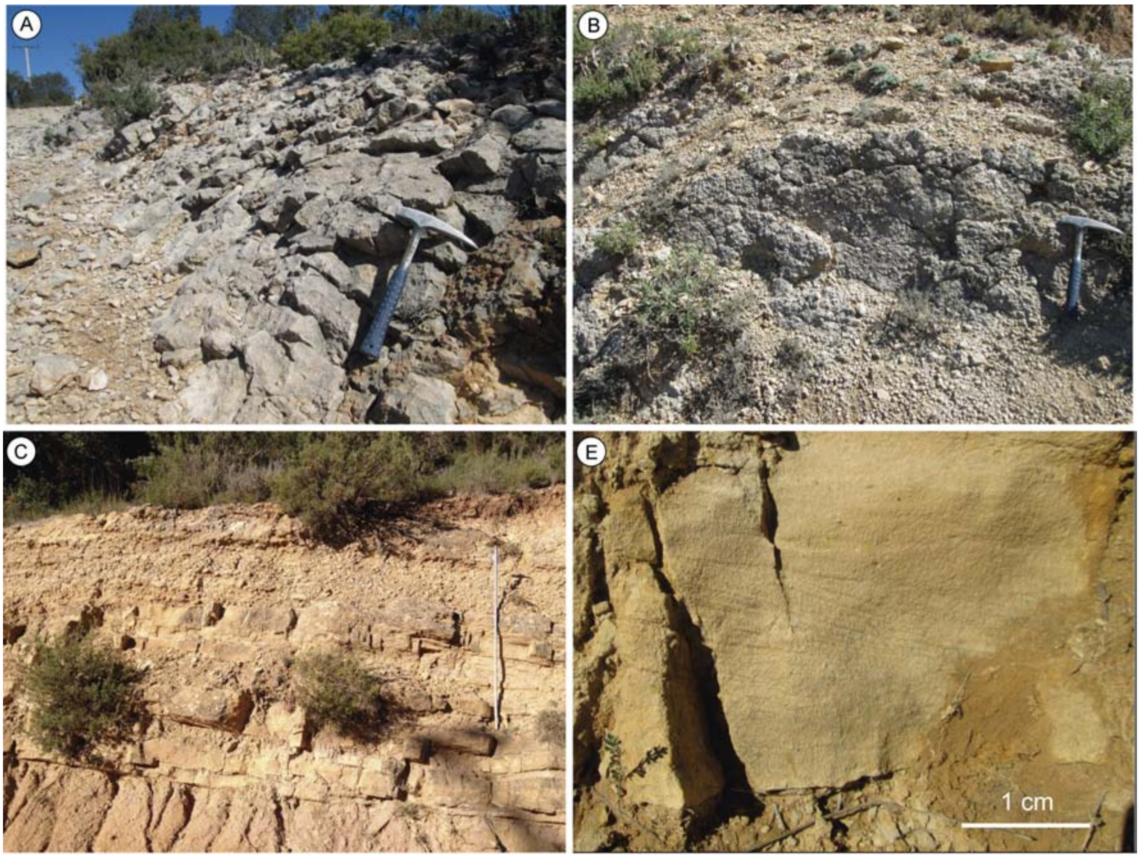
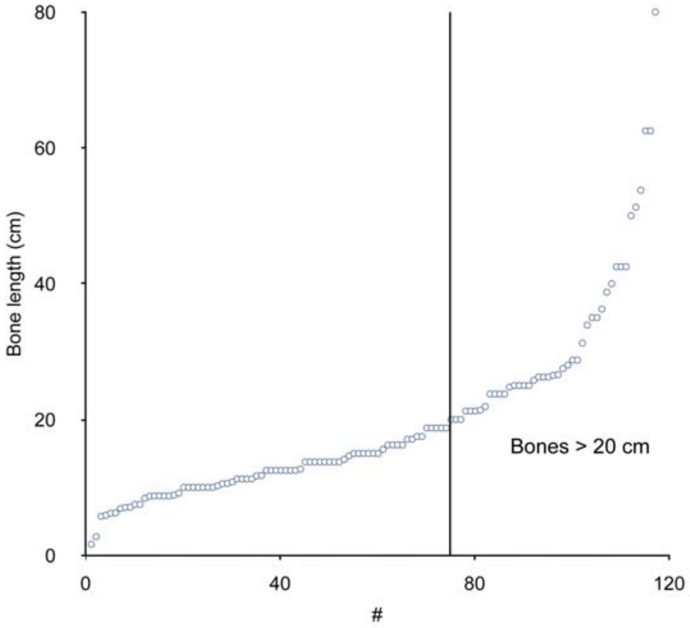
Supplementary Information

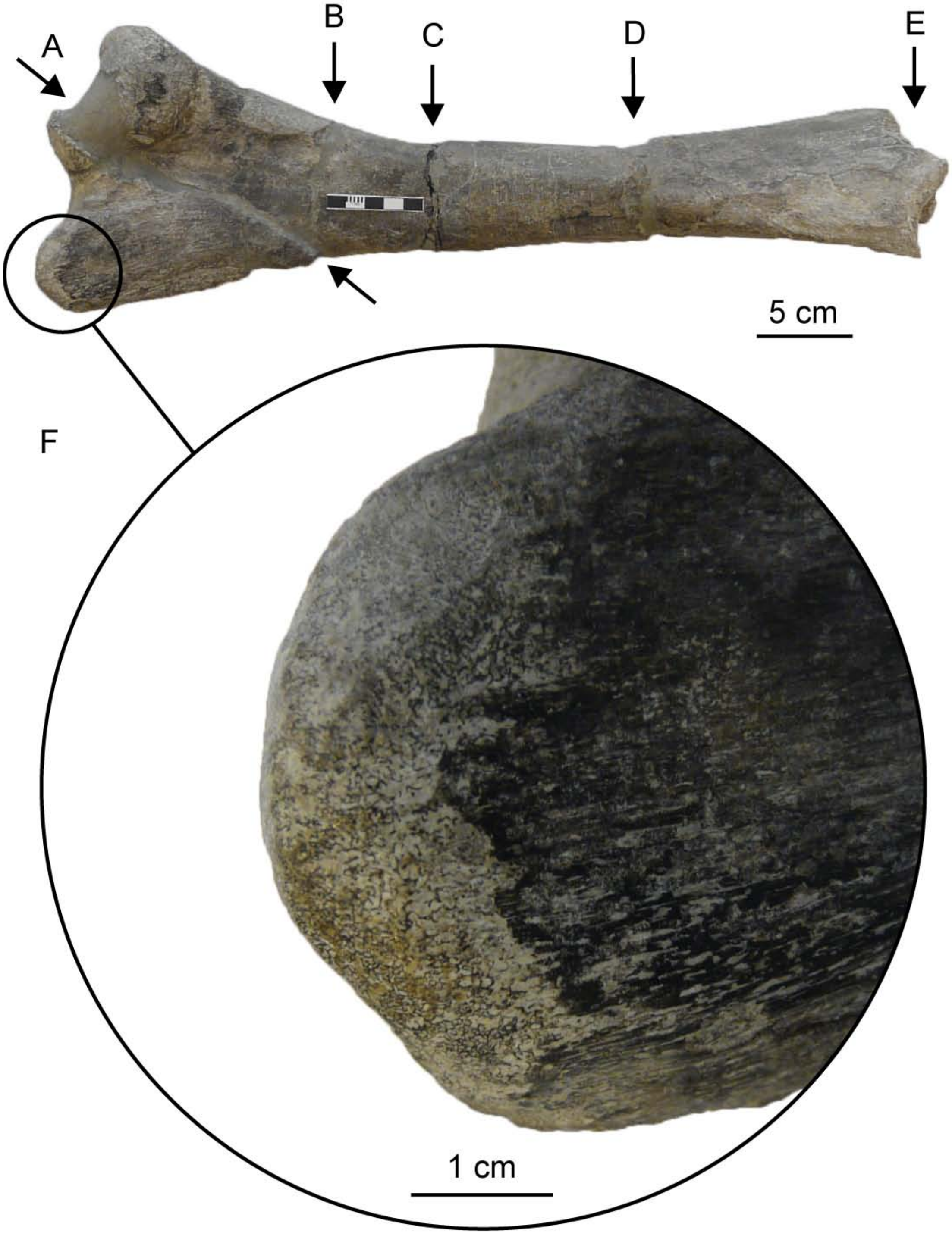
Supplementary Figure 1. Excavation in 2012.



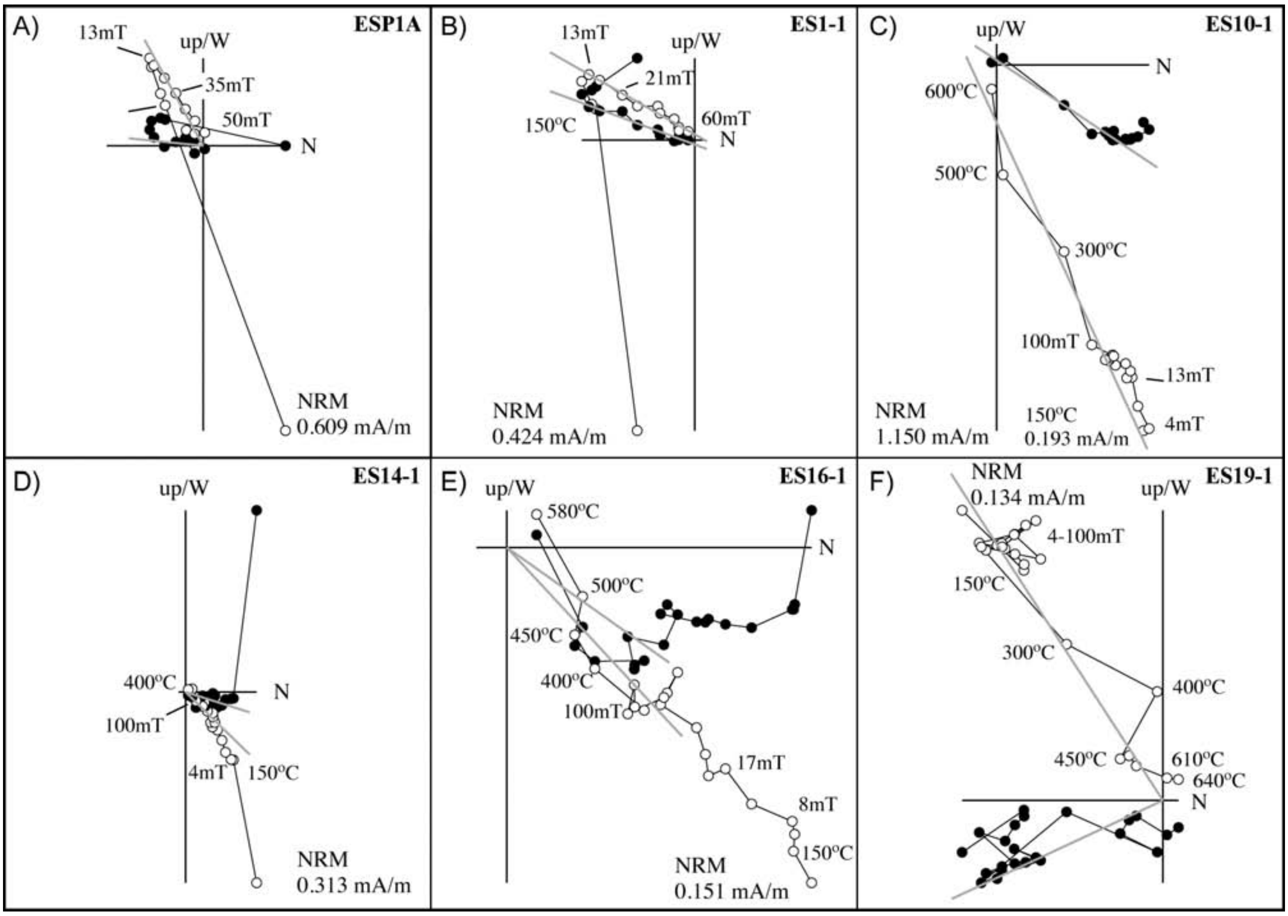
Supplementary Figure 2. Lacustrine limestones of the lower interval (**A**, **B**) and sandstones from the upper interval (**C**, **E**) described in the Torrent de L'Espinau section. **A**, wackestones. **B**, oncolites. **C**, sandstone body composed of inclined heterolithic stratification (IHS). The upper levels exhibit fine grained sands together with oncoids. **D**, detail of cross lamination in this sandstone.



Supplementary Figure 3: Histogram showing the bones used in the rose diagrams of Figure 10. The line indicates an inflection used to discrimine those bones conidered “longer”.



Supplementary Figure 4: Examples of bone breakage and abrassion in the right tibia ES-62. **A**, oblique fracture. **B**-**D**, transverse fractures. **E**, mixed oblique-transverse fracture. **F**, enlargement of the proximal end of the bone, showing an abraded surface that reveals the inner trabecular bone tissue.



Supplementary Figure 5. Representative in-situ orthogonal demagnetization diagrams from the studied Espinau sections. Samples follow a stepwise alternating field (AF) demagnetization protocol (4-100 mT) after a single heating step to 150ºC. For reddish lithologies thermal desmagnetization up to 640ºC proceed the previous protocol. The natural remanent magnetization (NRM) intensity and some demagnetization steps are indicated. Open and closed symbols indicate projections onto the upper and lower hemisphere respectively. The computed ChRM direction is shown by a solid grey thick line (reverse polarity for A, B and F; normal polarity for C, D and E).

Supplementary Table 1. Stratigraphic position**,** lithology, mineralogy and isotopic composition of the studied carbonates.

Sample	Stratigraphic position (m)	Lithology	Mineralogy	$\delta^{13}C$	$\delta^{18}O$
IESP1	15	Oncoid	Calcite + quartz (traces of nontronite)	-6.20	-6.53
IESP2	15	Oncoid	Calcite + quartz (traces of nontronite)	-7.25	-5.24
IESP3	15	Oncoid	Calcite (quartz)	-6.60	-6.25
IESP4	15	Oncoid	Calcite (quartz)	-6.19	-6.32
IESP5	15.3-15.7	Grey marls	Calcite + quartz (nontronite and traces of clinochlorite)	-5.87	-4.88

IESP6	15.3-15.7	Grey marls	Calcite + quartz (nontronite)	-6.16	-4.97
IESP7	15.3-15.7	Grey marls	Calcite + quartz (nontronite)	-6.14	-5.69
IESP8	15.3-15.7	Grey marls	Calcite + quartz (nontronite)	-6.26	-4.99
IESP9	15.3-15.7	Grey marls	Calcite + quartz (nontronite)	-6.23	-4.96
IESP10	15.3-15.7	Carbonate intraclast	Calcite (quartz + traces of nontronite)	-8.06	-3.65
IESP11	15.3-15.7	Carbonate intraclast	Calcite (quartz + traces of nontronite)	-8.44	-3.04
IESP12	15.3-15.7	Carbonate intraclast	Calcite (quartz)	-9.50	-1.78
IESP13	15.3-15.7	Carbonate intraclast	Calcite (quartz)	-7.76	-3.30
IESP14	15.3-15.7	Carbonate intraclast	Calcite (quartz)	-7.96	-2.92
IESP15	15.3-15.7	Carbonate intraclast	Calcite (quartz)	-7.80	-3.38
IESP16	15.3-15.7	Carbonate crust	Calcite + quartz (traces of nontronite)	-7.01	-3.35
IESP17	15.3-15.7	Carbonate crust	Calcite + quartz (traces of nontronite, microcline)	-6.80	-3.39
IESP18	15.3-15.7	Carbonate crust	Calcite (quartz)	-6.80	-3.18
IESP19	16	Pedogenic nodule	Calcite (quartz, goethite)	-7.99	-5.09
IESP20	17	Pedogenic nodule	Calcite + quartz + goethite	-7.26	-4.64
IESP21	21	Lacustrine limestone	Calcite	-7.59	-5.19
IESP22	21	Lacustrine limestone	Calcite	-7.63	-5.49
IESP23	21	Lacustrine limestone	Calcite	-7.80	-5.10
IESP24	21	Lacustrine limestone	Calcite	-7.75	-5.21

Magnetostratigraphy of the Maastrichtian continental record in the Upper Aude Valley (northern Pyrenees, France): Placing age constraints on the succession of dinosaur-bearing sites

8

El capítol 8 correspon a l'article publicat en la revista *Cretaceous Research* el gener de 2016, prèviament aparegut online el 10 de setembre de 2015:

Fondevilla, V., Dinarès-Turell, J., Vila, B., Le Loeuff, J., Estrada, R., Oms, O., Galobart, À. (2016). Magnetostratigraphy of the Maastrichtian continental record in the Upper Aude Valley (northern Pyrenees, France): Placing age constraints on the succession of dinosaur-bearing sites. *Cretaceous Research* **57**, 457-472.

En aquesta publicació V. F. ha realitzat treball de camp (mesura de les seccions estratigràfiques, i recollida de mostres) i ha coordinat les aportacions dels diferents autors. Ha escrit la major part del text, ha preparat les figures 1, 2, 3, 4 (conjuntament amb J. D.-T.), 8, 9 i 10 i ha discutit els resultats amb la resta de participants.

Aquest capítol està protegit (pàgines 137 a 160). Pot consultar-se en el següent enllaç:

http://www.sciencedirect.com/science/article/pii/S0195667115300525

DOI: http://dx.doi.org/10.1016/j.cretres.2015.08.009

THE CHRONOSTRATIGRAPHIC FRAMEWORK OF THE SOUTH-PYRENEAN MAASTRICHTIAN SUCCESSION REAPPRAISED: IMPLICATIONS FOR BASIN DEVELOPMENT AND END-CRETACEOUS DINOSAUR FAUNAL TURNOVER

9

El capítol 9 correspon a l'article publicat en la revista *Sedimentary Geology* l'abril de 2016, prèviament aparegut online el 15 de març de 2016:

Fondevilla, V., Dinarès-Turell, J., Oms, O. (2016). The chronostratigraphic framework of the South-Pyrenean Maastrichtian succession reappraised: Implications for basin development and end-Cretaceous dinosaur faunal turnover. *Sedimentary Geology* **337**, 55-68.

En aquest article V. F. ha realitzat treball de camp (mesura de seccions estratigràfiques, recollida de mostres) i de laboratori (desmagnetització de les mostres de paleomagnetisme) a l'Istituto Nazionale di Geofisica e Vulcanologia (INGV, Roma) durant l'estada breu. Ha coordinat les aportacions dels diferents autors. Ha escrit el text, ha preparat les figures 1, 2, 3, 4, 5, 7, 8, 9 i 10 i ha discutit els resultats amb la resta de participants.

Aquest capítol està protegit (pàgines 163 a 179). Pot consultar-se en el següent enllaç:

http://www.sciencedirect.com/science/article/pii/S0037073816000786

DOI: http://dx.doi.org/10.1016/j.sedgeo.2016.03.006

Dinosaur succession during the end-Cretaceous of southwestern Europe. A review.

10

El capítol 10 correspon a un article en preparació, encara no enviat a revisar.

Fondevilla, V. et al. (en preparació). Dinosaur succession during the end-Cretaceous of southwestern Europe. A review.

En aquest treball V. F. ha redactat el text i ha preparat totes les figures.

Dinosaur succession during the end-Cretaceous of southwestern Europe. A review.

