







Review

The Tetrapod Fossil Record from the Uppermost Maastrichtian of the Ibero-Armorican Island: An Integrative Review Based on the Outcrops of the Western Tresp Syncline (Aragón, Huesca Province, NE Spain)

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Abstract: The South-Pyrenean Basin (northeastern Spain) has yielded a rich and diverse record of Upper Cretaceous (uppermost Campanian–uppermost Maastrichtian) vertebrate fossils, including the remains of some of the last European dinosaurs prior to the Cretaceous–Paleogene (K–Pg) extinction event. In this work, we update and characterize the vertebrate fossil record of the Arén Sandstone and Tresp formations in the Western Tresp Syncline, which is located in the Aragonese area of the Southern Pyrenees. The transitional and continental successions of these sedimentary units are dated to the late Maastrichtian, and exploration of their outcrops has led to the discovery of numerous fossil remains (bones, eggshells, and tracks) of dinosaurs, including hadrosauroids, sauropods, and theropods, along with other tetrapods such as crocodylomorphs, testudines, pterosaurs, squamates, and amphibians. In particular, this fossil record contains some of the youngest lambeosaurine hadrosaurids (*Arenysaurus* and *Blasisaurus*) and Mesozoic crocodylomorphs (*Arenysuchus* and *Agaresuchus subjuniperus*) in Europe, complementing the lower Maastrichtian fossil sites of the Eastern Tresp Syncline. In addition, faunal comparison with the fossil record of Hațeg island reveals the great change in the dinosaur assemblages resulting from the arrival of lambeosaurine hadrosaurids on the Ibero-Armorican island, whereas those on Hațeg remained stable. In the light of its paleontological richness, its stratigraphic continuity, and its calibration within the last few hundred thousand years of the Cretaceous, the Western Tresp Syncline is one of the best places in Europe to study the latest vertebrate assemblages of the European Archipelago before the end-Cretaceous mass extinction.

Keywords: late Maastrichtian; Western Tresp Syncline; Southern Pyrenees; tetrapods; Ibero-Armorican island

1. Introduction

The Cretaceous–Paleogene (K–Pg) extinction event is undoubtedly one of the most debated topics in the evolutionary history of life on the planet. Ever since a catastrophic meteorite impact at the end of the Maastrichtian was proposed as the major cause of the extinction [1], scientific debate on this event has been of ongoing significance. At the end of the Cretaceous, a set of destabilizing events occurred on Earth, including a marine regression [2], climate changes [3,4], the volcanic activity of the Deccan Volcanic Province (India) with the emission of a huge amount of gases and volcanic material into the atmosphere [5–8], and the impact of an asteroid in Chicxulub (Mexico) 66 Ma ago [1,9–12]. Although all these causes seem to have contributed to the extinction to a certain degree, the meteorite impact hypothesis shows the most solid arguments for having been the major disturbing mechanism [12–16].

Whatever the cause, the K–Pg extinction eradicated nearly 70% of the living species on Earth [17,18]. Among vertebrates, this event led to the disappearance of several groups, including non-avian dinosaurs, enantiornithine birds, pterosaurs, mosasaurs, plesiosaurs, and several lineages of crocodylomorphs, among others [19–23]. However, the mechanism by which they became extinct and how fast they did so remain difficult questions for researchers, as is the issue of how determinant the Chicxulub impact was on the stability of the ecosystems. Except for the Hell Creek Formation in North America, whose vertebrate faunas are well known [22,24,25] and their chronostratigraphic framework is well constrained [26–29], the main difficulty in assessing the end-Cretaceous extinction is the lack of well-studied sedimentary formations with vertebrate remains encompassing the K–Pg boundary. In Europe, a great effort has been made in recent decades to characterize the terrestrial uppermost Cretaceous–Paleocene formations, especially in Spain, France, and Romania (e.g., [30–33]). The best-known deposits are those from the so-called Ibero-Armorican island, which encompassed the current south of France and the north-east of Spain (Languedoc, Provence, and the Pyrenees), and other outcrops in the east, northwest, and center of Spain and part of Portugal. Of these regions, the South-Pyrenean Basin is the best-known area. Since the end of the 20th century, several research teams have worked on the uppermost Campanian–Danian outcrops in this area, improving our knowledge of the biodiversity of fossil vertebrates, the environments they inhabited, and the chronostratigraphic framework [31,33,34].

The main objectives of this paper are to review the paleontological and stratigraphical data of the western sector of the Tremp Syncline (Figure 1a), which are characterized by the thickest and most continuous upper Maastrichtian succession in the South-Pyrenean Basin, and to integrate these data within the Ibero-Armorican Maastrichtian record as a whole. Work in this area has led to the discovery of more than 50 vertebrate fossil sites and the erection of four taxa. Such a record enables us to characterize the extinction patterns of the tetrapods of the Ibero-Armorican island, especially in the last few hundred thousand years of the Maastrichtian, and to ascertain how the ecological communities were affected by the asteroid impact and its consequences.

2. The Geological and Stratigraphic Framework of the Western Tremp Syncline (Aragonese Outcrops of the Tremp Fm)

The Western Tremp Syncline is the westernmost edge of the Tremp Syncline or Tremp–Graus Basin, the largest of the sub-basins into which the Southern Pyrenees was compartmentalized by several structural highs [35]. The Pyrenees is a mountain range located in the northeast of the Iberian Peninsula between Spain and France (Figure 1a). It is structured as an asymmetric range, a NW–SE oriented belt of folds and thrusts, which was formed as a product of the collision between the European plate and the Iberian microplate. This collision took place during the Alpine orogeny between the Late Cretaceous and the Miocene [36–39]. The thrust sheets of the orogen controlled the development of a series of compartmentalized foreland basins, parallel to the axis of the orogen, which were active in different tectonic stages. The South-Pyrenean Basin was active between the Late

Cretaceous and the Oligocene and was connected with the Atlantic Ocean until the Late Eocene [40]. For this reason, its sedimentary record consists mainly of marine sediments, although at the end of the Late Cretaceous, as a consequence of the global sea level fall [2], the basin was progressively filled with westward-prograding turbiditic and deltaic sediments (Santonian-Maastrichtian) [41] and transitional and continental deposits (lower to upper Maastrichtian) [35,42]. Continental sedimentation lasted up to the Paleocene.

The Tremp Syncline or Tremp-Graus Basin is limited in the north by the Bóixols thrust sheet and in the south by the Montsec thrust sheet (Figure 1a). In the Tremp Syncline, the uppermost Cretaceous-lowermost Paleocene transitional and continental deposits consist of two closely related stratigraphic units, the Arén and Tremp formations (see lithostratigraphy by [43]; Figure 1b). The uppermost Cretaceous outcrops of the Western Tremp Syncline (*sensu* [33]) studied here comprise those located between the rivers Noguera Ribagorçana and Ésera. Thus, they constitute the part of the Tremp Syncline situated within the region of Aragón (Huesca province) (Figure 1a).

The Arén Sandstone Fm [44] is a middle Campanian–Maastrichtian transitional unit constituted by a thick succession of calcarenites with large-scale cross-bedding, which is composed mainly of quartz grains and bioclasts [45]. It represents deposition in different transitional sedimentary environments including delta [46], barrier-island [45,47], and beach deposits [48,49]. These deposits pass laterally and vertically to the Tremp Fm, since their boundary is not isochronous.

The Tremp Fm [44], traditionally known as the ‘Garumnian Facies’ [50], is a coastal to continental heterogeneous and diachronous lithostratigraphic unit that ranges between the Maastrichtian and the Paleocene. It can be subdivided into four minor lithostratigraphic units, which have received different names in the successive stratigraphic subdivisions proposed (Figure 1b) [42–44,51,52]. The scheme used here is that of Rosell et al. (2001) [43], who divided the Tremp Fm into four informal units recognizable throughout the South-Pyrenean Basin.

The lowermost unit is the so-called “Grey Garumnian”, which is characterized by a succession of grey marls and mudstones, with intercalations of sandstones, limestones, and coal beds and a rich fossil content of brackish and continental invertebrate faunas. It is interpreted as transitional deposits, including lagoon, tidal mud flats, swamp and marsh sub-environments [42,43,47,51,53–56]. The overlying unit is the ‘Lower Red Garumnian’, which is composed of reddish, brown ochre, and multi-colored mudstones, with local paleosoils and intercalated lenticular sandstone packages, sometimes with channelized bases and point-bar deposits. There are also carbonate intercalations of lacustrine origin. The ‘Lower Red Garumnian’ has been interpreted either as fluvial and alluvial deposits [43,51,55] or as deltaic-plain and perilagoonal deposits in the Western Tremp Syncline [54]. The fluvial deposits show features indicative of a marked tidal influence in the basin [54,56–58]. The ‘Grey Garumnian’ and ‘Lower Red Garumnian’ successions studied here are of Maastrichtian age, having been dated by means of the biostratigraphy of planktonic foraminifera and charophytes [56,59–61] and by magnetostratigraphy [31,62–64]. Nevertheless, due to sedimentary evolution and syntectonic activity during the Maastrichtian, the age of these units varies throughout the basin, being younger westwards [41,63]. Thus, the lower Maastrichtian is only represented in the eastern part of the basin, whereas the upper Maastrichtian is much better recorded in its western part. This distribution implies the presence in the eastern part of a sedimentary hiatus within the ‘Lower Red Garumnian’, between chron C31r and chron C29r [63].

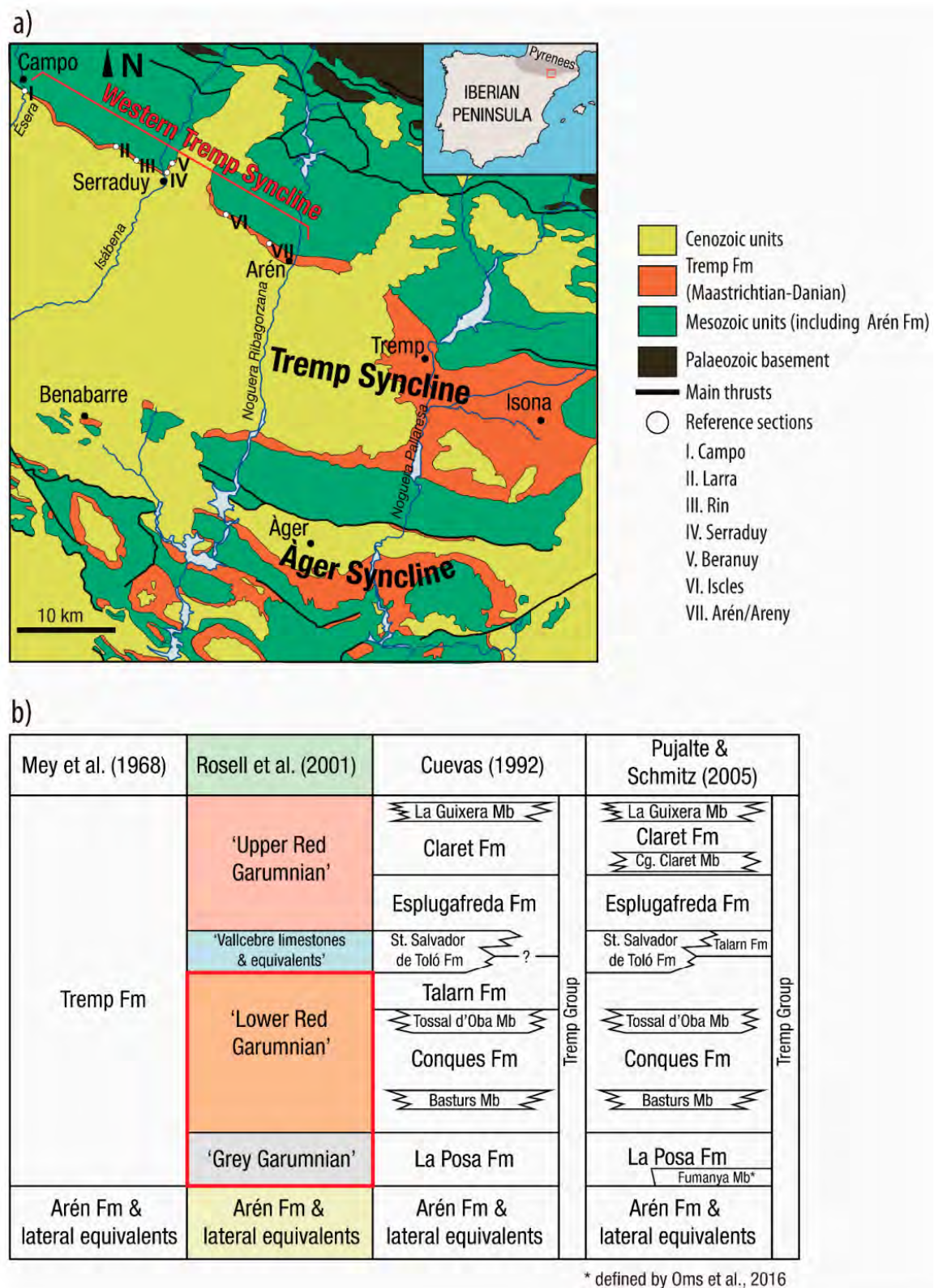


Figure 1. Geological and stratigraphic setting of the Tresp Syncline. (a) Geological map of the area of the South-Pyrenean Basin where the Tresp and Àger synclines are located. Reference sections of the Western Tresp Syncline are marked with Roman numerals: I Campo, II Larra, III Rin, IV Serraduy, V Beranuy, VI Isclès, VII Arén/Areny (map modified after [65]); (b) Stratigraphic proposals for the late Campanian-Paleocene deposits of the Tresp Syncline (modified after [66]).

The third unit of the Tresp Fm is the ‘Vallcebre limestones and equivalents’, which is a laterally discontinuous sedimentary unit of limestones with charophytes and *Microcodium* and which represents coastal lacustrine deposits [43,67]. In the Eastern Tresp Syncline, this unit has been dated as late Danian [56], which would indicate the existence of a disconformity. The K-Pg boundary would accordingly be situated somewhere between the topmost part of the ‘Lower Red Garumnian’ and the boundary with the ‘Vallcebre limestones’, with dinosaur-bearing sites lying just a few meters below the Vallcebre limestones ([31,64]; Figure 2). However, up to now, the boundary has never been recognized in the Tresp Syncline within this stratigraphic interval [43]. Finally, the last unit is the ‘Upper Red Garumnian’, which is a succession of red mudstones, sandstones, and conglomerates, with the occasional presence of paleosoils, gypsum, and limestones, representing fluvial and alluvial environments [43,51]. Its age is constrained in the Tresp Syncline between the Selandian and the late Thanetian [68,69], and at the top of the unit, the Paleocene-Eocene Thermal Maximum has been recognized [70]. It is also worth mentioning the Colmenar-Tresp Horizon [54], which is a stratigraphic level of caliche paleosoils and gypsum that can be traced across the basin. This horizon overlies the more modern sedimentary units westwards, marking a progressive unconformity within the Garumnian deposits.

The lithostratigraphic schemes used by other authors are indicated in Figure 1b. The ‘Grey Garumnian’ of Rosell et al. (2001) [43] (Figure 1b) is equivalent to the Posa Fm, whereas the ‘Lower Red Garumnian’ is equivalent to the Conques and Tarn formations of Cuevas (1992) [51]. Paleogene units also change their names. Thus, the ‘Vallcebre limestones and equivalents’ are equal to the Sant. Salvador de Toló and Suterranya formations, and the ‘Upper Red Garumnian’ is equivalent to the Esplugafreda and Claret formations. Furthermore, Cuevas (1992) [51] named as members the limestones intercalated with the mudstones of the Lower and Upper Red Garumnian, including (from older to younger) the Basturs, Tossal d’Oba, and la Guixera members (Figure 1b). Later, Pujalte and Schmitz (2005) [52] and Oms et al. (2016) [42] followed the proposal by Cuevas (1992) [51], with some modifications. Pujalte and Schmitz (2005) define the Claret Conglomerates member within the Claret Fm, and Oms et al. (2016) differentiate the Fumanya Member (lower Maastrichtian tidal flat deposits within La Posa Fm), which is preserved only in the eastern part of the South-Pyrenean Basin.

In the Western Tresp Syncline studied here, there are some sedimentological particularities that sometimes make it difficult to locate the formations and boundaries proposed in the Eastern Tresp Syncline. The boundary between the Conques and Tarn formations (equivalent units to the ‘Lower Red Garumnian’) is defined by the sharp contact between mudstones and conglomerates, or a swift change of light-colored mudstones to red mudstones and sandstones [51]; however, neither of these contacts can be observed in the Western Tresp Syncline. Moreover, chronostratigraphic data in the eastern part of the Tresp Syncline [63,71] restrict the Conques Fm to the early Maastrichtian (within chron C31r) and the Tarn Fm to the late Maastrichtian (chron C29r), a great part of the late Maastrichtian not being recorded (hiatus between C31r and C29r). By contrast, in the Western Tresp Syncline, the lateral equivalents to these units (‘Lower Red Garumnian’) are dated to within the late Maastrichtian chrons C30n–C29r [31,62,64,72], thus being the only part of the basin where chron C30n is recorded. According to the lithostratigraphic and depositional model proposed by Ardèvol et al. (2000) [41] and updated by Fondevilla et al. (2016) [63], the Tarn Fm is limited to the eastern part of the basin (see [63], Figure 8c). As a direct correlation is not possible, since part of the succession is overlaid by discordant Neogene conglomerates (Figure 1a), it is quite difficult to determine whether the ‘Lower Red Garumnian’ in the Western Tresp Syncline corresponds to an upper Maastrichtian Conques Fm or the Tarn Fm. A similar pattern is observed with the ‘Vallcebre limestone’ of the Western Tresp Syncline, which cannot be directly correlated with the St. Salvador de Toló and Suterranya formations to the east due to their lateral discontinuity. Finally, westwards, the continental deposits of the Tresp Fm pass laterally to the marine Laspún and Navarri formations [69,73].