1. Introduction

Southwestern Europe provides one of the few terrestrial records that allow a comprehensive study the Campanian-Maastrichtian dinosaur assemblages in terms of diversity, ecological and extinction patterns (Vila et al., 2016). A very rich fossil record with hundreds of sites have been found in the different sedimentary basins of Iberia (Portugal and north and central Spain), the Pyrenees (Spain and France) and the Languedoc and Provence areas (southeastern France; see Fig. 1A). These basins, together with other exposed massifs, conformed the Ibero-Armorican Island (Fig. 1B), the largest landmass of the western European archipelago (Philip et al., 2000).

The first attempt to establish a regional faunal succession by combining the dinosaur occurrences with chronostratigraphy was carried out by Le Loeuff et al. (1994a). These authors built a proposal of a major dinosaur faunal turnover that took place between the lower and the upper Maastricthtian of Spain and France. Further refinements of this succession kept the basis of the original hypothesis (e.g. Laurent et al., 1999; Vila et al., 2012; Vila et al., 2016). The current state of the art postulates that an assemblage of titanosaurian sauropods, rhabdodontid ornithopods, nodosaurid ankylosaurians, abelisaurid and dromeosaurid theropods dominated the Campanian-early Maastrichtian Ibero-Armorican landscapes until the beginning of the late Maastrichtian, when the appearance of a new assemblage composed by hadrosauroids and new titanosaurian taxa led a very rapid faunal replacement (Vila et al., 2016 and references therein). Le Loeuff et al. (1994a) proposed that the faunal turnover was related to environmental changes that led into a marine regression. The regressive context during the Maastrichtian in the Ibero-Armorican Island is well documented (e.g. Bilotte et al., 1983; Ardèvol et al., 2000; Laurent et al., 2001; Oms et al., 2007; Fondevilla et al., 2016a), and likely led palaeogeographical changes in the landmasses that allowed the arrival of dinosaur immigrants (Vila et al., 2016).

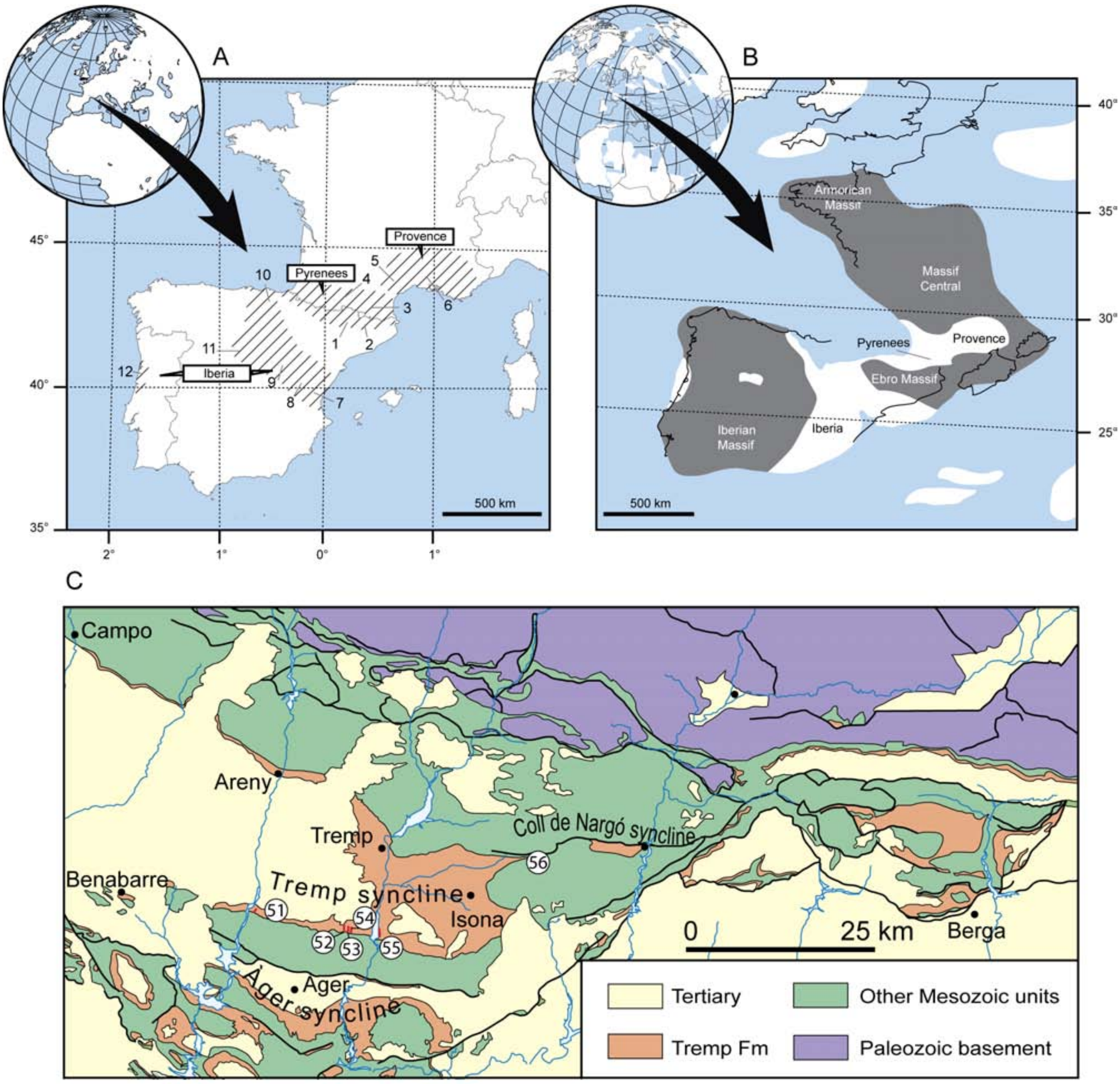


Figure 1. Present-day geography (**A**) and palaeogeographical setting (**B**) of the Ibero-Armorican Island (southwestern Europe) during the Campanian-Maastrichtian, with indication of the main considered sectors. Modified from Vila et al. (2016). **C**, enlargement of the South-Pyrenean area, with indication of some sections studied here (see the rest in Figure 2).

The narrative of Le Loeuff et al. (1994a) and subsequent works were based on a incomplete chronostratigraphic framework. Despite intense biostratigraphic and magnetostratigraphic research carried out in the last decade, critical points remain unresolved. This is the case of chron C31r in the Tremp Syncline (see Vila et al., 2012), an essential succession of sites to document the faunal shift in the Ibero-Armorican Island (Figs. 1B and 2A). Thus, the magnitude and duration of the proposed dinosaur faunal turnover was actually set up under limited chronostratigraphic data. However, recent studies by Díez-Canseco et al. (2014) and Fondevilla et al. (2016a) improved previous age constraints in the Tremp Syncline and provided an accurate dating of tens of key fossil sites around the time-interval in which the turnover took place (Fig. 2B). In light of these results, an updated succession of fossil sites in the Tremp Syncline is presented here. In addition, the dinosaur eggshell biostratigraphy, developed by Vianey-Liaud and Garcia (2000) and Garcia and Vianey-Liaud (2001), is revisited and amended here following the updated succession of dinosaur-bearing sites.

2. Sedimentary succession and chronostratigraphy

The chronostratigraphic framework of the Isona sector (eastern Tremp Syncline; Fig. 2B) published in Riera et al. (2009) and Vila et al. (2013) has been improved using planktonic foraminifera (Díez-Canseco et al., 2014) and new magnetostratigraphic studies (Fondevilla et al., 2016a for Isona and Canudo et al., 2016 for the lateral marine equivalents located westwards). The isochronous rudist horizons described in Vicens et al. (2004) have been used as key levels to physically correlate close spaced sections but also the different sectors of the basin (see also Caus et al., 2016 and Oms et al., 2016). As a result, we represented 56 stratigraphic columns (previously published in Riera et al., 2009; Riera, 2010; López-Martínez and Vicens, 2012; Blanco et al., 2016; Caus et al., 2016 and Fondevilla et al., 2016a) in three correlation panels: the northern, central and southern sectors of the Tremp Syncline (Figs. 3, 4 and 5). These new correlation schemes compile an unprecedented amount of geological data that permits to better observe differences in the sedimentary thickness within the basin depending on the location with respect to the depocentre, and thus avoid some correlation errors. As discussed in Fondevilla et al. (2016a), the new magnetostratigraphic dating of the Isona sector of the Tremp Syncline revealed that almost two thirds of the sedimentary succession (the entire Conques Fm) belong to the lower Maastrichtian, instead of the upper Maastrichtian considered in Vila et al. (2012), Dalla Vecchia et al. (2014) and Sellés and Vila (2015). As a consequence, several dinosaur fossil sites of the Tremp Syncline become older than previously considered.

The integration of the new calibration presented here together with all the available chronostratigraphic data from the rest of the Pyrenees, Iberia, the Languedoc and Provence areas (see Table 1 for references) allowed to ensamble the most complete Campanian-Maastrichtian dinosaur succession of southwestern Europe erected so far (Fig. 6). The dinosaur fossil record from Portugal has not been included due to the poorly known age calibration of the Viso, Aveiro and

Taveiro sites, although their palaeontological content is included in the main text. This general dinosaur succession allows a better comprehension of the faunal changes that took place within the Maastrichtian in some dinosaur groups of the studied region. Hence, the paleontological record of the different dinosaur groups that inhabited the region is reviewed below. In addition, the recently developed dinosaur eggshell biostratigraphy has been updated.

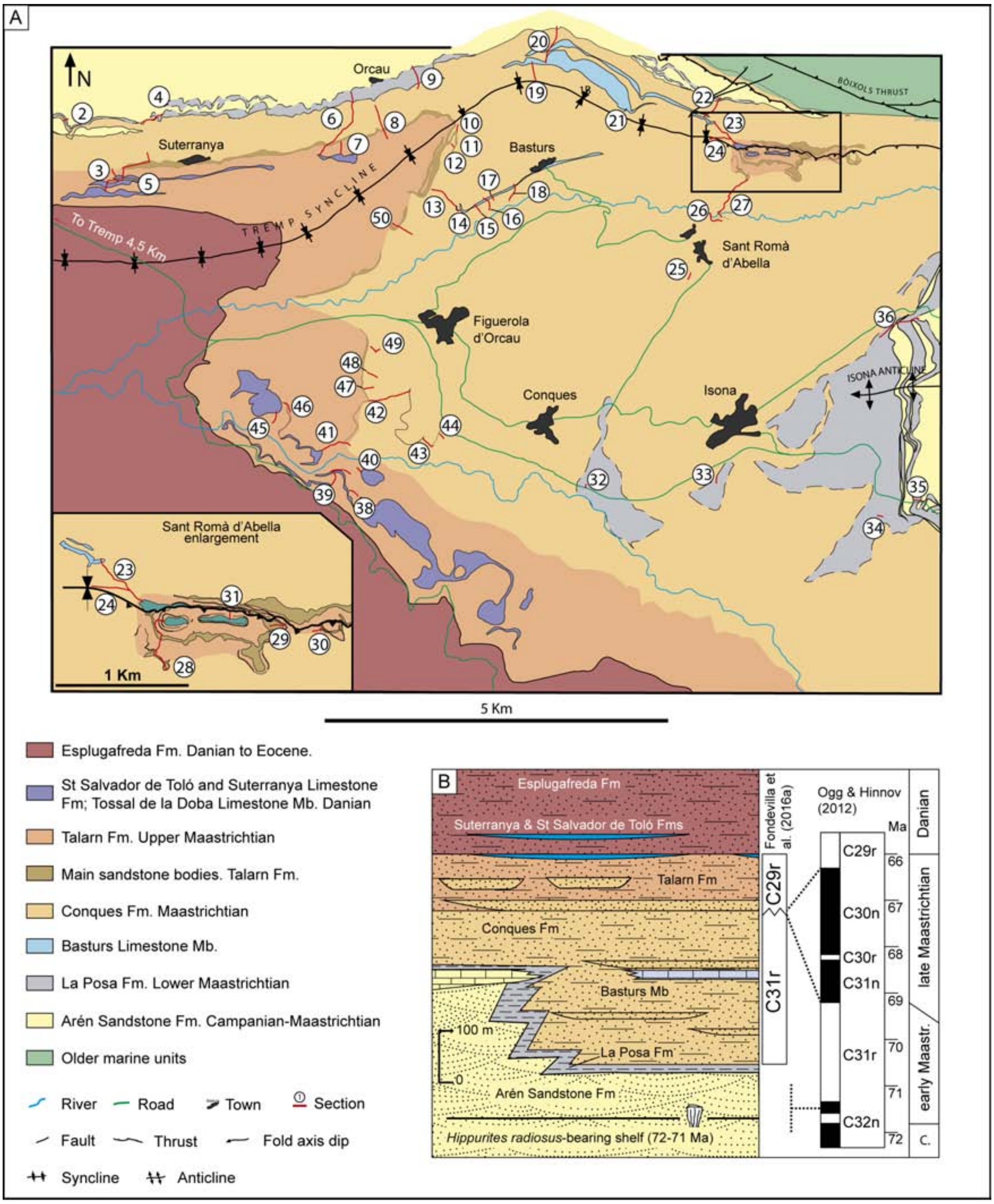


Figure 2. A, detailed geological map of the Isona sector (eastern Tremp Syncline), with location of the studied sections. Modified from Riera et al. (2009). **B**, chronostratigraphic scheme of the Isona sector. Modified from Fondevilla et al. (2016a).

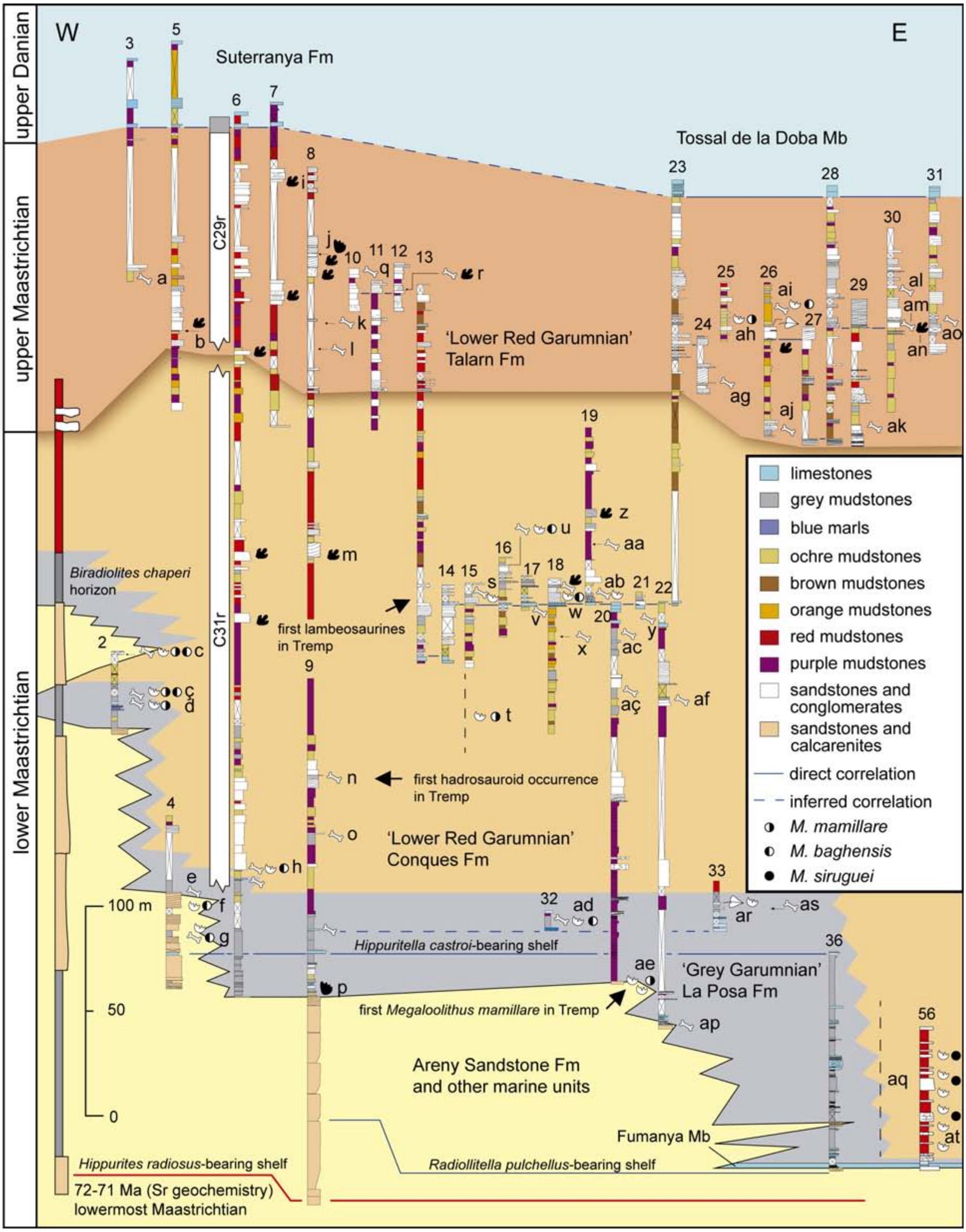


Figure 3. W-E correlation panel of the northern sector of the Isona area (Tremp Syncline), with indication of the fossil sites (plants, bones, tracks and egg remains). The megaloolithid oospecies are also indicated. Sections 32, 33 and 36 are projected. Correlation modified from Riera et al. (2009), Riera (2010) and Vila et al. (2013). Paleomagnetism after Fondevilla et al. (2016a). Sites: a, Les Serretes; b, Camí de les Planes, Serrat de Santó; c, Compuertas, Sant Bartomeu, Presa de Sant Antoni; ç, Vicari-4; d, Els Nerets; e, Suterranya-Mina de lignit, Suterranya-Camí de Montesquiu; f, La Llabusta; g, Suterranya-1 (L'Abeller); h, Orcau-1; i, Costa Roia; j, Serrat de Sanguín; k, Serrat de Sanguín-1, -2; l, Els

Esfons; m, Torrent de Carant; n, Casa Fabà; o, Orcau-3; p, Orcau-2; q, Barranc de Torrebilles-2; r, Barranc de Torrebilles-5; s, Serrat del Rostiar-1, -3; t, Costa de la Coma; u, Serrat del Rostiar-2; v, Magret; w, Basturs Poble, Basturs Est; x, Les Feixes; y, Costa de les Solanes; z, La Llau de la Costa; aa, Els Pous; ab, Les Torres, Les Torres-2; ac, Mare de Déu de l'Àrnec; aç, Barranc de la Costa Gran; ad, Barranc de la Boïga; ae, Basturs-1, -2; af, Lo Bas-1, -2; ag, Euroda Nord; ah, Tossal de Sant Romà; ai, Molí del Baró-1; aj, Molí del Baró-2; ak; Les Llaus; al, Serrat del Corb; am, Planta del Mestre; an, Tossal del Gassó; ao, Sant Romà d'Abella; ap, Costa de Santa Llúcia; aq; Barranc de la Fonguera-1, -2; ar, Isona Sud; as, Julí; at, Coll de Faidella.