3. The Upper Maastrichtian Tetrapod Fossil Record of the Western Tremp Syncline and Its Integration within the Ibero-Armorican Island Record

The sedimentary succession of the Tremp Fm in the Western Tremp Syncline here under study encompasses sedimentary rocks belonging to the ‘Grey Garumnian’ and ‘Lower Red Garumnian’, and therefore, the late Maastrichtian between the upper part of chron C30n and chron C29r (Figure 2). The studied area is the part of the Tremp Syncline where the thickest succession of the upper Maastrichtian is preserved (more than 210 m). In these upper Maastrichtian sediments, there is a diverse and significant record of vertebrate fossils, including avian and non-avian dinosaurs, crocodylomorphs, testudines, squamates, amphibians, and fishes. More than 1200 fossil remains have been recovered from the hilly outcrops, with 57 different fossil localities identified. In order to facilitate our explanation of the Western Tremp Syncline fossil record, we have clustered the paleontological sites by their closeness to certain reference stratigraphic logs, which are called the Campo (I), Larra (II), Rin (III), Serraduy (IV), Beranuy (V), Isclés (VI), and Areny (VII) sections (Figures 1a, 2 and 3). A table summing up the assemblage from all the sites can be found in the Supplementary Materials Table S1. All the fossils are housed at the Natural Science Museum of the University of Zaragoza (Spain) (MPZ) [74].

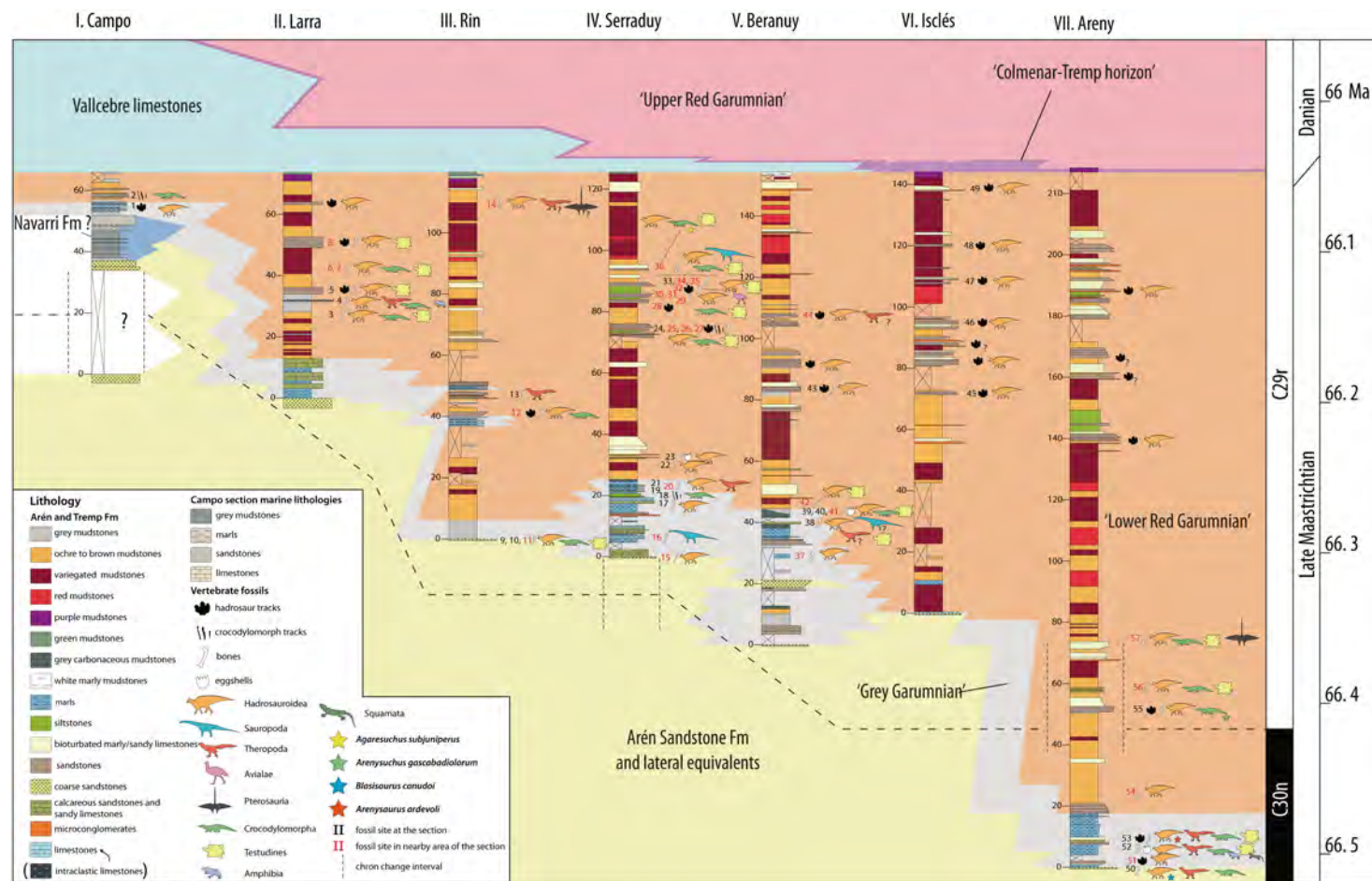


Figure 2. Correlation panel of the Western Tresp Syncline (W-E oriented) with the stratigraphic position of the vertebrate fossil sites: (1) Campo 1, (2) Campo 2, (3) Larra 3, (4) Larra 4, (5) Larra 5, (6) Larra 1, (7) Larra 2, (8) Larra 6, (9) Rin1, (10) Rin2, (11) Barranco Extremadura, (12) Pedregal, (13) Camino Rin 1, (14) Camino Rin 2, (15) Fuente San Cristobal, (16) Femur, (17) Barranco Serraduy 1, (18) Beranuy, (19) 172-i/04/d, (20) 172-i/04/c, (21) 172-i/04/e, (22) Barranco Serraduy 2, (23) 172-i/04/f, (24) Barranco Serraduy 3, (25) 172-i/04/a, (26) Color, (27) Serraduy Norte, (28) Dolor 1, (29) Dolor 2, (30) Dolor 3, (31) 172-i/04/b, (32) Amor 1, (33) Barranco Serraduy 4, (34) Barranco Serraduy 5, (35) Amor 2, (36) Amor 3, (37) Fornons 1, (38) Camino Fornons 1, (39) Camino Fornons 2, (40) Veracruz 1, (41) Fornons 2, (42) Sierra del Sis 1, (43) Sierra del Sis 2, (44) Fornons 3, (45) Isclés 1, (46) Isclés 2, (47) Isclés 3, (48) Isclés 4, (49) Isclés 5, (50) Blasi 1, (51) Areny 1, (52) Blasi 2a and 2b, (53) Blasi 3, (54) Blasi 3, 4, (55) Elias, (56) Blasi 4, (57) Blasi 5 (Larra log is modified from Puértolas Pascual et al. (2018), magnetostratigraphic data from [31,64,75]).

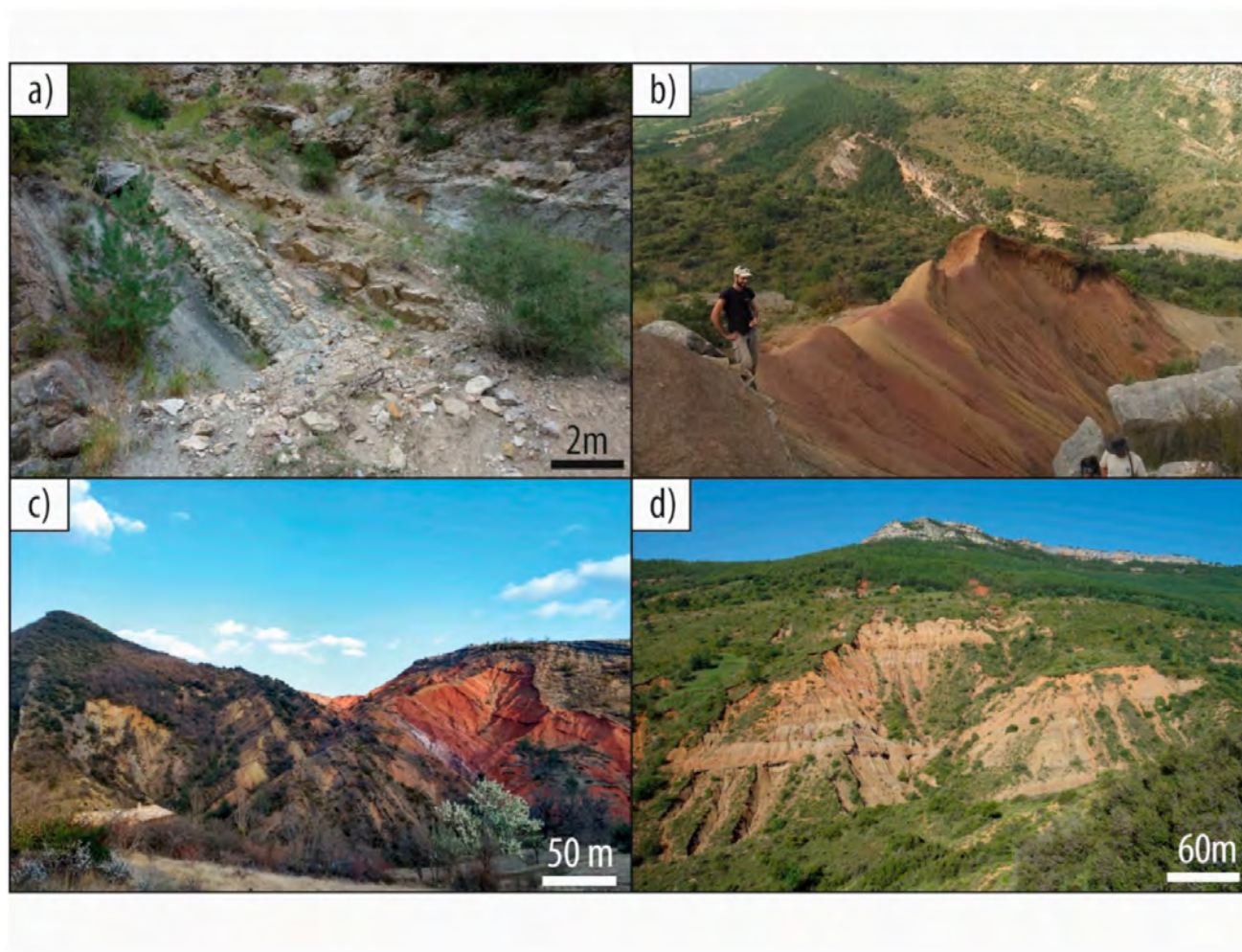


Figure 3. Upper Maastrichtian outcrops of the Western Tremp Syncline (Aragón, NE Spain). (a) Campo section (I); (b) Serraduy section (IV); (c) Isclés section (VI); (d) Arén/Areny section (VII).

3.1. Dinosauria

3.1.1. Hadrosauroidea

Hadrosauroid dinosaurs are the clade of Cretaceous ornithomorphs with the most abundant fossil record, especially in the Northern Hemisphere. In Europe, the best record of hadrosauroids has been recovered from France and Spain. In Spain, it is concentrated principally in the South-Pyrenean Basin (the provinces of Huesca and Lleida, NE Spain) [23,62,75–81].

In the Western Tremp Syncline, hadrosauroids are recorded in the upper Maastrichtian sediments of the Arén Sandstone Fm and the ‘Grey and Lower Red Garumnian’ of the Tremp Fm; these are among the youngest non-avian dinosaurs in the world [64]. The first hadrosauroid bones were found in the 1990s near the locality of Arén (Areny in Catalan) (Huesca, Aragón) by the geologists Lluís Ardèvol and Fabián López Olmedo during geological mapping work. Early work on several sites (Blasi 1 to 5 and Blasi 3,4) by a multidisciplinary team yielded fossil remains of indeterminate euhadrosaurids together with bones and eggshells of several dinosaurs and other terrestrial and aquatic vertebrates [72] (Figure 2). Later studies on specimens from the Blasi 1 and Blasi 3 sites resulted in the erection of two lambeosaurine hadrosaur species: *Blasisaurus canudo* Cruzado-Caballero, Pereda-Suberbiola, and Ruiz-Omeñaca 2010a [82] (Figures 3 and 4b)

and *Arenysaurus ardevoli* Pereda-Suberbiola, Canudo, Cruzado-Caballero, Barco, López-Martínez, Oms and Ruiz-Omeñaca [62,83] (Figures 3 and 4a,c). Both sites fall within the upper part of chron C30n [62]. These two species are recovered within Arenysaurini, which is a recently erected clade of lambeosaurines from Europe [84].

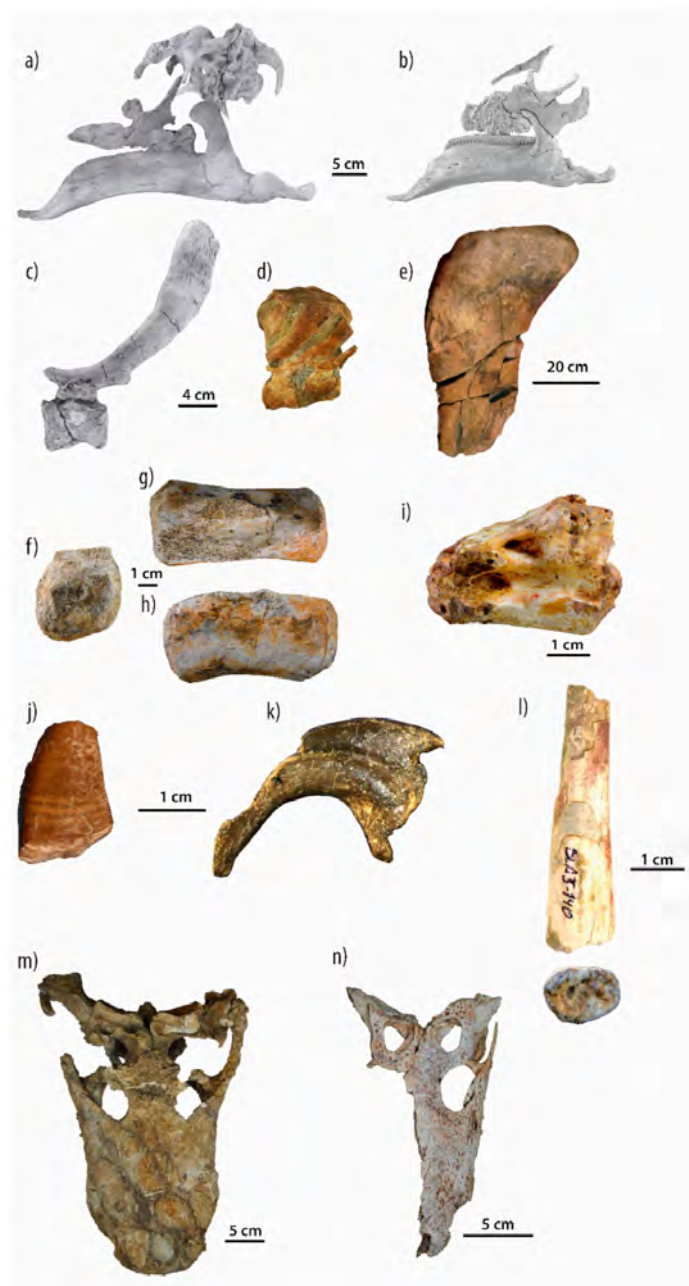


Figure 4. Main tetrapod remains from the Western Tremp Syncline. (a) Cranial elements of *Arenysaurus ardevoli* (MPZ2008/17, MPZ2008/256, MPZ2008/258, MPZ2008/259, MPZ2011/01), in left lateral view (modified from Cruzado-Caballero et al., 2013); (b) cranial elements of *Blasisaurus canudoii* (MPZ 99/664, MPZ 99/665, MPZ99/666a, MPZ99/666b, MPZ99/667, MPZ 2009/348), in left lateral view; (c) mid-caudal vertebra of *Arenysaurus* (MPZ204/480), in left lateral view (modified from Cruzado-Caballero et al., 2013); (d) articulated mid-caudal vertebrae of the small hadrosaurid from Serraduy (MPZ 2013-371), in left lateral view; (e) femur (proximal end) of *Titanosauria* indet. from Serraduy (MPZ 99/143), in posterior view (modified from Puértolas-Pascual et al., 2018); (f–h) posterior caudal vertebra of *Titanosauria* indet. (MPZ2021/1), in anterior view (f); dorsal view (g); left lateral view (h); (i) cervical vertebra of *Ornithuromorpha* indet. (MPZ 2019/264), in left lateral view; (j) cf. *Arcovenator* tooth (MPZ 2017/804), in lingual view; (k) pedal ungual II of *Dromaeosauridae* indet. (MPZ 2019/196), in lateral view; (l) fragmentary bone of *Pterosauria* indet. (MPZ 2021/54) (note the thin cortex in the transverse section); (m) skull of *Agaresuchus subjuniperus* (MPZ 2012/288), in dorsal view; (n) skull of *Arenysuchus gascabadiolorum* (MP Z2011/184), in dorsal view.

In addition to this, other remains of indeterminate hadrosaurids and euhadrosaurids have been described from the Blasi sites [76,78,85–87]. The findings from these sites have also led to the first description of a pathological bone from a hadrosaurid in Spain [88] and the first paleo-neuroanatomical description of a European lambeosaurine, *Arenysaurus ardevoli* [89]. Recent studies on the paleohistology of the hadrosauroids from the Blasi sites reveal the presence of hadrosaurid individuals at different ontogenetic stages, including early and late juveniles, subadults, and mature adults [90,91]. New areas with hadrosaurid remains have been found in the vicinities of Serraduy (Isábena, Huesca, Aragón) and Beranuy (Huesca, Aragón) (Figure 2) [23,64,77,79,92–94]. The new sites are characterized by the presence of fossil remains of the smallest adult hadrosaurids (maybe affected by insular dwarfism) from Europe, which coexisted alongside larger hadrosaurids [79] (Figure 4d).