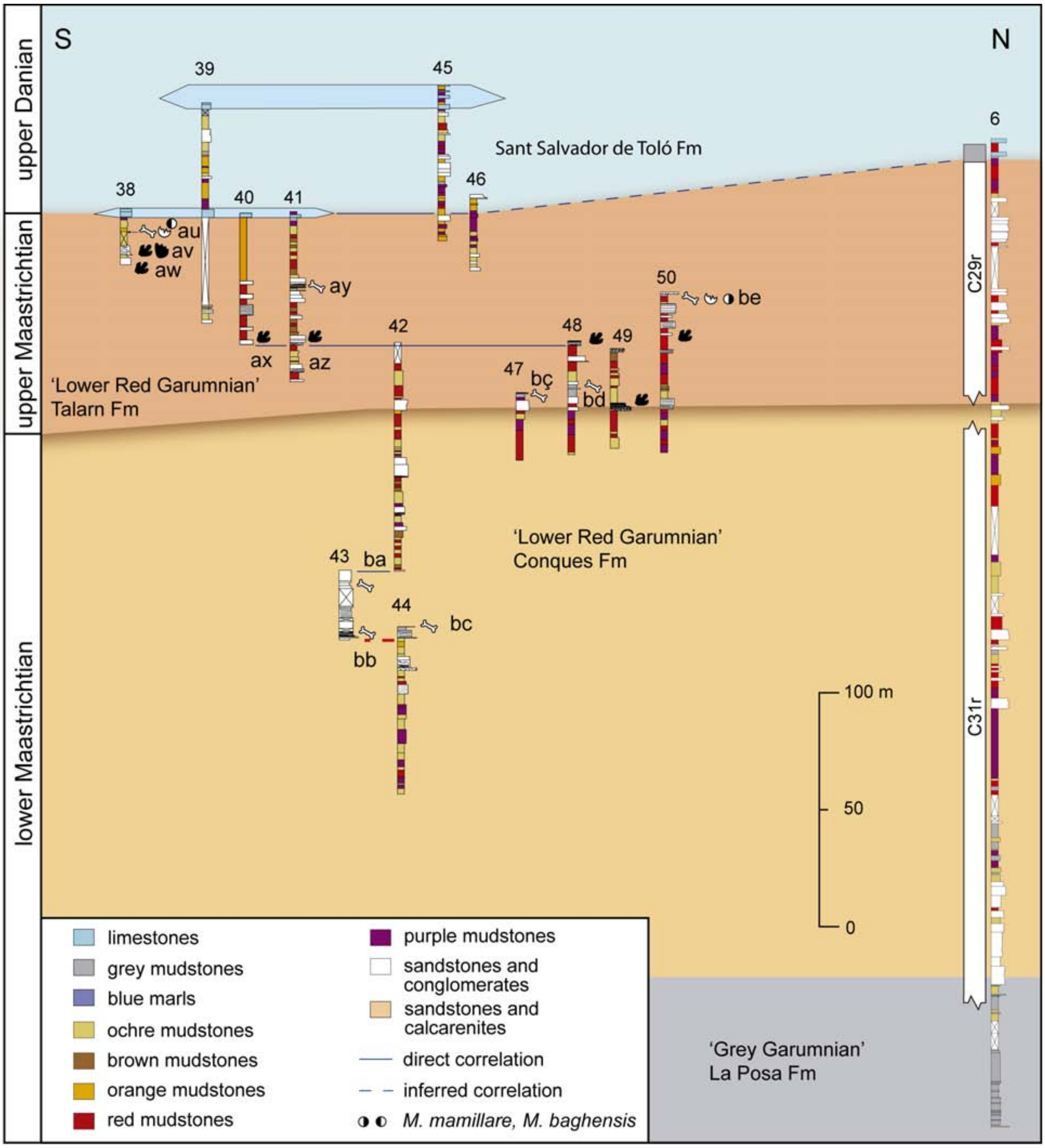


Figure 4. N-S correlation panel of the central sector of the Isona area (Tremp Syncline), with indication of the fossil sites (bones, tracks and egg remains). The megaloolithid oospecies are also indicated. This sector is correlated with

section 6 from the northern sector (Fig. 4). Correlation modified from Riera et al. (2009), Riera (2010) and Vila et al. (2013). Sites: au, Camí del Soldat; av, Barranc de Guixers-2; aw, Barranc de Guixers-1; ax, Barranc de Guixers-3; ay, Masia de Ramon; az, Masia de Ramon petjades; ba, Cabana de Gori-2; bb, Cabana de Gori-1; bc, Costa de Castelltallat; bç, Costa de la Serra-2; bd, Costa de la Serra-1; be, Serrat del Pelleu.

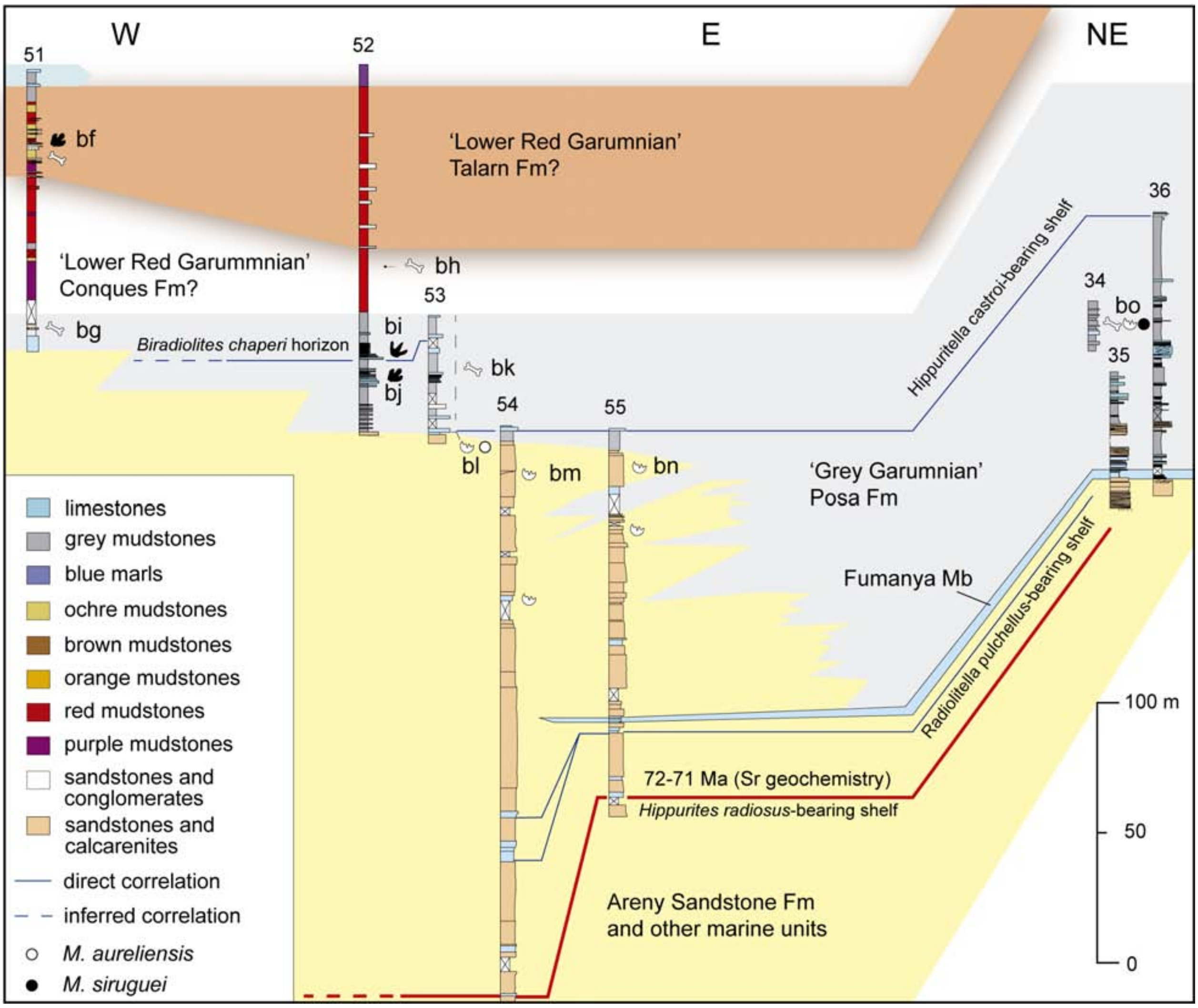


Figure 5. W-E-NE correlation panel of the southern margin of the Tremp syncline, with indication of the fossil sites (bones, tracks and egg remains). The megaloolithid oospecies are also indicated. This sector is correlated with section 36 from Figure 4. Correlation modified from Riera et al. (2009), Riera (2010), López-Martínez and Vicens (2012) and Vila et al. (2013). Sites; bf, Montrebei-1 (Montr-1); bg, Montrebei, Montrebei-2 (Montr-2); bh, L'Estanyó; bi, Moror A; bj, Moror B; bk, Moror; bl, Moror-1; bm, Serrat Pedregós; bn, Urbanització Montsec; bo, Biscarri.

3. Campanian and Maastrichtian dinosaur record of the Ibero-Armorican Island

The taxonomical diversity and temporal distribution of each dinosaur clade from southwestern Europe is presented and discussed here. See Figure 6 and 7 as references for the age calibrations of the key fossil sites and the dinosaur occurrences during the Campanian and the Maastrichtian in the region.

3.1. Hadrosauroids

The hadrosauroid record is very rich in the Maastrichtian deposits of the South- and North-Pyrenean areas (Vila et al., 2016) and consists of body fossils, tracks and spheroolithid egghsells (e.g. Prieto-Márquez et al., 2013; Vila et al., 2013; Sellés et al., 2014a). The lambeosaurine clade is by far the most important taxonomic group of the upper Maastrichtian, with four lambeosaurine species defined to date: *Pararhabdodon isonensis* (Sant Romà d'Abella, eastern Tremp Syncline, chron C29r; Casanovas-Cladellas et al., 1993), *Arenysaurus ardevoli* (Blasi-3, western Tremp Syncline, chron C30n; Pereda-Suberbiola et al., 2009a); *Blasisaurus canudoi* (western Tremp Syncline, chron C30n; Cruzado-Caballero et al., 2010); and *Canardia garonnensis* (Tricouté 3 and Larcan, Haute Garonne, uppermost Maastrichtian, probably the chrons C30n and C29r, respectively; Prieto-Márquez et al., 2013). *Koutalisaurus kohlerorum* was defined in base of a lambeosaurine dentary fragment (Les Llaus, eastern Tremp Syncline, chron C29r; Prieto-Márquez et al., 2006), but was regarded as a *nomen dubium* by Prieto-Márquez and Wagner (2009) and later as an indeterminate lambeosaurine by Prieto-Márquez et al. (2013). The latter authors also identified a maxilla of *P. isonensis* in Serrat del Rostiar-1 (eastern Tremp Syncline, chron C31r), thus expanding the temporal range of this taxon into the early Maastrichtian. Despite this apparent high lambeosaurine diversity, defining new species from fragmentary material has been resulted problematic, being *P. isonensis,* with several changes in its phylogenetic position in the last decade (Casanovas et al., 1999a; Prieto-Márquez et al., 2006 and Prieto-Márquez & Wagner, 2009), a good example of the difficulties involved in interpreting incomplete material and in determining its relationships with other taxa. Taxonomic difficulties are also extensible to the Blasi taxa, given the fact that these species have been defined by non-overlapping diagnostic elements. Hence, *B. canudoi* could be a junior synonym of *A. ardevoli* (Prieto-Márquez et al., 2013). Even, the same situation can be expected for both Arén taxa in respect to *P. isonensis* (Prieto-Márquez et al., 2013).

In addition to lambeosaurines, other hadrosauroid forms inhabited the Ibero-Armorican Island. In this respect, Cruzado-Caballero et al. (2014) identified a distinct euhadrosaurian taxon based on dentary material from Blasi-3.4 (western Tremp Syncline, chron C30n). Casanovas-Cladellas et al. (1999b) described a dentary from Fontllonga-R (uppermost Maastrichtian of the Àger Syncline, chron C29r) and attributed it to a non-hadrosaurid hadrosauroid. In a similar way, Valentin et al.

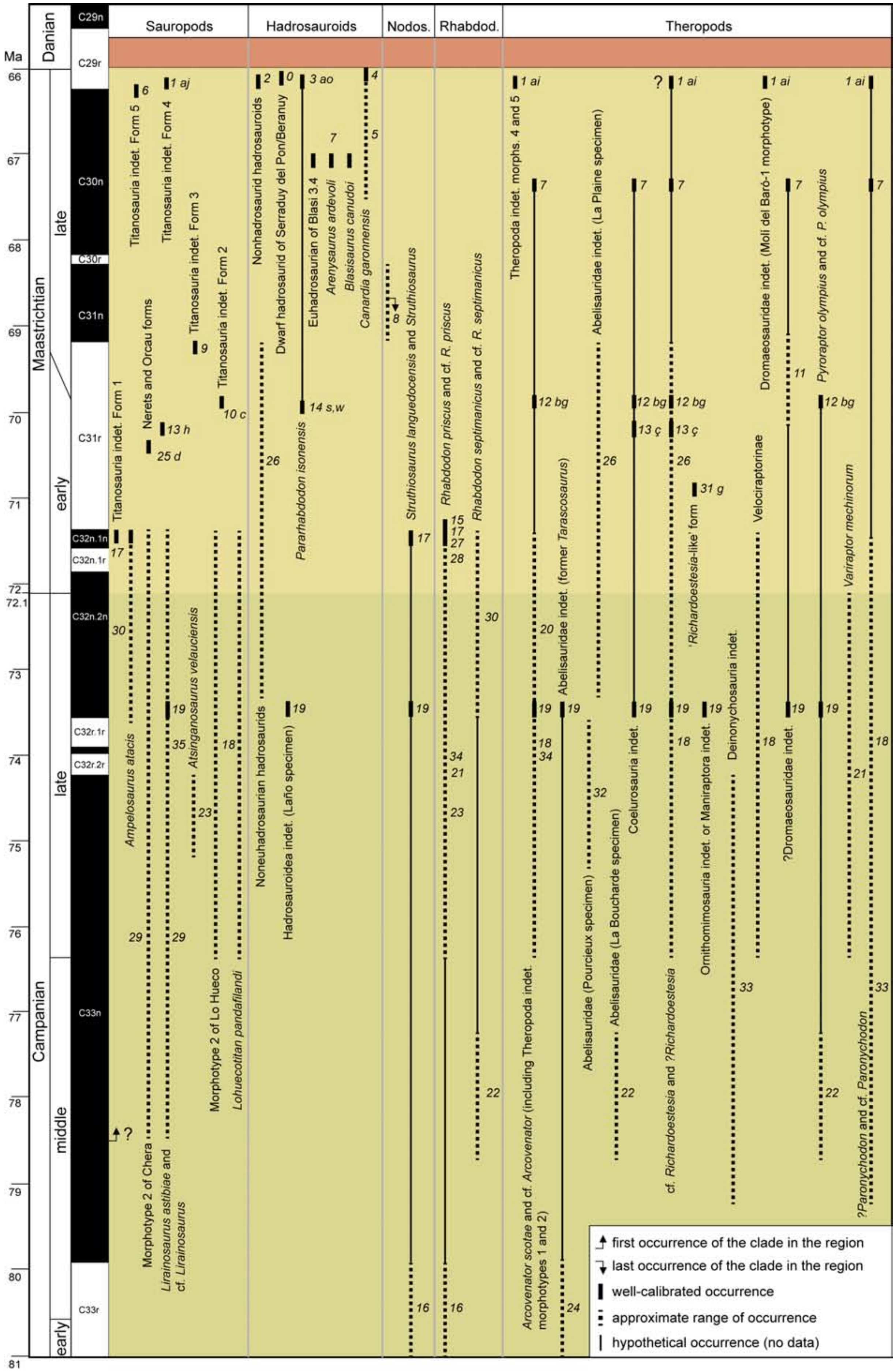
(2012) described dentaries of non-euhadrosaurian hadrosaurids in Vitrolles-La Plaine (Provence; lower to upper Maastrichtian, see below). Company et al. (2015) regarded small hadrosaurid material to a dwarf taxon in Serraduy del Pon and Beranuy (western Tremp Syncline; chron C29r). In a similar way, Blanco et al. (2015) referred a small morphotype of dentaries from Basturs Poble and other sites of the Tremp Syncline to adult individuals of a dwarfed non-hadrosaurid hadrosauroid, but Fondevilla et al. (2015) and V. F. work in progress reveal that these small individuals actually represent juveniles. Company et al. (1998) related a hadrosaurid dentary from La Solana (València, probably the upper Maastrichtian) with lambeosaurines, but Pereda-Suberbiola et al. (2009b) regarded it as a basal hadrosaurid.

The lowermost hadrosauroid bones found in the Tremp Syncline were recovered in the Casa Fabà site (Riera et al. 2009). This fossil locality clearly falls in the lower Maastrichtian (mid-part of the chron C31r, around 71-70 Ma) after the new calibration presented here, challenging a hadrosauroid first appearance restricted to the chron C31n as proposed by Vila et al. (2016). Furthermore, other important fossil sites with hadrosauroids such as Nerets or Basturs Poble also belong to the lower Maastrichtian (mid-part of chron C31r). Outside the Tremp Syncline, there are additional evidences of hadrosauroid occurrences in the chron C31r. One of them are the hadrosauroid-like tracks of Coll de Jou in the Vallcebre Syncline (Bernat Vila, personal communication). Their basal position within the Vallcebre section confirms a lower Maastrichtian age. The hadrosauroid-bearing L'Espinau bonebed of the southern Pyrenean range has been placed within the uppermost part of the chron C31r (Fondevilla et al., under review), although the site belongs to the upper Maastrichtian. In the Upper Aude Valley, some sandstone bodies calibrated with chron C31r show load structures that could represent hadrosauroid tracks (see Fig. 10 in Fondevilla et al., 2016b). According to these examples, the first appearance of the clade becomes older than previously suggested in Vila et al. (2016), at least in the Pyrenean area. Hence, hadrosauroids cannot be considered as a biostratigraphic marker of the upper Maastrichtian as previously concluded Vila et al. (2013). The first bones that can be unambiguously referred to lambeosaurine hadrosaurids come from Basturs Poble, Serrat del Rostiar-1 (Prieto-Márquez et al., 2013) and Costa de les Solanes (Fondevilla et al., 2013), 80 meters above the undetermined hadrosauroid remnants of Casa Fabà (see Fig. 4).

It has been hypothesized that the occurrence of hadrosauroids in the Pyrenean area (and also in the whole Ibero-Armorican Island) corresponds to a dispersal event (e.g. Laurent et al., 1997) in which Asian representatives such as tsintaosaurin and aralosaurin lambeosaurines (*P. isonensis* and *C. garonnensis,* respectively; Prieto-Márquez et al., 2013), but also North American-related forms (*A.*

ardevoli and *B. canudoi;* Cruzado-Caballero et al., 2013; Prieto-Márquez et al., 2013) arrived to the westernmost island of the European archipelago during the Maastrichtian. The basal hadrosauroid forms found in the Pyrenees and Provence areas, common in other Campanian-Maastrichtian landmasses of the archipelago (e.g. *Tethyshadros insularis*, from the Adriatic-Dinaric island, Italy; Dalla Vecchia, 2009) could represent relict forms that inhabited the European archipelago during the Late Cretaceous prior to the arrival of the lambeosaurines (Pereda-Suberbiola, 1999a) in the early Maastrichtian. The occurrence of a single hadrosauroid tooth from the upper Campanian of the Laño site (Condado de Treviño, northern Iberia; Pereda-Suberbiola et al., 2003; Pereda-Suberbiola et al., 2015) has been considered as a proof of the presence of hadrosauroids earlier than the Maastrichtian. In this respect, basal hadrosauroids have been documented in Europe since the Albian-Cenomanian (Company et al., 2009), so the Laño occurrence fits the notion of relict hadrosauroid taxa inhabiting Europe before the Asian and North American lambeosaurine arrival during the early Maastrichtian, as mentioned above. If this scenario is true, these relict hadrosauroids had to be a very rare herbivore clade during the Campanian of southwestern Europe, given the fact that their occurrences are very scarce. An accurate dating of the Vitrolles-La Plaine site should shed light on this proposal, since non-euhadrosaurian hadrosaurids have been recovered there. Tabuce et al. (2013) regarded the site as upper Maastrichtian, but according to the biostratigraphic data of Riveline et al. (1996) and the stratigraphic framework presented in Cojan and Moreau (2006), Vitrolles-La Plaine should be placed in the upper Campanian-lowermost Maastrichtian (Supp. Fig. 1). The basal forms likely evolved separately in each island of the European archipelago by vicariance rather than dispersal events, prior to the arrival of the Asian and American derived representatives as proposed in Pereda-Suberbiola (1999a) and Pereda-Suberbiola et al. (2003).