This rich osteological record of hadrosauroids in the Western Tremp Syncline is complemented by several track sites. These tracks appear in several levels from Arén to Campo (Huesca, Aragón), with large ornithopod footprints, many of which have been referred to the ichnogenus *Hadrosauropodus* [31,64,95,96] (Figures 3 and 5a,b), spanning from the top of chron C30n into chron C29r. Recently, in the Blasi 2B site, eggshells attributable to hadrosaurid dinosaurs have been tentatively referred to *Spheroolithus* aff. *europaeus* Sellés, Vila, Galobart 2014 [97,98].

3.1.2. Sauropoda

The sauropod remains in the Western Tremp Syncline are very scarce compared to those in the eastern part, where titanosaur bones, eggshells, and tracks are moderately abundant [33,71,99]. A remarkable specimen is the proximal half of a femur (MPZ 99/143) that probably corresponds to a large and indeterminate titanosaur [71,100] (Figure 4e). MPZ 99/143 was recovered northwest of the town of Serraduy, in the ‘Grey Garumnian’ unit (‘Femur’ site in Figure 2). Interestingly, the femur was originally correlated to the top of chron C30n, but the chronostratigraphical data indicate that this fossil lies within chron C29r [31,64]. Thus, this femur is one of the youngest records of titanosaurian sauropods in the Ibero-Armorican island, along with those recorded in fossil sites in the Catalonia region, including the ‘Molí del Baró-2’ femur [71], the vertebra from ‘El Portet’ site [101], and the skin impressions and footprints from the ‘Mirador de Vallcebre’ [102]. In addition, Cruzado-Caballero et al. (2012) [77] reported a caudal vertebral centrum that was found in the ‘Lower Red Garumnian’ unit near Serraduy and Beranuy. The caudal vertebra (MPZ 2021/1) is from the ‘Barranco Serraduy 4’ site (Serraduy) (Figures 2 and 4f–h), which is situated stratigraphically above the ‘Femur’ site, making it the youngest evidence of sauropods in the Western Tremp Syncline. MPZ 2021/1 is a slightly deformed centrum from a posterior caudal vertebra, which is elongated craniocaudally and compressed dorsoventrally. It is amphiplatyan, with both articular surfaces flat to slightly concave and with a rounded contour (Figure 4f,h). In anteroposterior view, the centrum has a subcircular outline (Figure 4f). Its ventral surface is slightly concave and lacks chevron facets (Figure 4h). Together with its length and the absence of transverse processes, this indicates that it was situated distally in the caudal series [103]. The neural arch is not preserved, but its attachment facets can be observed in the anterior area of the centrum (Figure 4g), which is a synapomorphy of Titanosauriformes [104]. The amphiplatyan condition in the middle and posterior caudal vertebrae is plesiomorphic within Titanosauria [104,105]. Some basal titanosaurs show this condition, as is the case of *Andesaurus* [106,107] or the distalmost vertebrae of *Lirainosaurus* [103]. Therefore, we tentatively refer it to Titanosauriformes indet., but for the reasons mentioned above, its ascription to Titanosauria cannot be ruled out.



Figure 5. Tetrapod tracks from the Western Tresp Syncline. (a) *Hadrosauropodus* trackway from the Areny 1 site; (b) foot cast of a hadrosaurid dinosaur from the 172-i/04/a site; (c) crocodylomorph tracks from the Serraduy Norte site.

3.1.3. Theropoda

Theropod fossils are scarce in the Western Tresp Syncline, and these are mainly represented by teeth, eggshells, and some isolated bones. Torices et al. (2015) [108] describe several teeth from the Blasi sites of Arén/Areny (Figure 2). They identify one

morphotype as Coelurosauria indet. (MPZ 98/79 to 82) and three morphotypes belonging to maniraptoran theropods, including *Richardoestesia* sp. (MPZ 98/72 to 74, MPZ 2004/7), cf. *Paronychodon* (MPZ 98/76 to 78), and Dromaeosauridae indet. (MPZ 2004/6). Finally, they describe two different morphotypes of large teeth whose assignation is problematic and that are referred to Theropoda indet. 1 (MPZ 98/67, MPZ 2004/3 to 5, 8) and Theropoda indet. 2 (MPZ 98/68), although a possible relation with neoceratosaurs is suggested. In fact, these two morphotypes were identified by Pérez-García et al. (2016) as cf. *Arcovenator* [109], which is an abelisaurid species from the Campanian of southern France. The Blasi sites 1, 2, and 3 are dated to within chron C30n [62] (Figure 2). Two more theropod teeth have been described from the fossil sites of 172-i/04/e (Serraduy) and Larra 4 (Valle de Lierp) [64]. The first tooth (MPZ 2017/804) (Figure 4j) is large and resembles the Theropoda indet. morphotype 1 (cf. *Arcovenator*) from Torices et al. (2015) [108], and the second one has been identified as Coelurosauria indet. Both sites are situated in outcrops of the ‘Lower Red Garumnian’ dated to within chron C29r [64].

Postcranial fossils of theropods are not very common and are usually fragmentary. A pedal ungual II (MPZ 2019/196) (Figure 4k) and the proximal part of an ulna (MPZ 2019/194) from a dromaeosaurid theropod were found at the Larra 4 site (Valle de Lierp, Huesca, Aragón, Spain) (Figure 2) [93]. Other sites in the Serraduy area have yielded fragmentary remains of indeterminate theropods (Figure 2). As regards avian theropods, a cervical vertebra from a large ornithuromorph bird has recently been described from the Tresp Fm outcrops between Serraduy and Bascas de Obarra (Beranuy, Huesca) (MPZ 2019/264) [110] (Figures 2 and 4i). It has been dated as uppermost Maastrichtian (C29r) [64] and represents the youngest record of a Mesozoic bird in Europe.

Up to now, theropod eggshells have only been found in the site Blasi 2B (‘Grey Garumnian’ at Arén/Areny, C30n; Figure 2). This site has a diverse theropod eggshell assemblage, which was briefly described by López-Martínez et al. (1999) [111]. The authors recognized up to six different types of primateolithid eggshells, whereas more recent research [98,112] recognized at least four different types (Figure 6a,b), including two different morphotypes attributable to the oogenus *Pseudogeckoolithus*, which has recently been referred to maniraptoran theropods [113]. Further research is necessary to ascertain the exact number of theropod ootaxa present at Blasi 2B.

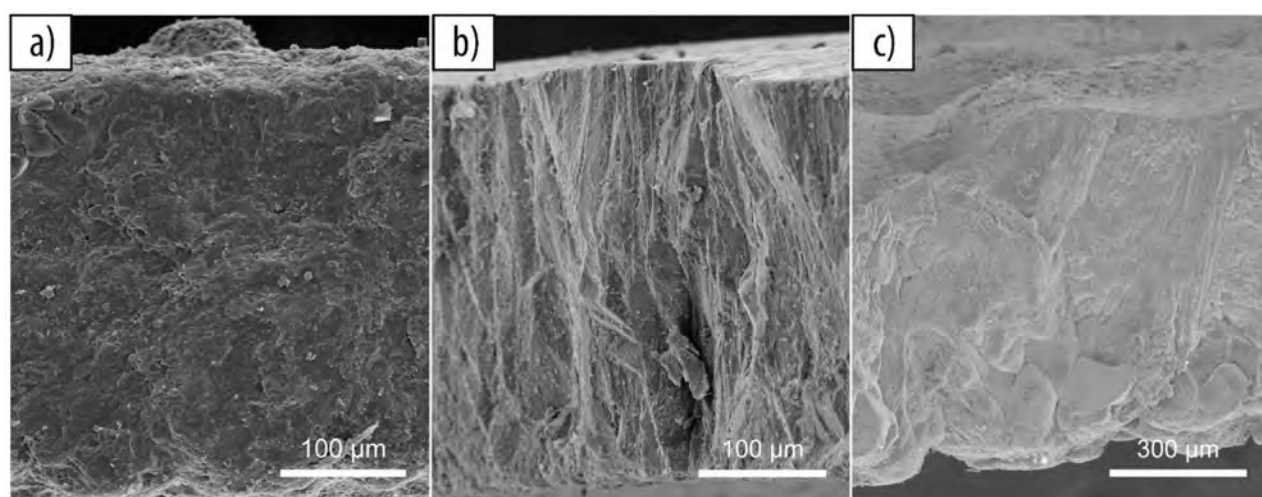


Figure 6. Tetrapod eggshells from the Western Tresp Syncline. (a) *Pseudogeckoolithus* sp. from the Blasi 2B site; (b) Prismatoolithidae indet. from Blasi 2B; (c) *Krokolithes* sp. from the Veracruz 1 site.