Finally, the predominance of lambeosaurines in the Pyrenean fossil record suggests that they rapidly occupied all paleoenvironments (the coastal and inland areas) and became the main herbivore group, but some basal hadrosauroid forms remained until the K-Pg extinction (e.g. the Fontllonga-R specimen).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Danian
Maastrichtian
Campanian
late
early
late
middle
early
C29n
C29r
C30n
C30r
C31n
C31r
C32n.1n
C32n.1r
C32n.2n
C32r.1r
C32r.2r
C33n
C33r
Sauropods
Hadrosauroids
Nodos.
Rhabdod.
Theropods
Titanosauria indet. Form 5
Titanosauria indet. Form 4
Titanosauria indet. Form 3
Titanosauria indet. Form 2
Titanosauria indet. Form 1
Nerets and Orcau forms
Ampelosaurus atacis
Atsinganosaurus velauciensis
Morphotype 2 of Chera
Lirainosaurus astibiae and cf. Lirainosaurus
Morphotype 2 of Lo Hueco
Lohuecotitan pandafilandi
Nonhadrosaurid hadrosauroids
Dwarf hadrosaurid of Serraduy del Pon/Beranuy
Euhadrosaurian of Blasi 3,4
Arenysaurus ardevoli
Blasisaurus canudoi
Canardia garonnensis
Pararhabdodon isonensis
Noneuhadrosaurian hadrosauroids
Hadrosauroidea indet. (Laño specimen)
Struthiosaurus languedocensis and Struthiosaurus
Rhabdodon priscus and cf. R. priscus
Rhabdodon septimanicus and cf. R. septimanicus
Theropoda indet. morphs. 4 and 5
Arcovenator scotae and cf. Arcovenator (including Theropoda indet. morphotypes 1 and 2)
Abelisauridae indet. (former Tarascosaurus)
Abelisauridae indet. (La Plaine specimen)
Abelisauridae (Pourcieux specimen)
Abelisauridae (La Boucharde specimen)
Coelurosauria indet.
cf. Richardoestesia and ?Richardoestesia
'Richardoestesia-like' form
Ornithomimosauria indet. or Maniraptora indet.
Deinonychosauria indet.
Dromaeosauridae indet. (Molí del Baró-1 morphotype)
Velociraptorinae
?Dromaeosauridae indet.
Pyroraptor olympius and cf. P. olympius
Variraptor mechinorum
?Paronychodon and cf. Paronychodon
1 aj
1 ai
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25 d
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31 g
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first occurrence of the clade in the region
last occurrence of the clade in the region
well-calibrated occurrence
approximate range of occurrence
hypothetical occurrence (no data)

Figure 6. Dinosaur succession of the Campanian-Maastrichtian from the Ibero-Armorican Island (southwestern Europe), with indication of the temporal occurrence of the main fossil sites. See Table 1 for taxonomic and chronostratigraphic references. Those sites from the Tremp Syncline include also the codes (letters) used in Figures 4, 5 and 6. Sites: *0*, Serraduy del Pon/Beranuy; *1 ai*, Molí del Baró-1, -2; *2*, Fontllonga-R; *3 ao*, Sant Romà d'Abella; *4*, Larcan; *5*, Tricouté 3; *6*, Serraduy; *7*, Blasi-1,-2,-3; *8*, Lestaillats; *9*, Peguera-1; *10 c*, Presa de Sant Antoni; *11*, Figuerola-2; *12 bg*, Montrebei; *13 h*, Els Nerets; *13 ç*, Vicari-4; *14 s*, Serrat del Rostiar-1; *14 w*, Basturs Poble; *15*, Gourg de l'Encantado; *16*, Villeveyrac-Meze; *17*, Bellevue; *18*, Lo Hueco, Armuña and Sacedón; *19*, Laño; *20*, Jas Neuf; *21*, Fox Amphoux; *22*, Trets-La Boucharde; *23*, Velaux-La Bastide Neuve; *24*, Le Beausset; *25 d*, Orcau-1; *26*, Vitrolles-La Plaine; *27*, Albières; *28*, Vitrolles-Couperigne; *29*, Chera; *30*, Cruzy; *31 g*, Suterranya-1 (L'Abeller); *32*, Porcieux; *33*, La Neuve; *34*, Armuña; *35*, Sacedón. Standard scale after Ogg and Hinnov (2012).

3.2. Ankylosaurians

Fossil remains of ankylosaurians are relatively common in the Campanian-Maastrichtian of southwestern Europe, being present in several fossil sites from Spain and southern France (see Vila et al., 2016 and references therein). Only the *Struthiosaurus languedocensis* has been defined to date, in the lower Campanian of Villeveyrac (Languedoc area, chron C33r; Garcia and Pereda-Suberbiola, 2003). Some specimens have been referred to *Struthiosaurus* sp. (e.g. in the La Nerthe and Laño sites, from southern France and Basque Country, respectively; Lapparent, 1947; Pereda-Suberbiola et al., 2000). The species *Taveirosaurus costai* (Taveiro, Portugal, upper Campanian to Maastrichtian; Antunes and Sigogneau-Russell, 1991) was related with pachycephalosaurs, with basal ornithischians (fabrosaurids; Galton, 1996) and later with nodosaurids (Antunes and Sigogneau-Russell, 1996) but was regarded as *nomen dubium* by Pereda-Suberbiola (1999b) due to the lack of diagnostic characters.

Most of the recovered remains have been referred to indeterminate nodosaurids, ankylosaurians or thyreophorans (e.g. Pereda-Suberbiola, 1992; Laurent et al., 2001; Buffetaut, 2005). In the lower Maastrichtian of the Tremp Syncline, remains attributed to ankylosaurians are limited to an isolated tooth in Biscarri (López-Martínez et al., 2000), appendicular bones in Suterranya-Mina de lignit (Escaso et al., 2010) and armor plates in Els Nerets (Santafé et al., 1997). The last occurrence of the group in the whole Ibero-Armorican Island is located in the Lestaillats site from the upper Maastrichtian of Haute Garonne (Laurent et al., 2002). This confirms a prolonged interval of coexistence of about 1-1.5 Ma between ankylosaurians and the new lambeosaurine immigrants, contradicting a rapid decline of the clade after the arrival of the new hadrosaurid forms (see Fig. 6).

3.3. Rhabdodontid ornithopods

Two species of rhabdodontid ornithopods have been defined to date. First species is *Rhabdodon priscus,* such as in the lower Campanian of Villeveyrac (Buffetaut et al., 1996), in the middle-late Campanian of Chera in València (Company et al., 2005), in the late Campanian of Armuña in Segovia (Pérez-García et al., 2016), in the upper Campanian-lower Maastrichtian of Fox Amphoux (Lapparent, 1947; de Broin et al., 1980), and in the lowermost Maastrichtian of Bellevue in Aude (Le Loeuff, 2005; Fondevilla et al., 2016b). The other species is *Rhabdodon septimanicus*, which has a more limited temporal range, being found in the mid-Campanian of La Boucharde, in Provence (Chanthasit, 2010) and the Campanian-Maastrichtian sites of Quarante and Montouliers in Cruzy, Hérault (Lapparent, 1947; Chanthasit, 2010 and references therein).

The last apparition of rhabdodontids is not well established. They occur in Vitrolles-La Plaine (Valentin et al., 2012), a site though to be upper Maastrichtian, but as explained above, it can be much older (upper Campanian or lowermost Maastrichtian). Interestingly, the rhabdodontid remains from Vitrolles-La Plaine were found together with non-lambeosaurine hadrosaurid dentaries, although the authors commented that rhabdodontid material could represent reworked elements from older rocks. In the Pyrenean area, the uppermost rhabdodontid evidence is a single tooth from Figuerola-2 (Llompart & Krauss, 1982), but its age is not well established. In any case, rhabdodontids seem to disappear from southwestern Europe earlier than ankylosaurians.

3.4. Titanosaurian sauropods

Titanosaurian sauropods have a continuous record from the middle-Campanian to the very end of the Maastrichtian (Vila et al., 2012; Sellés et al., 2016; Fondevilla et al., 2016c), with several occurrences in form of bones, tracks, eggshells and clutches, and even skin impressions (e.g. Garcia and Vianey-Liaud, 2001; Vila et al., 2005, 2012, 2013; Sellés et al., 2013, 2016; Díez-Díaz et al., 2015; Fondevilla et al., 2016c). Le Loeuff (1993) argued in favor of a post-Cenomanian titanosaurian extinction in order to explain the early Campanian gap in the Ibero-Armorican Island (see Fig. 6). However, Buffetaut et al. (1997) commented that this titanosaurian absence could correspond to a sampling bias instead of a hiatus.

The titanosaurian record from southwestern Europe is especially rich during the middle-late Campanian and the earlymost Maastrichtian, with four defined species to date: *Ampelosaurus atacis*

(Bellevue, Aude, chron C32n.1n; Le Loeuff, 1995), *Lirainosaurus astibiae* (Laño, Condado de Treviño, chron C32n.2n; Sanz et al., 1999), *Atsinganosaurus velauciensis* (Velaux-La Bastide Neuve, Provence, chron C33n; Garcia et al., 2010) and *Lohuecotitan pandafilandi* (Lo Hueco, Cuenca, likely the upper Campanian or the lower Maastrichtian; Díez Díaz et al., 2016). In addition, Vila et al. (2012) described a titanosaurian morphotype that probably represents a different taxon in Bellevue (Titanosauria indet. Form 1) and Díez Díaz et al. (2015) announced the presence of two additional morphotypes in Lo Hueco and Chera. This Campanian-lowermost Maastrichtian titanosaurian assemblage has been regarded as the producer of the oospecies *Megaloolithus aureliensis* and *M. siruguei* (since Chiappe et al., 1998 related the megaloolithid eggs to titanosaurians), as well as *Cairanoolithus roussetensis* and *C. dughii* (Sellés and Vila, 2015). Sellés and Galobart (2016) argued, however, that the *Cairanoolithus* oogenus was produced by ankylosaurians. According to Garcia and Vianey-Liaud (2001) and Sellés et al. (2013), the diverse megaloolithid and cairanoolithid assemblage found in the chrons C33n and C32n was followed by only one oospecies (*M. siruguei*) during the chron C31r in the region. This suggests a decreasing of the titanosaurian richness during the early Maastrichtian (but see below). The four titanosaurians described in Vila et al. (2012) (Titanosauria indet. Forms 2-5) were considered as the probable producers of *M. mamillare* and *M. baghensis* assemblage, thus representing the new titanosaurian forms after the faunal turnover.

According to the new calibration of Figures 3, 7 and 8, *Megaloolithus mamillare* and *M. baghensis* have a first appearance in the lower part of the chron C31r, around 71 Ma (e.g. in the fossil sites of Basturs-1 and -2; Fig. 5). This fact is against the former scheme of of Vila et al. (2011) and Sellés and Vila (2015), who considered that these oospecies did not appear until the upper Maastrichtian (around the C31r-C30n reversal). So that, the titanosaurian producers of *M. mamillare* and *M. baghensis* appeared in the lower Maastrichtian of southwestern Europe prior to the arrival of the lambeosaurine hadrosaurids. In the stratigraphic succession of the Isona sector, this difference is represented by at least 100 meters between the first *M. mamillare* and the first hadrosauroid remains, and 180 m considering the first unequivocal lambeosaurines (around one million year earlier following the sedimentary rates calculated in Fondevilla et al., 2016a; Fig. 3). Therefore, the dispersal events (e.g. the arrival of new titanosaurians and lambeosaurine hadrosaurids) that triggered the faunal turnover were not time-coincident between the different dinosaur clades.

3.5. Theropods

The theropod record from southwestern Europe is abundant and diverse, with several different taxa recognized to date (Fig. 6). However, in contrast with the former groups, theropod remains usually consist on isolated teeth, being cranial and postcranial remains much scarce. Small dromeosaurids are the most common representatives, with *Pyroraptor olympius* (Trets-La Boucharde, middle Campanian, probably within the chron C33n; Allain and Taquet, 2000) as the most complete specimen recovered to date. Another species, *Variraptor mechinorum* (Fox-Amphoux and Cruzy, Provence and Hérault; probably in the chrons C33n or C32n; Le Loeuff and Buffetaut, 1998) was considered as *nomen dubium* by Allain and Taquet (2000), but later was regarded as a valid taxon by Chanthasit and Buffetaut (2009). These authors also considered that *P. olympius* and *V. mechinorum* taxa could represent a single species due to the lack of overlapping elements. Torices et al. (2015) expanded the temporal range of the *Pyroraptor* genus to around the lower-upper Maastrichtian boundary by describing dental material from the Montrebei site (Tremp Syncline, probably in the upper part of chron C31r). These last authors also identified teeth of a distinct dromeosaurid morphotype (Dromeosauridae indet.), coelurosaurians (Coelurosauridae indet.) and the genus *Richardoestesia* in Campanian and Maastrichtian sites of the Pyrenees and Laño. The latter genus was also found in Vitrolles-La Plaine and Lo Hueco (Valentin et al., 2012; Ortega et al., 2015). Troodontid teeth of the genus *Paronychodon* have been found in Blasi 2B, Molí del Baró-1 (Tremp Syncline, C29r), Lo Hueco and La Neuve (Provence, upper Campanian) (Garcia et al., 2000; Torices et al., 2015; Ortega et al., 2015; Marmi et al., 2016). Marmi et al. (2016) also described different morphotypes of indeterminate theropods, dromeosaurids and a morphotype similar to *Richardoestesia* in the uppermost Maastrichtian site of Molí del Baró-1. A tooth from Suterranya-1 (Tremp Syncline, chron C31r) that was first referred as "*Richardoestesia*-like" (Prieto-Márquez et al., 2000) was later considered to be an indeterminate theropod by Torices et al. (2015). Other authors referred teeth material to indeterminate velociraptorines in Lo Hueco (Ortega et al., 2015) and deinonychosaurians in La Neuve (Buffetaut et al., 1986).

Concerning large theropods, the fossil record of the Ibero-Armorican Island is very fragmentary and scarce, and often lacks diagnostic characters. For example, *Tarascosaurus salluvicus* (Beausset Syncline, Bouches-du-Rhône, lower Campanian; Le Loeuff and Buffetaut 1991; Tortosa et al., 2014) was regarded as a ceratosaurian abelisaurid, as a *nomen dubium* (Allain and Pereda-Suberbiola, 2003; Rauhut, 2003) and as an Abelisauroidea *incertae sedis* (Carrano and Sampson, 2008). Later, Tortosa et al. (2014) considered the material to Abelisauridae. In addition, these last authors identified a considerable diversity of abelisaurids in the Campanian-Maastrichtian of the Provence area, including *Arcovenator scotae* from Pourrieres-Jas Neuf (chron C32n), the most complete specimen of the family found southwestern Europe so far. However, they suggested that some specimens could belong to the same genus, e.g. the Pourcieux abelisaurid could be *Arcovenator*. Concerning this taxon, Pérez-García et al. (2016) referred material previously classified as Theropoda indet. morphotypes 1 and 2 (see Torices et al., 2015) in the southern Pyrenees, Laño and Armuña as cf. *Arcovenator.* Thus, the temporal range of the genus *Arcovenator* likely spans from the middle Campanian to the late Maastrichtian as shows Figure 6.

Antunes and Sigogneau-Russell (1991) defined the species *Euronychodon portucalensis*, now considered a synonym of *Paronychodon* (Rauhut, 2002), in the Campanian-Maastrichtian site of Taveiro (Portugal). In addition, Antunes and Sigogneau-Russell (1992) identified seven morphotypes of theropod teeth in Aveiro, Taveiro and Viso.

Despite some possible synonyms, at least eight different theropod taxa have been identified in the Pyrenean area and Iberia during the Campanian-Maastrichtian (Torices et al., 2015), but this number could increase if we consider the Molí del Baró-1 assemblage (see Marmi et al., 2016) and the abelisaurid specimens of Tortosa et al. (2014) from France. The theropod record shows no evidence of any significant faunal change between the early and the late Maastrichtian. In this respect, most of the genus present in the upper Maastrichtian have also been found in the upper Campanian and the lowermost Maastrichtian (e.g. *Richardoestesia*, *Paronychodon* and *Arcovenator*). However, Sellés et al. (2014b) identified a gradual change between theropod ooassemblages (i.e. a replacement between prismoathoolitid oospecies) around the upper part of the lower Maastrichtian. The significance of this shift and their possible taxonomical implications is unclear given the apparent stasis in the theropod diversity during the Maastrichtian of southwestern Europe.

4. Implications for biostratigraphy and sauropod distribution

Vianey-Liaud and Garcia (2000) and Garcia and Vianey-Liaud (2001) defined three different ooassemblages with a potential biostratigraphic use for the Maastrichtian deposits of southwestern Europe. Their proposal was based on the occurrences of the megaloolithid and cairanolithid oopecies in southern France.

As mentioned above, an upper Campanian-lowermost Maastrichtian ooassemblage or oozone consisting of *Megaloolithus aureliensis, M. petralta*, *M. siruguei, Cairanoolithus dughii* and *C. rousetensis* was established. Later, *M. petralta* was regarded as a synonym of *M. aureliensis* by Sellés et al. (2013). Succeeding this assemblage, most of the lower Maastrichtian (chron C31r) was characterized by containing only *M. siruguei*. Then, an ooassemblage composed of *M. mamillare* and *M. pseudomamillare* (later referred to *M. baghensis,* see Sellés et al., 2013) was considered characteristic of the upper Maastrichtian. Vila et al. (2011) developed this biostratigraphy for the deposits of the Vallcebre Syncline in the southern Pyrenees, and later Sellés et al. (2013) and Sellés and Vila (2015) attempted to provide age calibrations to some sites and sections of the Coll de Nargó and Tremp Synclines. Recently, eggshell material has been used to better constrain the magnetostratigraphic results of the Aude area (see Fondevilla et al. 2016b).