3.2. Pterosauria

The presence of pterosaurs in the upper Maastrichtian of the Tresp Syncline has only been reported from the site of Torrebillas-2 in the Eastern Tresp Syncline, within chron

C29r [114]. In the Western Tremp Syncline, Puértolas-Pascual et al. (2018) [64] reported a possible mandible of a pterosaur from the upper part of the ‘Lower Red Garumnian’ near Serraduy (Isábena). This specimen has been reexamined, and although its identification as a dentary has been refuted, its affinity to a pterosaurian bone cannot be ruled out. However, until a future study identifies this bone more precisely, it cannot be assigned to Pterosauria. Nevertheless, we have identified a fragment of a long bone from the Blasi 5 site (Figures 2 and 4l) that shows a very thin cortex (thinner than the pterosaur bones from Barranc de Torrebilles-2 [114]) and is hollow inside. This bone could be the first pterosaur fossil identified in the Western Tremp Syncline. Blasi 5 is situated in the upper part of the ‘Lower Red Garumnian’ and is dated to within chron C29r (Figure 2) [62].

3.3. Crocodylomorpha

The crocodylomorph record in the Western Tremp Syncline is dominated by eusuchians. Two skulls belonging to two different genera have been identified. The first one is *Arenysuchus gascabadiolorum* Puértolas, Canudo, Cruzado-Caballero 2011 [115] (MPZ 2011/184) (Figure 4n), from the Elias site near Arén/Areny (‘Lower Red Garumnian’, C29r, Figure 2). Phylogenetically, MPZ 2011/184 was initially placed within Crocodyloidea (crown-group Crocodylia) [115], but later cladistic studies have situated it as a more basal eusuchian within Allodaposuchidae [116–120]. The second species is the allodaposuchid *Agaresuchus subjuniperus* Puértolas-Pascual, Canudo, Moreno-Azanza 2014 [121] (MPZ 2012/288) (Figure 4m). MPZ 2012/288 was initially identified as a member of the genus *Allodaposuchus* [121], but it was later reassigned to *Agaresuchus* [119]. This crocodylomorph comes from the Amor 3 site near the town of Serraduy, from one of the uppermost levels of the ‘Lower Red Garumnian’ (C29r, Figure 2). As such, it could be one of the youngest crocodylomorphs on the Ibero-Armorican island before the K-Pg extinction. In addition, allodaposuchids are also represented by isolated teeth in several sites throughout the C30n–C29r interval (Figure 2) [23,64,93,94,122]. All these teeth are conical with pointed crowns, showing the typical morphology of crocodylomorphs with a generalist diet. These dental morphologies have been observed in several allodaposuchid species from the Late Cretaceous of Europe (e.g., [122]). As the presence of other crocodylomorph clades with generalist dentition cannot be ruled out, these teeth were assigned to cf. Allodaposuchidae, since this is the most abundant clade in this region and time interval.

Gavialoidea is another clade of crocodylomorphs that may be present in the upper Maastrichtian of the Western Tremp Syncline. A few elongated conical teeth with basiapical ridges have been assigned to cf. *Thoracosaurus*. These are restricted to the transitional environments of the Arén Fm and the ‘Grey Garumnian’ unit of the Tremp Fm close to Arén/Areny, Beranuy and Serraduy (Figure 2) [23,64,122].

Hylaeochampsidae are represented by tribodont teeth from the Blasi 2B site, which were identified as cf. *Acynodon* (MPZ-2017/1137) [23,64,72,122]. The eusuchian record is augmented by teeth, osteoderms, and vertebrae from the Blasi and Serraduy sites, whose taxonomical position within Eusuchia is difficult to assign with precision. They are accordingly identified as Eusuchia indet. [23,64,72,122] (Figure 2).

López-Martínez et al. (2001) [72] pointed out the presence of “trematochampsid”-like and alligatoroid teeth from the sites of Blasi 1, 2, and 3 (Figure 2). However, although the authors did not provide pictures or specimen numbers, the morphotypes in question probably correspond to more recently erected taxa that had not been described at the time of publication of that paper. The “trematochampsid”-like teeth may correspond to non-eusuchian crocodylomorphs more typical of the Late Cretaceous of Europe, such as *Sabresuchus* or *Doratodon*, and the alligatoroid teeth probably correspond to allodaposuchids. In addition, Blanco et al. (2020) [122] mentioned the presence of a conical tooth (MPZ 2010/948) with enamel striations and crenulated carinae assigned to Mesoeucrocodylia indet.

There are also crocodylomorph eggshells from the Blasi 2 site (upper part of C30n, Figure 2). These were first reported as megaloolithid eggshells [111], but they were

later [123] described as having a crocodyloid morphotype and were identified as *Krokolithes* sp. Hirsch, 1985 [124], implying that these eggs were laid by crocodylomorphs. Something similar has occurred with the eggshells found at the Veracruz 1 site close to Biascas de Obarra, (Beranuy section, C29r, Figure 2), which were first identified as hadrosaurid eggshells [94] (Figure 6c), but after a more thorough study, their crocodylomorph affinities have been ascertained, and a description is in preparation.

Finally, the crocodylomorph record also includes several swimming and plantigrade tracks from the Serraduy, Beranuy, and Campo outcrops, all within chron C29r [23,125,126] (Figures 2 and 5c). This is the youngest record of crocodylomorph tracks in Europe. These tracks represent digit scratch marks produced by the manus and pes of buoyant crocodylomorphs, and they have been assigned to the ichnogenus *Characichnos*. One pedal impression has been assigned to cf. *Crocodylopodus*, and although its assignation cannot be confirmed with certainty due to the scarce material, this is the youngest occurrence of this ichnotaxon [125].

3.4. Testudines

Testudines are represented mainly by disarticulated plates of the carapace or the plastron, which appear at most of the paleontological sites from the topmost part of the Arén Fm to the upper levels of the ‘Lower Red Garumnian’ (Figure 2). Most of these remains show fine ornamentation comprising thin dichotomic grooves, which is a distinctive character of the bothremydids [127]. Among these remains, Murelaga and Canudo (2005) [128] describe several plates from the Blasi sites near Arén/Areny (Figure 2), including nuchal, pleural, and peripheral plates, a hyoplastron, a hypoplastron, and a xiphiplastron from bothremydid turtles. At the site of Rin 2, near the town of Serraduy (Isabena municipality), situated in the topmost part of the Arén Fm, Murelaga and Canudo (2005) [128] describe a xiphiplastron and a mesoplastron from a bothremydid. Pérez-Pueyo et al. (2019a, 2019b) [93,94] also describe indeterminate plates from this kind of turtle from the Larra 4 (Valle de Lierp) and Veracruz 1 (Biascas de Obarra, Beranuy) sites (Figure 2). Thus, the record of this group of pleurodiran turtles extends from the upper part of chron C30r to near the K-Pg boundary interval. It is also important to note that Murelaga and Canudo (2005) [128] identify a peripheral plate from a solemydid turtle from the Blasi 2 site (Figure 2). This shows its characteristic vermiculate ornamentation, although it is not well preserved.

3.5. Amphibia and Squamata

The Blasi 2 site has yielded a rich microvertebrate fossil assemblage, which includes the bones of small tetrapods, mainly amphibians and squamates [129] (Figure 2). Amphibian remains dominate, with at least one albanerpetontid (resembling the North American taxon *Albanerpeton nexuosum*) and two anurans, a discoglossid and a palaeobatrachid. The squamate remains comprise at least two undetermined lizards, one anguid lizard, and a snake. Blasi 2B is dated to the top of chron C30n in the ‘Grey Garumnian’ and is the only well-studied microvertebrate site in the Western Tremp Syncline. However, it is noteworthy that the Larra 4 site (Valle de Lierp) (C29r) has yielded remains from discoglossid amphibians [64], making it the youngest microvertebrate site in the Western Tremp Syncline.

3.6. The Tetrapod Fossil Record from the Upper Maastrichtian of the Ibero-Armorican Island

The tetrapod fossil record of the Western Tremp Syncline adds several unique taxa to the late Maastrichtian assemblages of the Ibero-Armorican island, yielding the youngest record of some groups prior to the Paleocene. To date, the upper Maastrichtian record of the Ibero-Armorican island is limited to the South Pyrenean Basin in northeast Spain; the Sobrepueña Fm, Torme Fm, and equivalent outcrops in northwest Spain [130,131]; east Spain near Tous (Valencia) [132,133]; and the Haute-Garonne and Aude departments in southern France [33,134]. During the Maastrichtian, the dinosaur faunas underwent a change in dominant herbivores during the so-called “Maastrichtian Dinosaur Turnover” [33,34,135].

During the early Maastrichtian, ecosystems were inhabited by rhabdodontid ornithopods, titanosaurian sauropods and ankylosaurs, whereas in the late Maastrichtian, these communities were replaced by hadrosaurid ornithopods and new titanosaurian forms. However, nodosaurid ankylosaurians still persisted up to chron C30r, coexisting with these new assemblages for nearly 2 Myr [33].