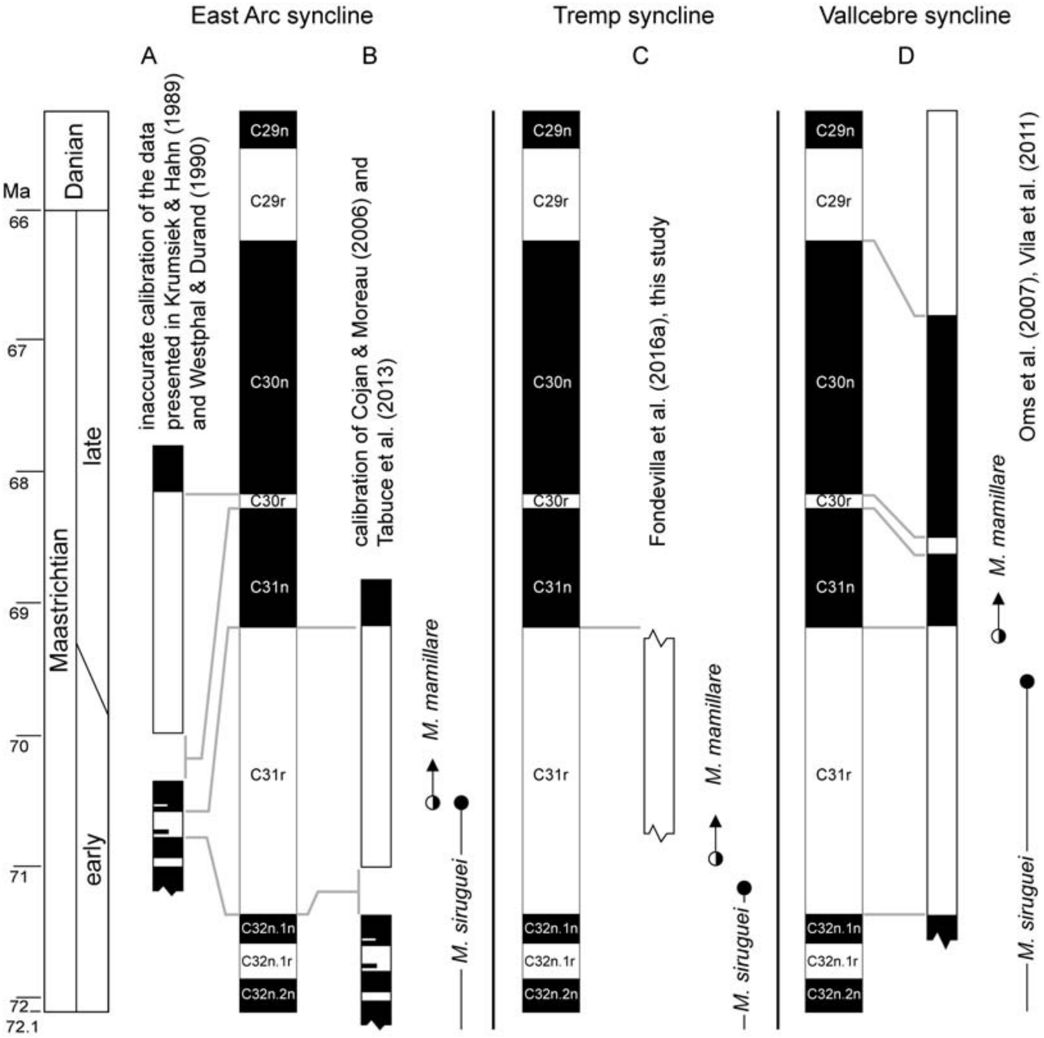


Figure 7. Calibrated stratigraphic ranges of *Megaloolithus siruguei* and *M. mamillare* in different areas of southwestern Europe, showing a diachronic replacement between the oospecies. **A**, inaccurate calibration of the East Arc Syncline of Krumsiek & Hahn (1989) and Westphal and Durand (1990), reproduced in Vianey-Liaud and Garcia (2000) and Garcia

and Vianey-Liaud (2001). **B**, paleomagnetic data after Krumsiek and Hahn (1989), Cojan and Moreau (2006) and Tabuce et al. (2013). **C**, chronostratigraphy of the Tremp Syncline after Fondevilla et al. (2016a) and this study. **D**, chronostratigraphy of the Vallcebre Syncline after Oms et al. (2007) and Vila et al. (2011). Standard scale after Ogg and Hinnov (2012).

However, the original proposal of Vianey-Liaud and Garcia (2000) and Garcia and Vianey-Liaud (2001), developed mainly in the Provence record, presents a major problem. In the East Arc Syncline, these authors followed the magnetostratigraphic calibration of Westphal and Durand (1990), who correlated a long reverse polarity zone of about 30-40 meters (originally found by Krumsiek and Hahn, 1989 above the Rognac limestone) with the short chron C30r of the upper Maastrichtian (Fig. 7A; see also fig. 15 in Vianey-Liaud and Garcia, 2000). Also, they considered a very short reverse zone of less than 10 meters as the long chron C31r of the early Maastrichtian. Thus, according to their correlation, *M. mamillare* appeared in the upper Maastrichtian (chron C31n), so it could be used as a biostratigraphic marker of that age. However, Cojan and Moreau (2006) revisited and improved the available paleomagnetic data from the East and West Arc Synclines and emended the previous interpretation of Westphal and Durand (1990). Hence, Cojan and Moreau (2006) correlated the long reverse zone of Krumsiek and Hahn (1989) with C31r (a long chron that spans about 2.1 million years af the early Maastrichtian, see Fig. 7B). This interpretation is considered here much more stronger than the original of Westphal and Durand (1990). Following this improved correlation, the chronostratigrafic panel of the Arc Syncline presented in Tabuce et al. (2013) clearly shows that *M. mamillare* first appeared in the lower part of chron C31r (Fig. 7B), in a similar stratigraphic position than in the Tremp Syncline (Fig. 7C). Nevertheless, Tabuce et al. (2013) authors still considered *M. mamillare* as indicative of an upper Maastrichtian age. Now, the new chronostratigraphy of the Tremp Syncline shows that this oospecies appeared in the lower Maastrichtian (see Fig 3 and 7). Regarding the West Arc Syncline, the calibration is more challenging due to some ambiguous paleomagnetic results. If the correlation proposed by Cojan and Moreau (2006) is correct, the first occurrence of *M. mamillare* is even older in that sector, being present in the upper Campanian-lowermost Maastrichtian (Supp. Fig. 1).

Following the dating of the Tremp Syncline presented by Díez-Canseco et al. (2014) and Fondevilla et al. (2016a), and the amended magnetostratigraphic dating of the Arc Syncline in Provence, a new proposal of eggshell biostratigraphy for southwestern Europe can be developed (see Fig. 7 and 8):

1) The ooassemblage composed of *Cairanoolithus dughii* and *C. roussetensis* is restricted to chrons C33n, C32r and C32n (but possibly present in the lowermost part of chron C31r). Hence, this ooassemblage seems to be characteristic of the middle-upper Campanian and the lowermost Maastrichtian. However, Sellés and Galobart (2016) related the oofamily Cairanolithidae with ankylosaurians, so findings of these eggshell material can be expected until the basal upper Maastrichtian (coinciding with the last occurrence of ankylosaurians in southwestern Europe). In consequence, cairanolithids can be only used to discard terminal Maastrichtian deposits (e.g. the chron C29r).

2) The ooassemblage composed by *Megaloolithus mamillare* and *M. baghensis* ranged from chron C31r (but possibly earlier) to the end-Maastrichtian. Since their first appearance is not isochronous and varies depending on the considered area (Figs. 7 and 8) they are not useful to discriminate between the lower and the upper Maastrichtian. Hence, they lose any potential biostratigraphic use. On the contrary, *M. siruguei* never appears in the chrons C31n, C30r, C30n and C29r, so its presence in a rock succession can be used to discard a late Maastrichtian age, in a similar way than cairanoolithid eggshells.

Taking into account the new temporal ranges of the oospecies, the results presented in Fondevilla et al. (2016b) in the Upper Aude Valley must be revisited. The correlation of a normal-reverse polarity sequence with the chrons C32n and C31r was sustained by the occurrence of *Cairanoolithus* oospecies and non-terminal Maastrichtian charophytes in the stratigraphic succession. According to the points announced above, this main correlation can be considered valid. However, the late Maastrichtian age inferred in the upper part of the section on the basis of the presence of *M. mamillare* is no longer supported as discussed above.

The diachronic appearance of *Megaloolithus mamillare* and *M. baghensis* in each sector of the Ibero-Armorican Island have implications in the local sauropod paleobiogeography during the Maastrichtian. In this respect, the Pyrenean area is very illustrative of a space partition between sauropod groups (Fig. 8). During the early stages of the chron C31r, *M. mamillare* and *M. baghensis* (and their producers) appeared in the Tremp Syncline but were absent in Coll de Nargó, Vallcebre and the Upper Aude Valley. At the same time, *M. siruguei* disappeared from the former area but persisted in the latters. Finally, around the early-late Maastrichtian boundary, *M. siruguei* become extinct in all areas and that space was occupied by the producers of *M. mamillare* and *M. baghensis.* This situation could reflect a habitat partition between different sauropod assemblages, who might compete for nesting areas. Hence, the producers of *M. siruguei* were first displaced and expulsed from the Tremp Syncline, which became the main nesting area for the new titanosaurian immigrants in the Ibero-Armorican Island.

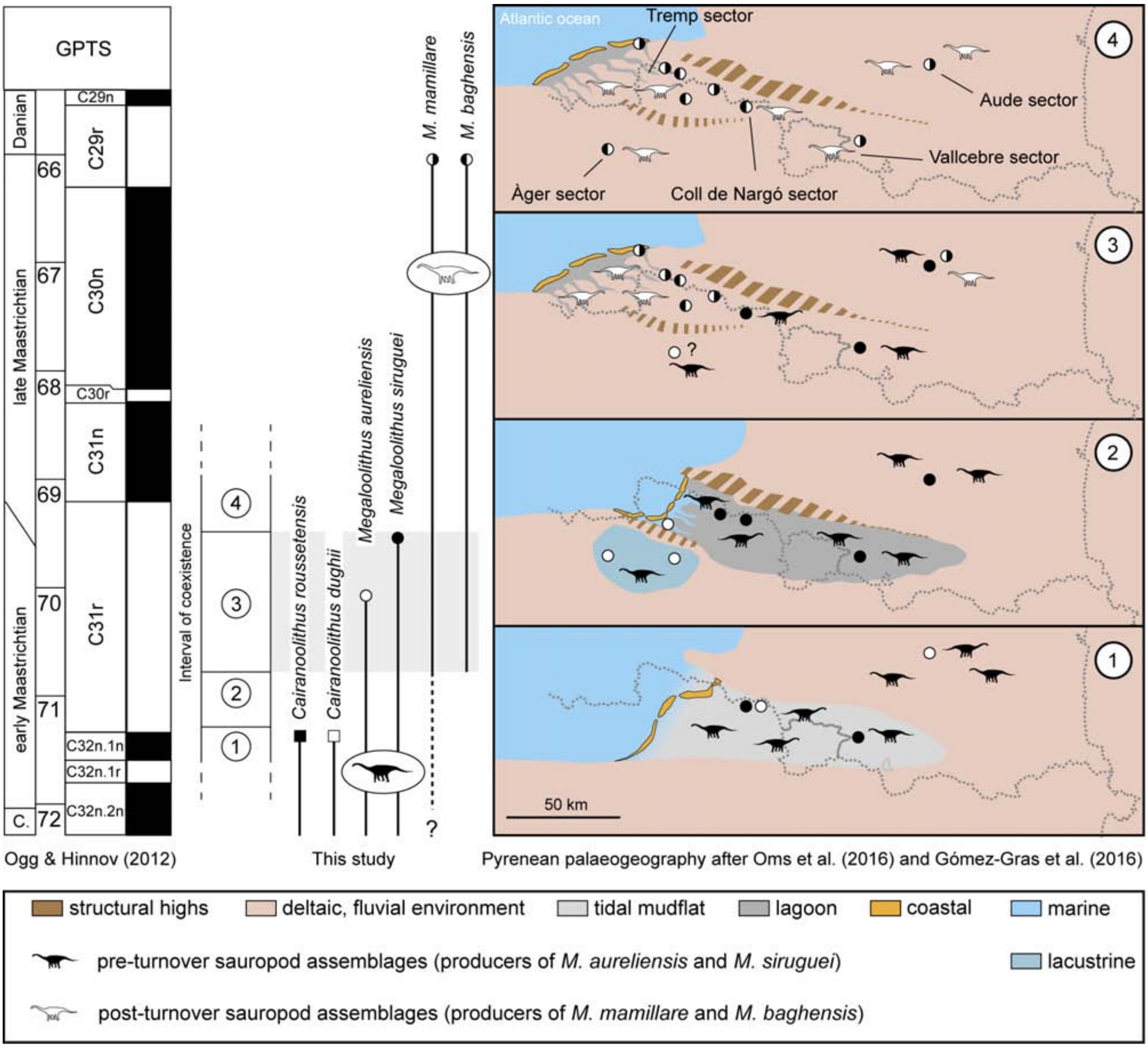


Figure 8. New refinements on the temporal and spacial distribution of the megaloolithid and cairanolithid oospecies. Standard scale after Ogg and Hinnov (2012).

The age calibration of the West and East Arc Synclines presented in Cojan et al. (2006) (see Supp. Fig. 1) also shows a diachronism in the apparition of *M. mamillare*. If the ages presented by these authors are true, then this habitat partition between the producers of *M. siruguei* and *M. mamillare* also occurred in Provence.

This hypothesis is still tentative, but there are tools to test it. Riera et al. (2013) studied the C and O isotopic composition of different megaloolithid eggshells from the Vallcebre and Coll de Nargó Synclines, which is a reflect of the food and water consumed by the animals during the oogenesis (e.g. Cojan et al., 2013). These authors found a similar isotopic signal for *M. siruguei, M. mamillare* and *M. baghensis*, suggesting that the titanosaurian producers had a similar diet. This fact seems to agree with a competence for food resources between titanosaurian assemblages that resulted in a habitat partition during the chron C31r. However, the values shown in Riera et al. (2013) for *M. mamillare* and *M. baghensis* were obtained from a very small sample. Hence, a more detailed isotopic study should be conducted in the future.

5. Conclusions

The new Campanian-Maastrichtian dinosaur succession presented here (Fig. 6) amends the timing and duration of the faunal turnover that took place in southwestern Europe during the Maastrichtian. New chronological and geological data indicate that the faunal changes that took place from the early to the late Maastrichtian involved a prolongued interval of coexistence rather than a rapid faunal replacement as previously postulated by Le Loeuff (1994a) and Vila et al. (2016). The episodes of extinction and new appearances (likely immigrant arrivals) took place diachronously for each main taxonomic group during the Maastrichtian. These changes or events can be summarized as follows (Figs. 6, 7 and 8):

- The Campanian and the earlymost Maastrichtian (until chron C32n) of the Ibero-Armorican Island was dominated by titanosaurian sauropods -producers of the oospecies *M. aureliensis* and *M. siruguei*-, ankylosaurians, rhabdodontids and small and medium-sized theropods. Hadrosauroids seem to be extremely rare during this period.

- During the first stages of the chron C31r (around 71 Ma), new titanosaurian sauropods - producers of *M. mamillare* and *M. baghensis*- arrived to the island. New and older sauropod forms cohabited the region (but presumably did not inhabited the same local areas) until the end of the early Maastrichtian (around 70-69 Ma). Then, producers of *M. siruguei* finally disappeared.

- Around 70 Ma (mid-part of chron C31r, still in the early Maastrichtian) lambeosaurine hadrosaurids first appeared in southwestern Europe and rapidly became the main herbivore group of the whole region. Rhabdodontid dinosaurs disappeared no long before this moment.

- Ankylosaurians became extinct probably during chron C31n (around 69 Ma), coexisting with lambeosaurine hadrosaurids for about 2 Ma.

- The theropod taxa appear to be unafected by any major change during this time interval. Thus, most of the Campanian forms were still present during the late Maastrichtian in the Ibero-Armorican Island.

Migration episodes took place in at least two different waves (new titanosaurian sauropods and later lambeosaurine hadrosaurids) separated by around one million year. Despite the new scenario of replacement presented here, the general observations and conclusions presented in Vila et al. (2016), concerning the structures of the herbivore dinosaur communities and their taxonomic diversity before and after the turnover, are essentially valid.

Table 1. List of dinosaur taxa used in Figure 6, with references for taxonomy and ages. This table is modified from Sellés et al. (2014). Most of the references have been taken from Vila et al. (2016).

Theropods

Taxa	Localities (may include multiple sites)	References	References for age
Arcovenator escotae cf. *Arcovenator*	Armuña (Spain; late Campanian)	Pérez-García et al., 2016	Pérez-García et al., 2016
	Pourrières-Jas Neuf (France; late Campanian - early Maastrichtian)	Tortosa et al., 2014	Tortosa et al., 2014
	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Ortega et al., 2015	Ortega et al., 2015
Theropoda indet. Morph. 1-2	Montrebei (Spain; early-late Maastrichtian -C31r-) Blasi (Spain; late Maastrichtian -C30n-)	Torices et al., 2015	Pereda-Suberbiola et al., 2009a; this study
Abelisauridae indet. (La Plaine specimen)	Vitrolles-La Plaine (France; early-late Maastrichtian -C31r-)	Valentin et al., 2012; Tortosa et al., 2014	Tabuce et al., 2013; Tortosa et al., 2014, see Supp. Fig. 1
Abelisauridae indet. (La Boucharde specimen)	La Boucharde (France; mid-Campanian; -C33n-)	Tortosa et al., 2014	Tortosa et al., 2014
Abelisauridae indet. (Porcieux specimen)	Porcieux (France; late Campanian; -C33n to C32r-)	Tortosa et al., 2014	Tortosa et al., 2014
Abelisauroidea *incertae sedis*, (*Tarascosaurus salluvicus*)	Villeveyrac (France; early Campanian - mid-Campanian -C33r-)	Le Loeuff and Buffetaut, 1991	Benammi et al., 2006; Tortosa et al., 2014;
Tarascosaurus sp.	Laño (Spain; late Campanian -C32n.2n-)	Pereda-Suberbiola et al., 2015	Corral et al., 2016
cf. *Paronychodon*	La Neuve (France; mid-Campanian -C33n-)	Garcia et al., 2000	Garcia et al., 2000
	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Ortega et al., 2015	Ortega et al., 2015
	Blasi-2B (Spain; late Maastrichtian -C30n-)	Torices et al., 2015	Pereda-Suberbiola et al., 2009a
	Molí del Baró-1 (Spain; late Maastrichtian -C29r-)	Marmi et al., 2016	Marmi et al., 2016
Euronychodon portucalensis	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1991	Antunes and Sigogneau-Russell, 1991

Coelurosauria indet.	Laño (Spain; late Campanian -C32n.2n-)	Torices et al., 2015	Corral et al., 2016
	Vicari-4 (Spain; early Maastrichtian -C31r-)	Torices et al., 2015	This study; Fondevilla et al., 2016a
	Montrebei (Spain; early-late Maastrichtian -C31r-)	Torices et al., 2015	This study
	Blasi-2B (Spain; late Maastrichtian -C30n-)	Torices et al., 2015	Pereda-Suberbiola et al., 2009a Torices et al., 2015
aff. Coeluridae indet. A	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
aff. Coeluridae indet. B	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
aff. Coeluridae indet. C	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
Deinonychosauria indet.	La Neuve (France; mid-Campanian -C33n-)	Buffetaut et al., 1986	Garcia et al., 2000
cf. Dromaeosauridae indet.	Laño (Spain; late Campanian -C32n.2n-)	Torices et al., 2015	Corral et al., 2016
	Fontllonga-6 (Spain; early-late Maastrichtian)	Torices et al., 2015	Torices et al., 2015
	Figuerola-2 (Spain; early-late Maastrichtian)	Torices et al., 2015	Torices et al., 2015
	Blasi (Spain; late Maastrichtian -C30n-)	Torices et al., 2015	Pereda-Suberbiola et al., 2009a
Dromaeosauridae indet. (Portugal)	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
Dromaeosauridae indet. (Molí del Baró-1 specimen)	Molí del Baró (Spain; late Maastrichtian -C29r-)	Marmi et al., 2016	Marmi et al., 2016
Velociraptorinae indet.	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Ortega et al., 2015	Ortega et al., 2015
Pyroraptor olympius cf. *Pyroraptor olympius*	Trets-La Boucharde (France; middle Campanian)	Allain and Taquet, 2000	Tortosa et al., 2014
	Laño (Spain; late Campanian -C32n.2n-)	Torices et al., 2015	Corral et al., 2016
	Montrebei (Spain; early-late Maastrichtian -C31r-)	Torices et al., 2015	This study
Variraptor mechinorum	Fox-Amphoux (France; late Campanian - early Maastrichtian)	Le Loeuff and Buffetaut, 1998; Chanthasit and Buffetaut, 2009	Díez Díaz et al., 2012
Ornithomimosaurus sp. or Maniraptora indet.	Laño (Spain; late Campanian -C32n.2n-)	Torices et al., 2015; Pereda-Suberbiola et al., 2015	Corral et al., 2016
‘*Richardoestesia*-like’ form	L'Abeller (=Suterranya-1 of Ardèvol et al., 1995 ="Suterranya" of Torices et al., 2015) (Spain; early Maastrichtian -C31r-	Prieto-Márquez et al., 2000	This study, Fondevilla et al., 2016a
Richardoestesia, cf. *Richardoestesia* and ?*Richardoestesia*	Blasi-2B (Spain; late Maastrichtian -C30n-)	Torices et al., 2015	Pereda-Suberbiola et al., 2009a
	Laño (Spain; late Campanian -C32n.2n-)	Torices et al., 2015	Corral et al., 2016
	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Ortega et al., 2015	Ortega et al., 2015
	Vicari-4 (Spain -C31r-)	Torices et al., 2015	This study, Fondevilla et al., 2016a
	Vitrolles-La Plaine (France; early-late Maastrichtian -C31r-)	Valentin et al., 2012	Tabuce et al., 2013; but see Supp. Fig. 1
	Montrebei (Spain; early-late Maastrichtian -C31r-)	Torices et al., 2015	This study
	Molí del Baró (Spain; late Maastrichtian -C29r-)	Marmi et al., 2016	Marmi et al., 2016

Theropoda indet. (morphotypes 4 and 5 of Molí del Baró-1)	Molí del Baró (Spain; late Maastrichtian -C29r-)	Marmi et al., 2016	Marmi et al., 2016
Theropoda indet. A (=*Megalosaurus* cf. *pannonensis*)	Viso and Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
Theropoda indet. B	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991
cf. Troodontidae indet.	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1992	Antunes and Sigogneau-Russell, 1991

Sauropods

Taxa	**Localities (may include multiple sites)**	**References**	**References for age**
Lirainosaurus astibiae cf. *Lirainosaurus*	Laño (Spain; late Campanian -C32n.2n-)	Sanz et al., 1999	Corral et al., 2016
	Chera; La Castellana (Spain; mid-Campanian - late Campanian)	Company, 2004; Company et al., 2009	Company et al., 2005
	Sacedón (Spain; late Campanian - early Maastrichtian)	Ortega and Pérez-García, 2009	Ortega and Pérez-García, 2009
Morphotype 2 of Chera	Chera (Spain; mid-Campanian - late Campanian)	Díez Díaz et al., 2015	Company et al., 2005
Ampelosaurus atacis	Bellevue C3 (France; early Maastrichtian -C32n.1n-)	Le Loeuff et al., 1995; Le Loeuff, 2005	Fondevilla et al., 2016a
Atsinganosaurus velauciensis	Velaux-La Bastide Neuve (late Campanian - early Maastrichtian -C32n-)	Garcia et al., 2010	Tortosa et al., 2014; Cincotta et al., 2015; Martin et al., 2016, this study*
Lohuecotitan pandafilandi	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Díez Díaz et al., 2016	Ortega et al., 2015
Morphotype 2 of Lo Hueco	Lo Hueco (Spain; late Campanian - early Maastrichtian)	Díez Díaz et al., 2015	Ortega et al., 2015
Titanosauria indet. Form 1	Bellevue C3 (France; early Maastrichtian -C32n.1n-)	Vila et al., 2012	Fondevilla et al., 2016b
Titanosauria indet. Form 2	Presa de Tremp (Spain; early-late Maastrichtian -C31r-)	Vila et al., 2012	This study; Fondevilla et al., 2016a
Titanosauria indet. Form 3	Peguera-1 (Spain; late Maastrichtian -C31r-C31n-)	Vila et al., 2012	Vila et al., 2012
Titanosauria indet. Form 4	Molí del Baró-2 (Spain, late Maastrichtian -C29r-)	Vila et al., 2012	This study; Fondevilla et al., 2016a
Titanosauria indet. Form 5	Serraduy (Spain; late Maastrichtian -C30n-C29r-)	Vila et al., 2012	Vila et al., 2012
Nerets and Orcau-1 forms	Nerets and Orcau (Spain; early Maastrichtian -C31r-)	Work in progress	This study; Fondevilla et al., 2016a

Hadrosauroids

Taxa	**Localities (may include multiple sites)**	**References**	**References for age**
Pararhabdodon isonensis	Sant Romà d'Abella (Spain; late Maastrichtian -C29r-)	Casanovas-Cladellas et al., 1993; Prieto-Márquez et al., 2013	This study; Fondevilla et al., 2016a
	Serrat del Rostiar-1 (Spain; early Maastrichtian -C31r-)	Prieto-Márquez et al., 2013	This study; Fondevilla et al., 2016a
	Basturs Poble (Spain; early Maastrichtian -C31r-)	Dalla Vecchia pers. comm, V. F. work in progress	This study; Fondevilla et al., 2016a

Canardia garonnensis	Tricouté 3 (France; late Maastrichtian)	Prieto-Márquez et al., 2013	Prieto-Márquez et al., 2013
	Larcan (France; late Maastrichtian -C29r?-)	Prieto-Márquez et al., 2013	Prieto-Márquez et al., 2013
Arenysaurus ardevoli	Blasi-3 (Spain; late Maastrichtian -C30n-)	Pereda-Suberbiola et al., 2009a; Prieto-Márquez et al., 2013	Pereda-Suberbiola et al., 2009a
Blasisaurus canudoi	Blasi-1 (Spain; late Maastrichtian -C30n-)	Cruzado-Caballero et al., 2010; Prieto-Márquez et al., 2013	Pereda-Suberbiola et al., 2009a
Dwarf hadrosaurid of Serraduy	Serraduy del Pon/Beranuy (Spain; late Maastrichtian -C29r-)	Company et al., 2015	Vila et al., 2013
La Solana hadrosaurid	La Solana (Spain; probably late Maastrichtian)	Company et al., 1998; Pereda-Suberbiola et al., 2009b	Company, 2004
Noneuhadrosaurian hadrosaurid	Vitrolles-La Plaine (France; early-late Maastrichtian -C31r-)	Valentin et al., 2012	Tabuce et al., 2013; but see Supp. Fig. 1
Nonhadrosaurid hadrosauroids	Fontllonga-R (Spain; late Maastrichtian -C29r-)	Casanovas et al., 1999b	López-Martínez et al., 1998

Rhabdodontid ornithischians

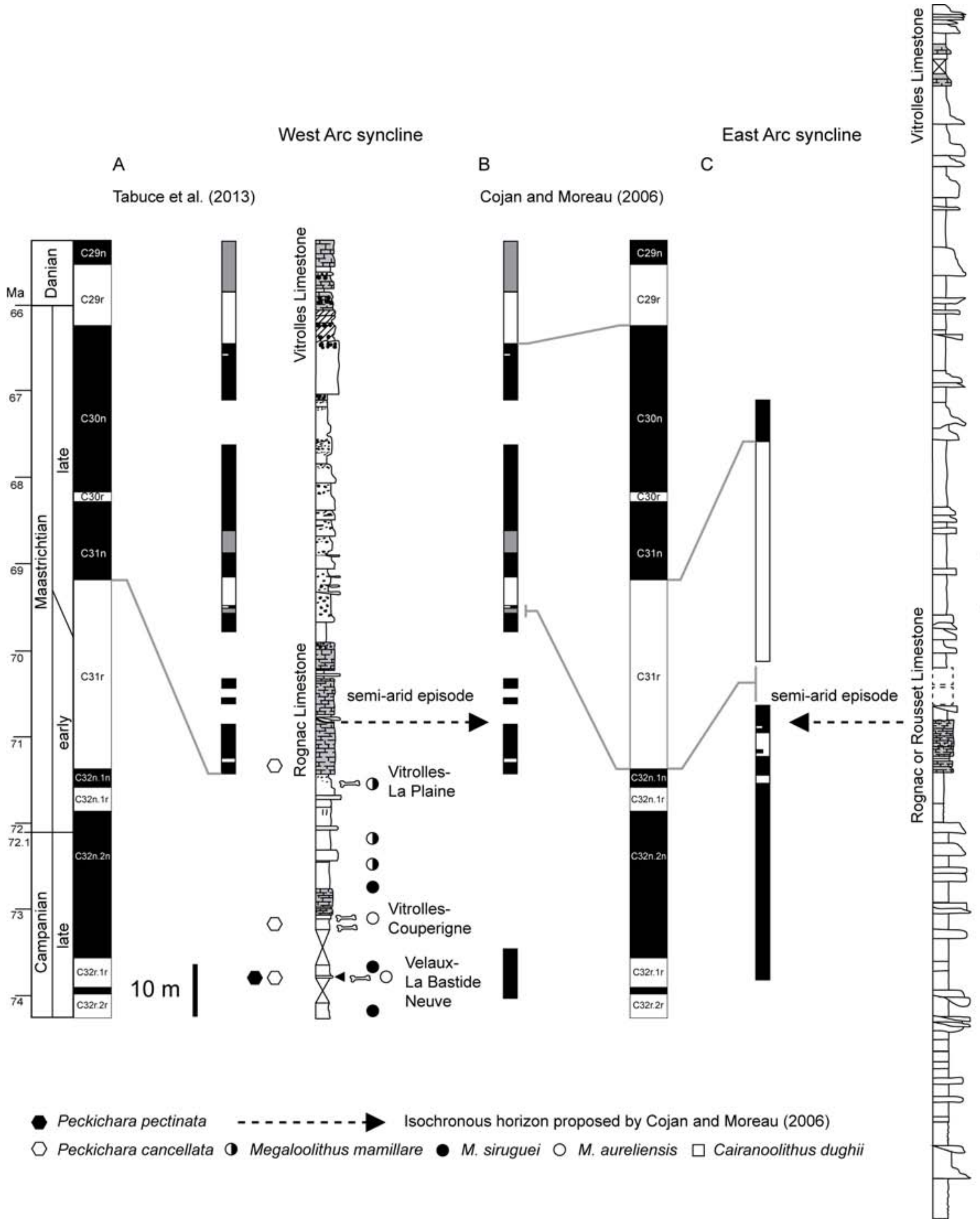
Taxa	**Localities (may include multiple sites)**	**References**	**References for age**
Rhabdodon priscus and cf. *R. priscus*	Villeveyrac (France; early Campanian - mid-Campanian -C33r-)	Buffetaut et al., 1996	Benammi et al., 2006
	La Boucharde (France; mid-Campanian)	Allain, 1998; Allain and Pereda-Suberbiola, 2003	Tortosa et al., 2014
	Chera (Spain; mid-Campanian - late Campanian)	Company, 2004	Company et al., 2005
	Armuña (Spain; late Campanian)	Pérez-García et al., 2016	Pérez-García et al., 2016
	Gabre (France; late Campanian)	Villatte et al., 1985	Villatte et al., 1985
	Arauzo de Miel-El Cogorro (Spain; late Campanian - early Maastrichtian)	Quintero Amador et al., 1982	Quintero Amador et al., 1982
	Basségat-F3 (France; late Campanian - early Maastrichtian)	Lapparent, 1947; Chanthasit, 2010	Chanthasit, 2010
	Fox Amphoux-F1 (France; late Campanian - early Maastrichtian)	Lapparent, 1947; de Broin et al., 1980	Díez Díaz et al., 2012
	Velaux-La Bastide Neuve F3 (France; late Campanian - early Maastrichtian -C32n-)	Laurent et al., 2001; Chanthasit and Buffetaut, 2009; Chanthasit, 2010;	Cincotta et al., 2015; this study
	Bellevue C3 (France; early Maastrichtian -C32n.1n-)	Le Loeuff, 1995, 2005	Fondevilla et al., 2016b
	Vitrolles-Couperigne VCO, B8 and B2 (France; early Maastrichtian)	Garcia et al., 1999; Pincemaille-Quillevere, 2002; Chanthasit, 2010	Tabuce et al., 2013; but see Supp. Fig. 1
	La Valdieu (France; early Maastrichtian -C32n.1n-)	Le Loeuff et al., 1997	Fondevilla et al., 2016b
	Gourg de l'Encantado (France; early Maastrichtian -C31r-)	Le Loeuff et al., 1994b; Le Loeuff, 1998; Pincemaille-Quillevere, 2002; Chanthasit, 2010	Fondevilla et al., 2016b
	Albières (France; early Maastrichtian -C32n.1n-)	Lapparent, 1967	Fondevilla et al., 2016b
	Cubilla (Spain; early Maastrichtian)	Lapparent et al., 1957	Floquet, 1991
	La Nerthe (France; early Maastrichtian?)	Matheron, 1869	Pincemaille-Quillevere, 2002

Rhabdodon septimanicus and cf. *R. septimanicus*	Cruzy area - Quarante and Montouliers sites (France; late Campanian - early Maastrichtian)	Lapparent, 1947; Buffetaut and Le Loeuff, 1991; Pincemaille-Quillevere et al., 2006; Chanthasit, 2010	Buffetaut and Angst, 2016
	La Boucharde (France; mid-Campanian)	Chanthasit, 2010	Tortosa et al., 2014

Nodosaurid ankylosaurians

Taxa	**Localities (may include multiple sites)**	**References for taxonomy**	**References for age**
Struthiosaurus languedocensis	Villeveyrac (France; early Campanian)	Garcia and Pereda-Suberbiola 2003	Benammi et al., 2006
Struthiosaurus	Laño (Spain; late Campanian -C32n.2n-)	Pereda-Suberbiola et al., 2000	Corral et al., 2016
	La Nerthe (France; early Maastrichtian?)	Lapparent, 1947	Pincemaille-Quillevere, 2002
Taveirosaurus costai (*nomen dubium*)	Taveiro (Portugal; Campanian to Maastrichtian)	Antunes and Sigogneau-Russell, 1991; Pereda-Suberbiola, 1999b	Antunes and Sigogneau-Russell, 1991

*Regarding the age of Velaux-La Bastide Neuve, the deposits in which the site is allocated (the Begudian) were first calibrated with chron C33n after Westphal and Durand (1990) and Cojan and Moreau (2006). Thus, Tortosa et al. (2014) placed the site in that chron. Cincotta et al. (2015), however, performed a magnetostratigraphic study in the section that contains the fossil site, identifying a normal polarity zone. These authors calibrated this magnetozone with chron C32n, despite they also reported the occurrence of the *Peckichara pectinata* charophyte species in the section, which has been correlated with chrons C33n-C32r (Riveline et al., 1996). Martin et al. (2016) cite the species *Saportanella maslovi, P. pectinata, P. cancellata, Platychara caudata* and *?Amblyochara begudiana* in the site according to a personal communication given by Monique Feist. All these species, together with the normal polarity zone, support the correlation of Velaux-La Bastide Neuve with the upper part of chron C33n (since no *P. pectinata* is found in chron C32n).



Supplementary Figure 1. Discrepances in the age calibration of the West Arc syncline, with the implications for the dating of the Vitrolles-La Plaine site. **A**, proposal of Tabuce et al. (2013) and Garcia and Vianey-Liaud (2001), implying a diachrony between the limestone units of the West and East Arc syncline. **B**, proposal of Cojan and Moreau (2006), implying isochrony for the limestone units. An isochronous horizon (semi-arid episode) was proposed. **C**, calibration of the East Arc syncline after Cojan and Moreau (2006). Lithostratigraphy after Garcia and Vianey-Liaud (2001) and Cojan and Moreau (2006). Paleomagnetism after Westphal and Durand (1990), Cojan et al. (2003), Cojan and Moreau (2006) and Cincotta et al. (2015). Charophyte biostratigraphic data after Riveline et al. (1996) and Tabuce et al. (2013). The position of the Velaux-La Bastide Neuve site (projected in the section) is taken from Martin et al. (2016).

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DISCUSSIÓ INTEGRADA

11

Els capítols anteriors han aportat una sèrie de resultats referents a l'ocupació dels paleoambients per part dels diferents grups de dinosaures que habitaven la Península ibèrica i el sud de França durant el Maastrichtià, conjuntament amb noves dades cronostratigràfiques que han permès millorar el coneixement del marc temporal dels dipòsits continentals de la regió. En aquest capítol es discuteixen aquestes noves aportacions per tractar de resoldre els objectius enunciats en el Capítol 2.

Els resultats presentats en el Capítol 5 mostren una clara predominància dels hadrosaures en els ambients fluvials del Maastrichtià del sud dels Pirineus, amb moltes evidències de petjades i rastres (32 jaciments) representats per l'icnogènere *Hadrosauropodus* en els subambients de plana d'inundació, canals i dipòsits de desbordament. Així, en aquest ambient, aquest grup de dinosaures predomina clarament pel que fa a petjades o icnites respecte a l'altre gran grup d'herbívors de la regió, els sauròpodes. Aquests últims presenten evidències *in situ* (incloent-hi impressions de pell, Capítol 6) en només 6 jaciments, malgrat les evidències fòssils de sauròpodes en els ambients fluvials d'aquesta àrea geogràfica s'incrementen notablement si comptem el ric registre oològic del grup (veure Capítol 10). Tot i això, el grup dels hadrosaures segueix sent, de llarg, el clade de dinosaures dominant en els ambients continentals de l'illa Ibero-Armoricana, en concordança amb Vila et al. (2016).

Amb tot, depenent del període de temps considerat es poden observar diferències en l'ocupació dels hàbitats disponibles. En el Campanià superior i els inicis del Maastrichtià inferior del sud-oest europeu els sauròpodes estan ben representats en molts jaciments d'origen fluvial, com ara Bellevue (veure Capítol 8), Velaux-La Bastide Neuve (Garcia et al., 2010) o Lo Hueco (Díez Díaz et al., 2016), mentre que els hadrosaures són extremadament rars durant aquest període (una ocurrència al jaciment fluvial de Laño, i un altre possible cas a Vitrolles-La Plaine, veure Capítol 10).