Lambeosaurine hadrosaurids were present in the Ibero-Armorican island from the late early Maastrichtian, mostly recorded from the Pyrenees (Spanish and French). The lambeosaurine from Els Nerets (Vilamitjana, Catalonia, NE Spain) is the oldest evidence of hadrosaurids in Europe, which was dated to within chron C31r [81]. Lambeosaurines are also present within chron C29r, with some fossils falling very close to the K-Pg boundary. At present, there are five species of lambeosaurine hadrosaurids described from the region, comprising *Adynomosaurus* from the Costa de Les Solanes site (Basturs, Catalonia) [136], *Arenysaurus* [62], *Blasisaurus* [82] from Areny and Blasi sites (Ribagorça, Aragón, NE Spain), *Pararhabdodon* from the Sant Romà d'Abella site (Lleida, Catalonia, NE Spain) [80,137–139], and *Canardia* from the Lacarn and Tricouté sites (Haute-Garonne, southern France) [80]. Additional hadrosauroid remains include the aforementioned lambeosaurinae from Els Nerets [81] and other indeterminate lambeosaurines from Basturs Poble and Les Llaus (Lleida, Catalonia) [80,140–142]; a non-hadrosaurid hadrosauroid from Fontllonga-R (Fontllonga, Catalonia, NE Spain) [75]; an indeterminate euhadrosaurid from Blasi 3,4 [78]; and a small hadrosaurid from Serraduy [79]. Outside the Pyrenees, there is a dentary from La Solana (Tous, Valencia, E Spain) that has been identified as belonging to an indeterminate hadrosaurid [75,143]. Finally, there is a hadrosauroid femur from the Albaina site (Laño, Condado de Treviño, Burgos, NW Spain) [144]. With six to twelve taxa, hadrosauroids are the most speciose clade of dinosaurs in the Tremp Basin, five to eight of them being lambeosaurine hadrosaurids (Table 1, Figures 7 and 8).

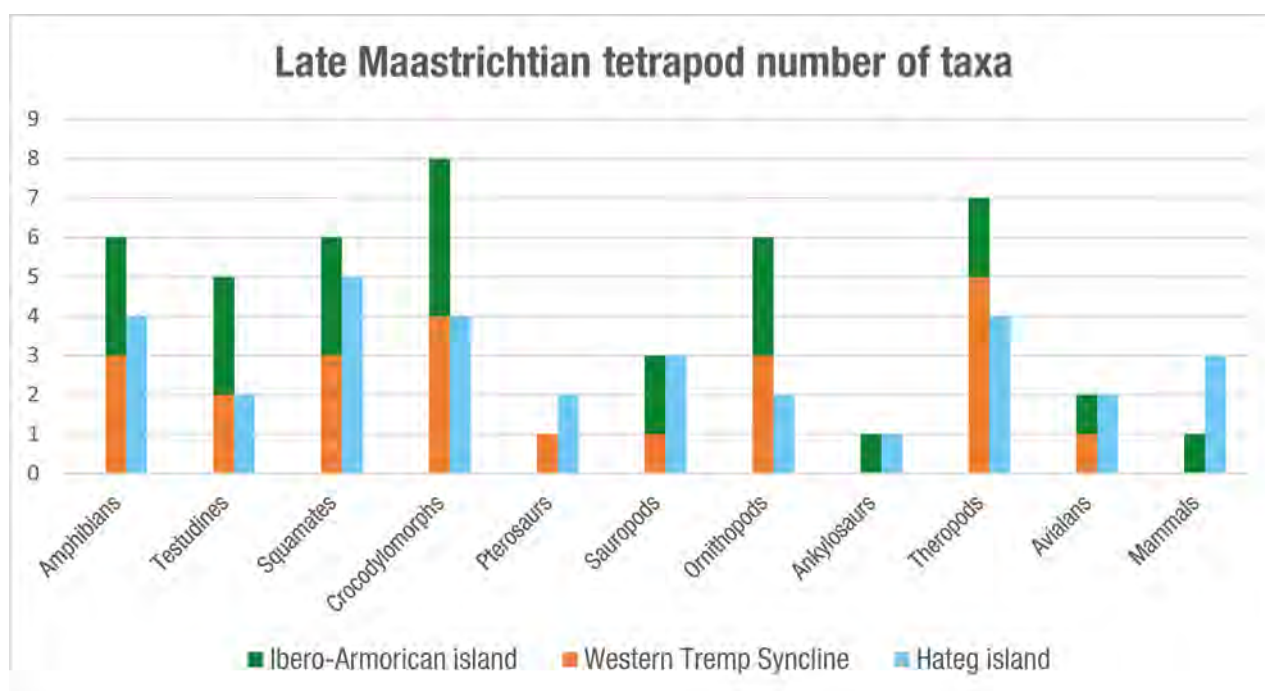


Figure 7. Bar chart with the minimum number of tetrapod taxa (genera) present in the Ibero-Armorican island and Hateg island during the late Maastrichtian.

Table 1. Number of tetrapod taxa present on the Ibero-Armorican and Hațeg islands during the late Maastrichtian. Red numbers mark possible additional taxa.

Taxon	Ibero-Armorican Island	Western Tresp Syncline	Hațeg Island
Amphibia	6	3	4
Anura	4	2	3
Albanerpetontidae	1	1	1
Salamandridae	1	—	—
Squamata	6 + 2?	3 + 2?	5
‘Scincomorpha’	1	1?	1
Anguimorpha	1	1	1
Teiioidea	1	—	1
Borioteiioidea	—	—	1
Scleroglossa	1	1	—
Iguanidae	1	1?	—
Amphisbaenia	1?	—	—
Varanoidea	1?	—	—
Alethinophidia	1	1	1
Testudines	5	2	2
Meiolaniformes	—	—	1
Pan-Pleurodira	3	1	1
Pan-Cryptodira	2	1	—
Crocodylomorpha	8	4	4
Notosuchia (<i>Doratodon</i>)	1	—	1
Neosuchia (‘Atoposauridae’)	1	—	1
Basal Eusuchia	4	2	1
(Allodaposuchidae)			
Basal Eusuchia			
(Hylaeochampsidae, cf. <i>Acynodon</i>)	1	1	1
Eusuchia (Gavialoidea)	1	1	—
Pterosauria	1	1	2
Azhdarchidae	1	1	2
Dinosauria	18 + 1? (6)	10 (1)	12 + 1? (3)
Sauropoda	3	1	3
Titanosauria	3	1	3
Theropoda	8 + 1?	6	6 + 1? (3)
Alvarezsauridae	—	—	1?
Abelisauroidae	1	1	—
Coelurosauria indet.	1	1	—
Maniraptora	5	3	3 (2)
Paraves with uncertain affinities (<i>Balaur</i> , <i>Elopteryx</i>)	—	—	1 (1)
Enantiornithes	1?	—	1
Ornithuromorpha	1	1	1
Ornithopoda	6 (6)	3 (1)	2
Rhabdodontidae	—	—	1
Hadrosauroidae	6 (6)	3 (1)	1
Ankylosauria	1	-	1
Nodosauridae	1	—	1
Mammalia	1?		3
Multituberculata	—	—	3
Theria	1?	—	—

Ankylosaurs are represented during the late Maastrichtian by isolated and fragmentary material referred to nodosaurids from several sites in the Southern Pyrenees within the Lleida province (Catalonia, NE Spain), including Els Nerets [145], Fontllonga-6 [111], and Biscarri [146]. They are also present at the Lestaillats site, in the Petite Pyrénées (Haute-

Garonne, southern France) [134]. Their last occurrence is documented at the Fontllonga-6 and Lestaillats sites, dated to within chrons C30r and C30n (Figure 8).

Titanosaurs from the upper Maastrichtian of the Ibero-Armorican island consist mainly of three undetermined but distinct taxa represented by three femur morphotypes [71] (Figures 7 and 8). The femur from Serraduy corresponds to a large titanosaur, whereas the other two femora represent small-medium titosaurs. Although not formally described, these titosaurs represent different taxa from those of the early Maastrichtian assemblage [71]. This distinction is additionally supported by the distinct ootaxa association reported from the pre- and post-turnover assemblages, respectively [33,99].

Theropods from the late Maastrichtian of the Ibero-Armorican island are mainly abelisaurids and maniraptorans [64,93,108,147,148], and they have been found only in the South-Pyrenean Basin. Due to their fragmentary and incomplete nature, the number of taxa is difficult to determine. Based on tooth morphotypes from the Southern Pyrenees, at least one abelisaurid taxon inhabited the island during the late Maastrichtian (Theropoda indet. 1 and 2 or cf. *Arcovenator*; [108]) (Figures 7 and 8). Maniraptorans are also represented mainly by teeth from the Southern Pyrenees, with at least three taxa identified in this way (*Richardoestesia*, *Paronychodon*, and Dromaeosauridae indet. from [108]), and by the troodontid *Tamarro insperatus* Sellés, Vila, Brusatte, Currie and Galobart 2021 [149], which were recently described on the basis of skeletal remains (Table 1, Figures 7 and 8). However, the real abundance of theropods is hard to establish, since there are several fragmentary skeletal remains attributable to undetermined dromaeosaurids, and an oological record comprising several ootaxa of maniraptoran-like eggshells, including *Prismatoolithus trempii* Sellés, Vila, Galobart 2014 [150], and *Pseudogeckoolithus* Vianey-Liaud and López-Martínez 1997 [151] ([98,113,150]). Avialan dinosaurs are represented by the giant ornithuromorph bird from Beranuy [110] and a putative enantiornithine from southern France [152] (Table 1, Figures 7 and 8).