Si ens centrem en l'ambient costaner, també s'observen variacions pel que fa al grup de dinosaures dominant depenent del període de temps considerat. Durant els primers estadis del Maastrichtià inferior gairebé exclusivament trobem icnites i postes d'ou de sauròpodes en ambients propers a la línia de costa (platges, planes mareals fangoses i lagoons, veure Sanz et al., 1995, Marmi et al., 2014 i Oms et al., 2016), essent-hi els hadrosaures completament absents. Això canvia cap a finals del Maastrichtià inferior i durant tot el Maastrichtià superior: els hadrosaures passen a ser, amb molta diferència, el grup més nombrós en aquest tipus d'ambient tant pel que fa a icnites com ossos, amb multitud d'exemples a la vessant sud dels Pirineus com Moror A (Capítol 5), L'Espinau

(Capítol 7) i els jaciments de Blasi (Blain et al., 2010). Això també es compleix a la nord, amb exemples com Tricouté i Larcan (Laurent et al., 2002; Prieto-Márquez et al., 2013). Aquestes diferències de dominància segons l'intèrval de temps considerat segueixen la línia proposada per Le Loeuff et al. (1994), els quals defensaven un canvi faunístic durant el Maastrichtià on els hadrosaures esdevenien el grup herbívor dominant del sud-oest europeu, tot desplaçant els sauròpodes. No obstant, Riera et al. (2009) i Riera (2010) proposaven que el canvi de dominància podria ser aparent, i que podia explicar-se com la conseqüència d'un biaix ambiental. Aquests autors consideraven que els sauròpodes mostraven una preferència pels hàbitats propers al mar basant-se entre d'altres en el ric registre icnològic trobat en jaciments com Fumanya Nord i Sud (veure Capítol 5 i Vila et al., 2005). D'aquesta manera, l'escassedat dels dipòsits costaners en la regió (causada per una regressió marina) explicaria la poca abundància de sauròpodes a finals del Maastrichtià. Al contrari, la preferència dels hadrosaures per l'ambient fluvial, molt ben representat en les formacions Maastrichtianes de la regió, afavoria la seva aparent predominància tant en icnites i ossos en la majoria de jaciments. Tal com s'ha comentat anteriorment, però, la preferència pels ambients costaners dels sauròpodes no està ben fonamentada. Per exemple, en el cas dels jaciments costaners de Fumanya (situats en el cron C32n.1n, fa uns 71,5 milions d'anys), les dades presentades en el Capítol 8 ens mostren que durant el mateix període de temps els sauròpodes tenien una presència destacada i dominant també en l'ambient fluvial de les àrees properes. Aquesta observació està en consonància amb l'estudi estadístic de Vila et al. (2014), el qual descarta una preferència pels ambients propers al mar per part dels sauròpodes de la regió.

L'evidència recollida fins ara ens mostra que els sauròpodes generalment estan ben representats en tot tipus d'ambients durant el Maastrichtià, tot i que durant la fase final del Maastrichtià inferior els hadrosaures lambeosaurins passen a dominar tots els ecosistemes disponibles (costaner i fluvial). Amb el predomini dels lambeosaurins, el clade dels sauròpodes experimenta un cert declivi però no desapareix del medi costaner ni fluvial, sinó que segueix estant representat fins a finals del Cretaci (veure Vila et al., 2012, Sellés et al., 2016 i Capítols 5 i 6). Vila et al. (2016) comenten que aquest declivi pot estar ocasionat per la competència per l'espai dins un mateix ambient més que no pas per la competència per l'aliment, donada la diferència de mides i aparells masticatoris entre sauròpodes i hadrosaures.

A diferència de sauròpodes i hadrosaures, els anquilosaures mostren un desplaçament d'hàbitat durant el Maastrichtià inferior. Mentre que en el Campanià i el Maastrichtià inicial els ossos d'anquilosaure freqüentment es troben en ambients fluvials (per exemple veure Capítol 8 i Pereda-

Suberbiola et al., 2015), durant gran part del Maastrichtià inferior i el superior només s'han recuperat ossos d'anquilosaure en ambients costaners. Exemples d'això els trobem en forma de dents i ossos aïllats en diversos jaciments *lagoonals* de la Formació Posa del Sinclinal de Tremp, (veure López-Martínez et al., 2000 i Escaso et al., 2010) i ossos a Lestaillats, a l'Alta Garona (Laurent et al., 1999, 2002). Aquest fet pot correspondre a un desplaçament d'hàbitat produït per la competència amb els hadrosaures lambeosaurins. Així, els anquilosaures s'haurien concentrat en ambients marginals on van poder perdurar i coexistir temporalment amb altres grups de dinosaures fins a la seva extinció al Maastrichtià superior (veure Capítol 10 i a sota). Aquesta proposta és encara molt temptativa i s'hauria de contrastar amb nous estudis estadístics.

En cas dels rhabdodòntids, el Capítol 8 suggereix una preferència d'aquest grup pels ambients fluvials, ja que el seu registre en formacions costaneres durant el Campanià superior i el Maastrichtià inferior és molt escàs. Acceptant com a vàlida aquesta premisa, es pot hipotetitzar que un cop els lambeosaurins apareixen a la regió del sud-oest europeu aquests van competir amb els rhabdodòntids ja sigui per l'espai o pels recursos en l'ambient fluvial. Això podria ser una causa de la ràpida extinció dels rhabdodòntis atès que aquest grup no sembla haver estat capaç de colonitzar i refugiar-se en l'ambient costaner com sí van fer els anquilosaures. En aquest sentit, Vila et al. (2014) també donen suport a una preferència per ambients continentals per aquests dinosaures.

Vila et al. (2016) proposen que els hadrosaures poden ser els causants de l'extinció dels dinosaures rhabdodòntids i anquilosaures en el sud-oest europeu en ocupar els seus nínxols ecològics. Aquests autors comenten que la major eficiència dels hadrosaures per a processar l'aliment (veure Mallon i Anderson, 2013) pot explicar el domini dels hadrosaures lambeosaurins a partir del Maastrichtià inferior en l'illa Ibero-Armoricana. Alternativament, Vila et al. (2016) plantegen que els hadrosaures podrien haver assolit una preponderància en extingir-se els rhabdodòntids i els anquilosaures per altres causes desconegudes.

Finalment, pel que fa al grup dels teròpodes, aquests no mostren aparentment cap preferència de tipus paleoambiental, ja que les seves restes s'han recuperat en tot tipus d'ambients (veure referències del Capítol 10).

La nova successió de dinosaures del Campanià-Maastrichtià presentada al Capítol 10 esmena l'inici i la durada del reemplaçament faunístic que es va donar lloc a l'illa Ibero-Armoricana a finals del Cretaci (Fig. 11.1). Així, en comptes d'un reemplaçamet ràpid de faunes concentrat al voltant del canvi de crons C31r-C31n (fa uns 69 milions d'anys), tal i com proposa Vila et al. (2016), les dades presentades en aquesta tesi doctoral (Capítols 9 i 10) demostren que aquest fenomen es va produir durant un intèrval de temps més prolongat. A més, el canvi faunístic es va iniciar abans, durant el Maastrichtià inferior (abastant entre els 71 i els 69 milions d'anys). Aquesta tesi també millora el coneixement sobre la temporització de les aparicions i desaparicions de clades de dinosaure. En aquest sentit, el fet clau és que les primeres aparicions de nous grups no són coincidents en el temps, sinó que són esdeveniments diacrònics. Aquestes aparicions de faunes són probablement causades per episodis d'immigració com ara l'arribada de nous tàxons de sauròpodes titanosaures i hadrosaures lambeosaurins. De la mateixa manera, l'extinció dels rhabdodòntids i els anquilosaures, amb les dades disponibles, no és coincident en el temps.

Els principals esdeveniments que caracteritzen el reemplaçament faunístic es poden resumir així:

- El Campanià i l'inici del Maastrichtià inferior (fins el cron C32n, al voltant dels 71,5 Ma) del sud-oest europeu estava dominat per sauròpodes titanosaures, probablement els productors de l'associació oològica formada per *Megaloolithus siruguei* i *M. aureliensis*, ornitòpodes rhabdodòntids i anquilosaures nodosàurids. Els hadrosaures, probablement tàxons basals similars als de la resta de l'arxipèlag europeu, haurien representat un clade extremadament rar a la regió.

- En els primers estadis del cron C31r (en el Maastrichtià inferior, al voltant de 71 Ma) noves formes de sauròpodes titanosaures, productores d'una nova associació oològica de *M. mamillare* i *M. baghensis*, van arribar a l'illa Ibero-Armoricana. Formes antigues i noves de titanosaure van coexistir a la regió fins als inicis del Maastrichtià superior, tot i que possiblement no van compartir els mateixos espais locals. Entre els 70 i els 69 Ma l'associació de sauròpodes antiga s'extingeix (evidenciat per la desaparició de l'oospècie *M. siruguei*).

- Al voltant de fa 70 Ma (part mitjana del cron C31r, encara al Maastrichtià inferior), els hadrosaures lambeosaurins apareixen a l'illa i ràpidament esdevenen el grup herbívor dominant, ocupant tots els ecosistemes. Poc temps després, el clade dels rhabdodòntids s'extingeix a la regió.

- Els anquilosaures nodosàurids s'extingeixen durant el cron C31n (al voltant dels 69 Ma), coexistint amb els lambeosaurins durant al menys un milió i mig d'anys en els ambients costaners, però no en els continentals, on aquests dinosaures cuirassats són absents.

- El clade dels teròpodes no pateix cap canvi significatiu durant l'intèrval de temps en el qual es produeix el canvi de faunes, ja que la majoria de gèneres i famílies documentats al Campanià estaven també presents al Maastrichtià superior del sud-oest europeu.

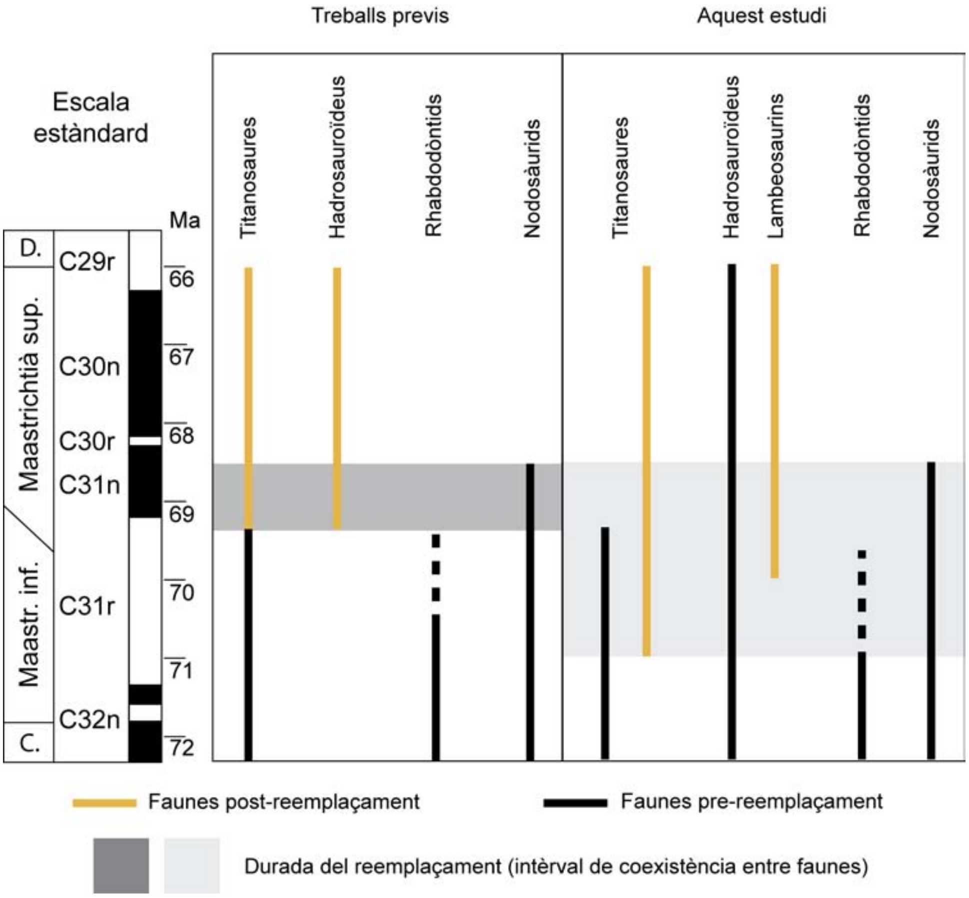

Figura 11.1. El reemplaçament faunístic entre comunitats de dinosaures herbívors del Maastrichtià del sud-oest europeu. Es mostra el punt de partida de treballs anteriors i la nova proposta desenvolupada en aquesta tesi.

Aquest escenari implica que durant el Maastrichtià es van donar al menys dos esdeveniments o onades d'immigració a la regió separats per un milió d'anys aproximadament en base a les taxes de sedimentació calculades al Sinclinal de Tremp en el Capítol 9. Una primera (o més) va estar composta per sauròpodes titanosaures i una altra (o més d'una) per lambeosaurins. Pel que fa als primers, la paleobiogeografia no està clara tot i que es proposa una connexió entre les faunes de Gondwana i les trobades a Europa (Csiki-Sava et al., 2015 i referències allí incloses). Pel que fa als lambeosaurins, els diferents tàxons trobats a la regió tenen relació amb clades d'Àsia i Nord

Amèrica. Mentre el tsintaosaurini *Pararhabdodon isonensis,* membre d'un clade original d'Àsia, apareix al Maastrichtià inferior, l'aralosaurini *Canardia garonnensis,* també relacionat amb tàxons asiàtics, no apareix fins el Maastrichtià superior. De manera similar, els lambeosaurinis *Arenysaurus ardevoli* i *Blasisaurus canudoi*, emparentats amb clades del Cretaci Superior nord americà (Prieto-Márquez et al., 2013; Cruzado-Caballero et al., 2013) no apareixen fins el Maastrichtià superior. Aquestes diferències d'edat poden implicar també un diacronisme pel que fa a les dispersions que van portar els diferents grups de lambeosaurins a Europa, tot i que probablement són un producte de la manca de dades en el registre.

La causa que va precipitar el reemplaçament faunístic sovint s'ha buscat en canvis ambientals al voltant del Maastrichtià inferior-superior (per exemple Le Loeuff et al., 1994). Durant aquest període (al voltant dels 69 milions d'anys), el registre marí mostra un esdeveniment climàtic a escala global (*Mid-Maastrichtian Event*, MME, veure Voigt et al., 2012). Amb tot, aquest esdeveniment no té una expressió en els ambients continentals de la regió, tal com mostren els resultats d'isòtops estables de carboni i oxigen de nòduls edàfics de Riera et al. (2013). Ans al contrari, aquests autors argumenten que al llarg del Maastrichtià, al menys al sud dels Pirineus, hi va dominar una estabilitat climàtica. A més, tal com mostren els Capítols 9 i 10, el reemplaçament s'inicià abans del MME, per tant, cal buscar altres causes més enllà del clima per explicar el canvi faunísitc a l'illa Ibero-Armoricana. En aquest sentit, l'eliminació de les barreres geogràfiques produïda per caigudes del nivell del mar documentades durant el Maastrichtià (veure Miller et al., 2003) s'ha proposat com un dels factors que podrien afavorir aquests episodis de migració a l'arxipèlag europeu (Csiki-Sava et al., 2015).

El Capítol 10 també revela que la biostratigrafia basada en les closques d'ou de dinosaure té un ús més limitat del que inicialment s'havia plantejat. La proposta original de Garcia i Vianey-Liaud (2001) permetia calibrar successions fins al punt de determinar a quin cron podien pertànyer unes roques amb restes de closques, ja que es basava en esdeveniments isòcrons (aparicions i extincions d'oospècies) a tot el sud-oest europeu. L'actualització del marc cronostratigràfic presentat al Capítol 9 mostra que aquestes primeres aparicions i desaparicions no ocorren al mateix temps en cada àrea de la regió, sinó que probablement obeeixen a factors paleoecològics encara poc coneguts (com ara la competència i partició d'ecosistemes entre els titanosaures productors). Donat que les aparicions de noves oospècies sovint no són isòcrones, moltes d'elles perden el seu valor biostratigràfic. Aquest és el cas de *Megaloolithus mamillare* i *M. baghensis*. Amb tot, d'altres oospècies mantenen certa utilitat, com ara *M. siruguei* i els representants de l'oofamília

Cairanolithidae. En aquest sentit, aquestes closques d'ou de dinosaure no apareixen mai en successions sedimentàries del Maastrichtià terminal, de manera que es poden emprar per identificar el Campanià o el Maastrichtià inferior (i possiblement la base del superior).

El reemplaçament de faunes que es va produir a finals del Cretaci en l'illa Ibero-Armoricana no té cap equivalent en la resta de l'arxipèlag europeu. En aquest sentit, Csiki-Sava et al. (2015, 2016) contrasten aquests canvis entre grups d'herbívors amb una aparent estabilitat faunística en l'illa de Haţeg, en l'actual Romania. En aquesta regió la successió de faunes no mostra canvis pel que fa a la diversitat de tàxons de dinosaure al llarg del Maastrichtià, sinó que rhabdodòntids com ara *Zalmoxes* i *Mochlodon* conviuen amb l'hadrosaure *Telmatosaurus* i titanosaures com ara *Magyarosaurus* i *Paludititan* durant tot l'estatge. Aquesta, però, podria ser una observació parcial o esbiaixada a causa d'una manca de registre geològic del Maastrichtià superior. Així, mentre el Maastrichtià inferior està ben representat a la regió, amb seccions calibrades amb datacions absolutes i paleomagnetisme (Panaiotu i Panaiotu, 2010; Csiki-Sava et al., 2016), el Maastrichtià superior es troba o bé incomplet pel que fa a l'estratigrafia (per exemple en la Formació Sînpetru) o bé inexistent o no acuradament datat (per exemple a la conca Rusca Montană). Sovint, les formacions que inclouen el Maastrichtià inferior estan escapçades per sediments miocens. D'aquesta manera, els darrers milions d'anys del Maastrichtià de la regió no han estat ben identificats fins ara i podrien no haver quedat enregistrats o desaparegut en gran mesura per erosió.

La menor disponibilitat de seccions estratigràfiques del Maastrichtià superior respecte de l'inferior sembla ser una característica comuna en el registre geològic continental de l'illa Ibero-Armoricana i potser també en el registre de l'illa de Hateg. Al Capítol 9 s'esmenta que moltes de les seccions estratigràfiques del Cretaci terminal continental presenten hiatus o successions condensades durant el Maastrichtià superior. Aquest fet, aparentment no restringit al sud-oest europeu, suggereix un esdeveniment o fenomen comú més enllà de l'activitat tectònica regional (com podria ser la fase tectònica compressiva en la zona dels Pirineus). Per exemple, un context de regressió marina general en tot Europa durant el Maastrichtià superior afavoriria l'erosió, la no sedimentació i/o *by pass* en les conques deposicionals, cosa que derivaria en un menor registre geològic per aquest estatge. En aquest sentit, Miller et al. (2003) identifiquen almenys dos regressions durant el Cretaci terminal, una d'elles a inicis del Maastrichtià superior que podria estar relacionada amb les erosions i progradacions de les conques sedimentàries de l'arxipèlag europeu. Davant d'aquesta circumstància, la poca disponibilitat de successions estratigràfiques amb un registre complet del Maastrichtià terminal i de la transició Cretaci-Paleogen posa en valor les seccions occidentals del

Sinclinal de Tremp i tota la successió de Vallcebre. El ric registre paleontològic que contenen (veure Capítols 5 i 6, Blanco et al., 2015, Sellés et al., 2016 i Canudo et al., 2016) esdevé un dels únics i més importants per estudiar les darreres comunitats de dinosaures del món més enllà del registre de Nord Amèrica.

GENERAL CONCLUSIONS / CONCLUSIONS GENERALS

12

Paleoenvironments and dinosaur record

- The ichnogenus *Hadrosauropodus*, linked to hadrosaurs, has been identified as the most profuse dinosaur track in the end-Cretaceous fluvial environments (channel and floodplain facies) of the South-Pyrenean area. This record includes tracks few meters below the Cretaceous-Paleogene transition (K-Pg).

- In addition to the fluvial environment, hadrosaurs are well represented in the coastal settings of the upper Maastrichtian. One example is the L'Espinau site, a cohesive flow-induced bonebed produced near the coastline. In this respect, hundreds of hadrosaur bones appear mixed with other terrestrial and marine fauna in a lagoon. Further, hadrosaur tracks also occur in lagoonal settings, but they are much scarcer.

- The sauropod track record is abundant in the coastal environment of the southern Pyrenees (e.g. tidal mudflats and lagoonal settings of Fumanya), and scarce in the fluvial one. As in hadrosaurs, this latter setting includes examples of sauropod tracks, but also skin impressions, in channel facies very close to the K-Pg transition.

- There is no evidence of any preference for the coastal environment in sauropods. During the Campanian and the early Maastrichtian, the sauropod record is abundant in both inland and coastal settings recorded in southwestern Europe (Provence, Pyrenees and Iberia).

- The other herbivorous groups of the region, the rhabdodontid ornithopods and the nodosaurid ankylosaurians, could have had a habitat preference. The former group predominantly appears in inland settings, while the latter seems to be restricted to the coastal environment from most of the early Maastrichtian (chron C31r). However, these observations should be tested numerically in the future.

Chronostratigraphy

- The integrated stratigraphic and paleomagnetic study carried out in the end-Cretaceous sections of the Upper Aude Valley (northern Pyrenees) allowed to achieve an accurate dating. Important dinosaur sites from the area (e.g. Bellevue) fall in the lowermost

Maastrichtian (chron C32n, probably the C32n.1n). After this age calibration, this French fossiliferous area can be integrated in the precise Pyrenean chronostratigraphic framework, together with other well-calibrated sections from the south (e.g. Vallcebre).

- The inconclusive paleomagnetic results from the Isona sector of the Tremp Syncline have been revisited in a new magnetostratigraphic study carried out in Orcau. The obtained long reverse magnetozone agrees with the recent planktonic foraminifera biozones identified in the same area. The magnetozone correlates with chron C31r (lower Maastrichtian), implying that those deposits are older than previously though.

- The new age calibrations of the Tremp Syncline show that the basin had important sedimentary hiatus. Most of the upper Maastrichtian is absent in its eastern sector (Orcau-Isona sections), but well represented in the west (Blasi and Campo sections).

- Several Maastrichtian sedimentary successions from southwestern Europe show hiatus, facies shifts and/or low depositional rates during the late Maastrichtian. Even, the Romanian end-Cretaceous formations seems to exhibit a similar feature.

- The dinosaur eggshell biostratigraphy, developed during the last years, proved to be less resolutive than initially though after the new age calibrations achieved here.

Dinosaur succession of southwestern Europe

- Lambeosaurine hadrosaurs arrived to the Ibero-Armorican Island during the early Maastrichtian. Their appearance in the Tremp Syncline, in the mid-/upper portion of the C31r (around 70 Ma), more or less coincides with the explosion of the hadrosaur track record. The hadrosaur dominance in the late Maastrichtian was likely driven by lambeosaurines.

- Sauropods were the dominant clade in both coastal and inland settings during the Campanian and the earlymost Maastrichtian. Since both environments are well represented in the Campanian and the early/late Maastrichtian, the sauropod decline during the Maastrichtian can not be explained as the product of an environmental bias. Coinciding with the lambeosaurine apparition, hadrosaurs became the new herbivore dominants in all settings thus displacing sauropods.

- The Maastrichtian dinosaur faunal turnover of southwestern Europe took place in a extended period of about two million years. During this interval, newer and older herbivore dinosaur clades cohabited the Ibero-Armorican Island. Hence, the extinction and apparition (immigrant arrivals) of dinosaur groups were not time coincident.

- The turnover started earlier than the global event known as mid-Maastrichtian Event (MME). During the replacement, stable climatic conditions have been reported for southwestern Europe. Hence, the faunal turnover is not linked to a global or local climatic event.

Paleoambients i registre de dinosaures

- L'icnogènere *Hadrosauropodus,* produït per hadrosaures, representa l'empremta de dinosaure més abundant en els ambients fluvials del Cretaci terminal (en fàcies de canal i de plana d'inundació) de l'àrea sud-pirinenca. Aquest registre inlou nivells de petjades molt pocs metres per sota de la transició K-Pg.

- Els hadrosaures també estan ben representats en els ambients costaners. Un exemple és el jaciment de L'Espinau, un *bonebed* produït per un flux cohesiu iniciat prop de la línia de costa. Centenars d'ossos d'hadrosaure es troben barrejats amb altres restes de vertebrats terrestres i marins en un *lagoon*. A més a més, també apareixen petjades d'hadrosaure en ambients de *lagoon*, tot i que són molt més escasses.

- El registre de petjades de sauròpode és abundant en els ambients costaners dels Pirineus (per exemple en planes mareals i *lagoons*, com a Fumanya), i escàs en el medi fluvial. D'igual manera que en els hadrosaures, en aquest darrer ambient s'hi troben exemples de petjades de sauròpode (i també impressions de pell) molt properes a la transició K-Pg.

- No s'ha trobat evidència sobre una preferència pels ambients costaners per part dels sauròpodes a la regió. Durant el Campanià i el Maastrichtià basal, el registre de sauròpodes del sud-oest europeu és abundant tant en medis continentals com en costaners.

- Altres grups d'herbívors de la regió, com ara els ornitòpodes rhabdodòntids i els anquilosaures nodosàurids podrien mostrar preferències per algun tipus d'ambient. Els primers predominantment s'han trobat en medis fluvials, mentre que els segons semblen estar restringits als ambients costaners durant la major part del Maastrichtià inferior (en el cron C31r). Amb tot, aquestes observacions requereixen de suport estadístic en el futur.

Cronostratigrafia

- L'estudi estratigràfic i paleomagnètic realitzat en les seccions de l'Alta Vall de l'Aude (vessant nord dels Pirineus) han permès obtenir una datació acurada. Jaciments importants com ara Bellevue queden situats a la part més baixa del Maastrichtià inferior, en el cron

C32n (probablement el C32n.1n). Amb aquesta calibració d'edat, el registre d'aquesta àrea del sud de França es pot integrar en un marc cronostratigràfic conjuntament amb la resta de seccions del sud dels Pirineus (per exemple Vallcebre).

- Els resultats paleomagnètics poc concloents del sector Isona del Sinclinal de Tremp s'han revisat en un nou estudi magnetostratigràfic dut a terme a la secció d'Orcau. La llarga magnetozona de polaritat inversa que s'ha obtingut està d'acord amb les recents dades biostratigràfiques de foraminífers plantònics de la zona. Aquesta magnetozona es pot correlacionar amb el cron C31r, que engloba la major part del Maastrichtià inferior. Això implica que els dipòsits sedimentaris d'Isona són més antics del que s'havia considerat inicialment.

- La nova datació del Sinclinal de Tremp mostra que la conca presenta importants hiatus sedimentaris. La major part del Maastrichtià superior es troba absent en la seva part oriental (secció Orcau-Isona), però en canvi sí que està ben desenvolupat en el sector occidental (seccions de Blasi i Campo).

- Moltes successions sedimentàries del sud-oest europeu mostren hiatus, canvis de fàcies i/o taxes deposicionals baixes durant el Maastrichtià superior. Aparentment, fins i tot el registre Maastrichtià de Romania mostra aquesta característica.

- La biostratigrafia d'ous de dinosaure, desenvolupada en els darrers anys, resulta ser menys resolutiva del que s'havia considerat inicialment tenint en compte les noves datacions obtingudes.

Successió de dinosaures al sud-oest europeu

- Els hadrosaures lambeosaurins van arribar a l'illa Ibero-Armoricana durant el Maastrichtià inferior. La seva aparició al Sinclinal de Tremp, al voltant de la meitat/part superior del cron C31r, coincideix més o menys amb l'expansió del registre de petjades d'hadrosaure. Això suggereix que el predomini dels hadrosaures a partir d'aquest moment va estar causat per l'arribada dels lambeosaurins.

- Els sauròpodes representaven el clade herbívor dominant en els ambients costaners i fluvials del Campanià i el Maastrichtià més basal. Donat que els ambients fluvials i costaners estan ben representats tant al Campanià com al Maastrichtià inferior i superior de la regió, el declivi del grup dels sauròpodes durant el Maastrichtià no es pot explicar com un producte d'un biaix ambiental. Coincidint amb l'aparició dels lambeosaurins, els hadrosaures esdevigueren el grup herbívor dominant a la regió, tot desplaçant els sauròpodes en tots els ambients.

- El reemplaçament faunístic que es va produir durant el Maastrichtià del sud-oest europeu es va perllongar durant uns dos milions d'anys. En aquest intèrval, nous i vells clades de dinosaures herbívors van coexistir a l'illa Ibero-Armoricana. Així, les extincions i aparicions (episodis migratoris) de grups de dinosaures no van coindicir en el temps.

- El reemplaçament faunístic va iniciar-se abans de l'esdeveniment climàtic global conegut com a Esdeveniment del Maastrichtià mitjà. Durant el període de canvi faunístic s'han proposat condicions climàtiques estables al sud-oest europeu. D'aquesta manera, el reemplaçament faunístic no està lligat a un canvi climàtic d'abast global o regional.

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14

AGRAÏMENTS

Em disposo a tancar el volum de la tesi doctoral i m'adono, dos dies abans de l'entrega, que encara no he fet el darrer capítol... els agraïments. Aquests últims dies -febrils-, entre feines d'edició i de correcció d'errades imprevistes, i entre sopars i dinars de Nadal, he intentat enumerar mentalment tota la gent que s'ha creuat en el camí de la meva tesi. Ara mateix lamento no haver fet un llistat de mica en mica! Són les 9 del vespre d'un dissabte de gener i he de deixar constància, ara sí, per escrit, de tots vosaltres...

En primer lloc, com no podia ser d'una altra manera, vull agrair als directors de tesi la confiança que van dipositar en mi quan van decidir que jo era la persona indicada per dur a terme les tasques del projecte.

Oriol Oms, vull agrair-te la llibertat que m'has donat per desenvolupar la recerca a la meva manera. Totes les facilitats, la comprensió i el bon humor a l'hora d'afrontar els moments més difícils. El teu suport quan volia canviar el món amb una magneto. Encara me'n recordo d'aquella tarda al teu despatx, després de molt temps sense veure'ns, on em vas plantejar les feines que faríem plegats si aconseguia la beca... Des de llavors, en aquests gairebé cinc anys puc dir que he passat grans moments, intensos, ja sigui en visites al teu despatx deu minuts abans que marxesis, ja sigui en dies de camp a Tremp i a Espéraza, o fins i tot per Skype. L'última, aquest mateix matí.

Àngel Galobart, vull agrair que pensessis en mi per anar a excavar aquell estiu del 2011. Pràcticament no ens coneixíem però vas considerar que podia ser un bon reforç per l'Espinau (bé, el meu cap vol pensar que va ser així). Potser gràcies a aquesta primera presa de contacte vaig fer números per a que em confiessis un treball de màster sobre material del Mesozoic... i potser gràcies a això vaig acabar tenin-te de codirector de la tesi! Gràcies per la confiança, la comprensió i l'ajuda rebuda durant les meves visites a l'ICP de Sabadell. I gràcies també per donar-me l'oportunitat de conèixer de primera mà les tomaqueres de Tòrrec!

En segon lloc, vull agrair-li al Jaume Dinarès l'atenció i ajuda que m'ha proporcionat quan hem treballat plegats al camp, en els intercanvis de correus i, sobretot, durant la meva estada breu a l'INGV. Aprofitant el paràgraf, vull agrair al Leo Sagnotti la confiança que em va prestar durant la meva visita a Roma. I parlant d'italians, també aprofito per agrair els bons moments de camp al Massimiliano Ghinassi (Gino).

Gràcies als membres del Departament de Geologia de la UAB per la seva disponibilitat davant qualsevol problema o dubte al llarg d'aquests anys. Vull agrair especialment la Rita Estrada, les secretàries i els membres del Laboratori de làmines primes per les facilitats rebudes i la feina ben feta.

Vull donar les gràcies als companys del Mesozoic de l'ICP amb qui he coincidit aquests anys. Gràcies per la feina feta plegats, les col·laboracions passades i espero que futures, i el bon ambient que sempre m'heu mostrat quan apareixia per allà. Josep Marmi, Bernat Vila, Albert G. Sellés, Alex Blanco, Novella Razzolini, Arnau Bolet, gràcies i a reveure! No sé si en Josep Fortuny entra en aquesta categoria, però aprofito per agrair-li els consells que de tant en tant anava deixant caure (les bromes pesades potser no...). També vull dedicar un espai a altres membres de l'ICP, passats i presents, als qui de tant en tant he anat veient i amb qui he compartit alguns moments. Gemma Prats, Carolina Cancelo, Marc Furió, Salvador Moyà, Meike Köhler, David Alba, Soledad de Esteban, Marta March, Carmen Nacarino, Blanca Moncunill, Guillem Orlandi i Luján. Ja he anomenat a l'Alex, però el rescato per agrair-li les genials estones cervesa en mà a Sabadell o a Espéraza.

Hi ha tres persones més que mereixen unes línies apart. Tots tres formen part de l'excels grup de Primats de l'Eocè: en Joan Femenias (que va en pack amb la Joana), na Judit Marigó (i l'Èlia) i en Raef Minwer Barakat (indestriable d'una senyora Guapíssima). Vau ser de les primeres persones amb qui em vaig fer en l'inici d'aquesta aventura i són moltíssims els moments que hem passat junts/xerrat via Whatsapp. Són especialment memorables els sopars a casa del Raef expressant la nostra opinió sobre el món. Gràcies per ser-hi i haver-hi estat.

Mereixen una especial menció els companys Precaris (i Becaris). Andreu Badia, Andreu Vinyoles, Laura Burrel, Pablo Rodríguez, Jordi Pérez, Mireia Domènec, Dídac Navarro, Isaac Corral, Lucia Struth, Miquel Poyatos, Marc Viaplana, Camilo. Gràcies per tot aquest temps! El Salvador Boya i l'Eudald Mujal entren dins d'una categoria apart. Gràcies pels inicis junts al despatx! Ah, i la Marta Roigé. Quan anem a mostrejar?

Me'n recordo també dels companys d'Aragosaurus de la Universidad de Zaragoza. Diego Castanera, Eduardo Puértolas, Tony Alonso, José Manuel Gasca, Pablo Navarro, Miguel Moreno, Penélope Cruzado, i la petita Jara Parrilla (:P). I a l'Iñaki Canudo. Ens hem vist en congressos, excavant, i també per casualitat...

També a les dues Albes de la UB: Alba Vicente i Alba Sánchez. Malgrat no ens hem vist gaire, us vull fer esment. Gràcies!

Vull recordar també les persones que han participat en les excavacions paleontològiques de Costa de les Solanes i L'Espinau durant aquests anys: la Irina Fernández, la Laura Romero, el Francesco (Ciccio) Battista, el Xavier Mir, el Fernando Ari, el Pere xic, i tots els alumnes de pràctiques que d'alguna manera o altra han col·laborat.

Canviant d'òrbita, vull afegir aquí els Lleidatans pel món, l'incombustible grup humà responsable de les més grans tardes (i matins, i nits) de pèrdues de temps al Whatsapp, que de vegades servien per treure el cap de l'ordinador. Tot i que potser massa sovint. Tapis, Betet, Andrés, Burón, Soro, Sisc, PauVilaFernández, A.R., Pabloff i G.B.R. Un Xurrasco a 8,5€?

Les persones de la següent llista s'han guanyat un lloc després d'haver aguantat al menys un cop les meves queixes sobre com n'és de dura la vida del becari investigador. O per haver mostrat interès en el que estava fent (que sempre s'agraeix). Dani Gavaldà, Rocío Romero, Nohemi Gómez, Mikel Iriondo, Leire Iriondo, Albert Alins, Marta Mesonero, Rubén Cierco, Núria Chic, Marla Singer a.k.a. Sílvia Ripoll, Bortx Holgado, Albert Herrera, Pilar Palacín, Pilar i Neus de Nadal, Alba de Nadal, Llorenç de Nadal i José i Biel de Codina.

A la resta de veïns de Castanesa i Vilaller. A Javi, allà on siguis.

Als meus pares, Joaquín i Ana. A la meva padrina Montserrat. Als meus tiets i cosins. Al Cristian i la Tanja. Al petit Max. Gràcies per tot el suport durant aquesta etapa.

Tan sols he escrit tres pàgines i el rellotge marca el punt de la mitjanit. Si no t'has trobat a la llista, perdona'm. No es poden deixar les coses per a l'últim moment...

The upper Maastrichtian dinosaur fossil record from the southern Pyrenees and its contribution to the topic of the Cretaceous–Palaeogene mass extinction event

A 1

L’annex 1 correspon a l’article publicat en la revista *Cretaceous Research* el gener de 2016, prèviament aparegut online el 9 de juliol de 2015:

Canudo, J. I., Oms, O., Vila, B., Galobart, À., **Fondevilla, V**., Puértolas-Pascual, E., Sellés, A. G., Cruzado-Caballero, P., Dinarès-Turell, J., Vicens, E., Castanera, D., Company, J., Burrel, L., Estrada, R., Marmi, J., & Blanco, A. (2016). The upper Maastrichtian dinosaur fossil record from the southern Pyrenees and its contribution to the topic of the Cretaceous–Palaeogene mass extinction event. *Cretaceous Research* **57**, 540-551.

En aquest article, V. F. ha participat en tasques de camp a la secció de Campo. A més, ha contribuït redactant la descripció de les diferents seccions estratigràfiques que s’estudien i ha preparat les dues figures del treball. Ha discutit els resultats amb la resta de coautors.

Aquest annex està protegit (pàgines 283 a 300). Pot consultar-se en el següent enllaç:

http://www.sciencedirect.com/science/article/pii/S0195667115300173

DOI: http://dx.doi.org/10.1016/j.cretres.2015.06.013

TRANSITIONAL ENVIRONMENTS OF THE LOWER MAASTRICHTIAN SOUTH-PYRENEAN BASIN (CATALONIA, SPAIN): THE FUMANYA MEMBER TIDAL FLAT

A 2

L'annex 2 correspon a l'article publicat en la revista *Cretaceous Research* el gener de 2016, prèviament aparegut online el 12 d'octubre de 2015:

Oms, O., **Fondevilla, V**., Riera, V., Marmi, J., Vicens, E., Estrada, R., Anadón, P., Vila, B., & Galobart, À. (2016). Transitional environments of the lower Maastrichtian South-Pyrenean Basin (Catalonia, Spain): The Fumanya Member tidal flat. *Cretaceous Research* **57**, 428-442.

En aquest article, V. F. ha realitzat tasques de camp i ha mesurat les seccions de Figuerola de Meià, Terradets, part de la secció d'Isona i Llordà. Ha realitzat el comptatge de làmines de la secció de Terradets i ha realitzat la restitució paleogeogràfica de la conca en base a talls geològics compensats dels diferents sinclinals. Ha preparat les figures 1, 2, 3, 4 i 6, les figures suplementàries 1, 2 i 6 i ha realitzat part de la compilació de jaciments que apareixen en la Taula suplementària 1. Ha discutit els resultats amb la resta de coautors.

La majoria de les seccions estratigràfiques que apareixen en el treball pertanyen a la tesi doctoral de V. R., així com la interpretació general de l'ambient que es descriu a l'article. Per aquest motiu, s'ha decidit de no incloure'l dins el cos de la tesi, sinó únicament en l'annex a mode de referència donada la importància d'aquest article en la resta de capítols.

Aquest annex està protegit (pàgines 303 a 338). Pot consultar-se en el següent enllaç:

http://www.sciencedirect.com/science/article/pii/S0195667115300628

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