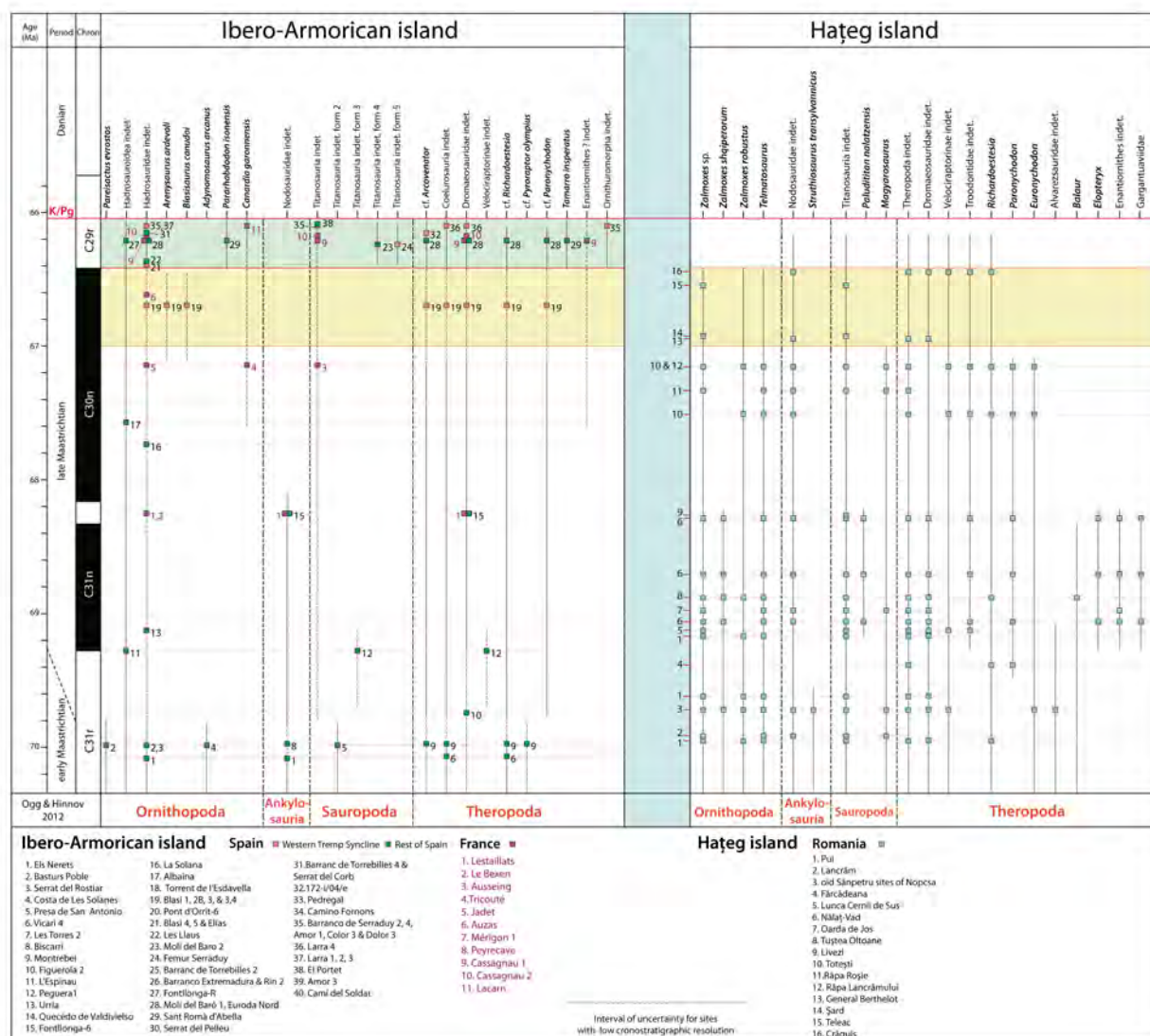


Figure 8. Dinosaur groups and species occurrences in the Ibero-Armorican island and Hațeg island during the late Maastrichtian. Hațeg island data are based on [32] with updated information. The yellow band marks the temporal interval used for comparison, whereas the green band marks the last ≈ 350 ka of the Maastrichtian, with a record only in the Ibero-Armorican island. Magnetostratigraphic scale based on [153] and calibration for the K-Pg boundary based on [28].

The pterosaur record in the late Maastrichtian is scarce, with some isolated and fragmentary bones from the Pyrenees of France [154–156] and Spain [114] and from the upper Maastrichtian outcrops near Valencia (Spain) [157,158] (Figure 9). All of them have been identified as belonging to undetermined giant azhdarchids.

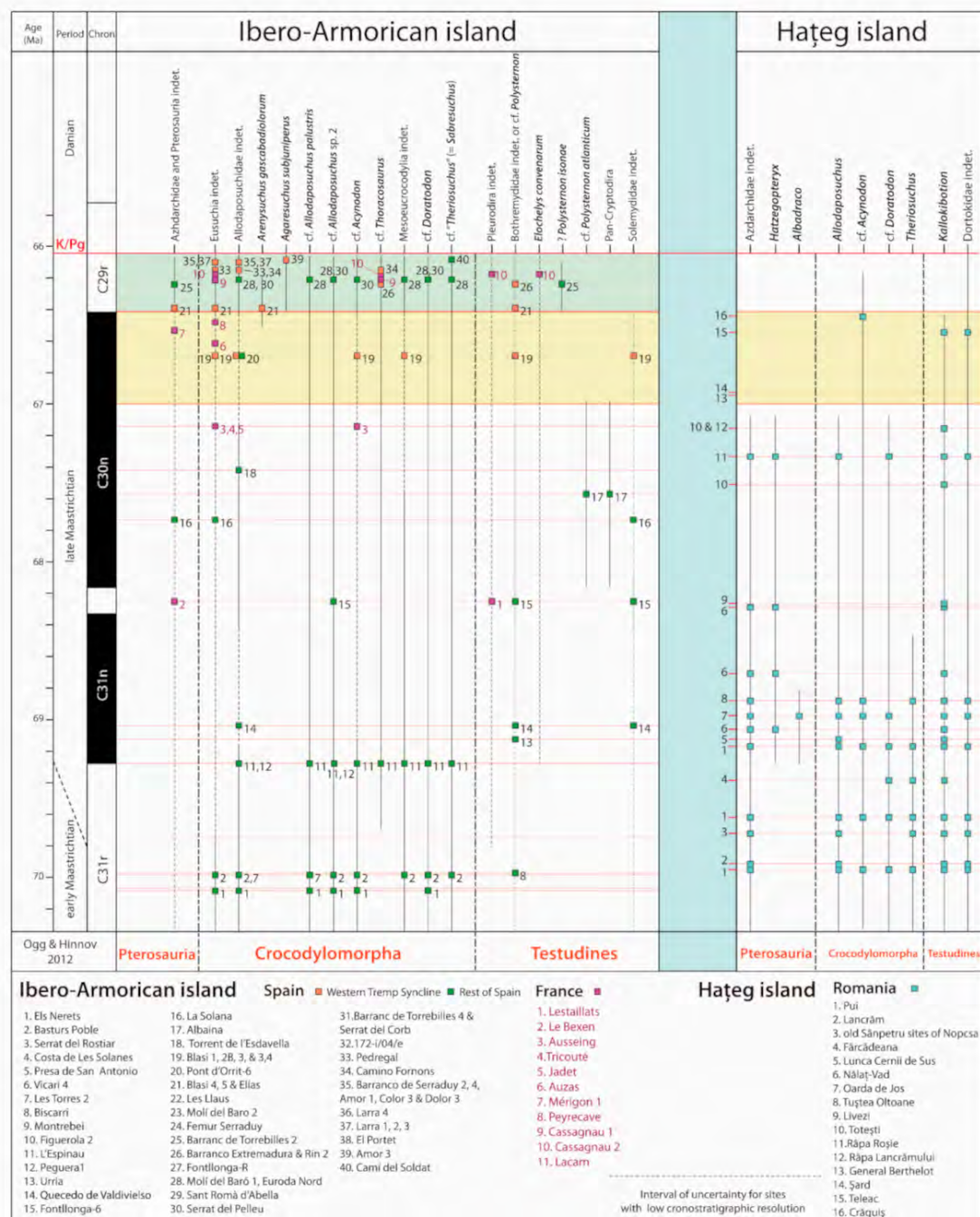


Figure 9. Pterosaur, crocodylomorph, and testudines groups and species occurrences in the Ibero-Armorican island and Hațeg island during the late Maastrichtian. Hațeg island data based on [32] with updated information. The yellow band marks the temporal interval used for comparison, whereas the green band marks the last ≈ 350 ka of the Maastrichtian, with a record only in the Ibero-Armorican island. Magnetostratigraphic scale based on [153] and calibration for the K-Pg boundary based on [28].

During the late Maastrichtian, the crocodylomorphs of the Ibero-Armorican island show great abundance, with a similar number of taxa to that during the early Maastrichtian [23]. The best-represented clade is the eusuchian Allodaposuchidae, with two taxa described from the Western Tresp Syncline (*Agaresuchus subjuniperus* and *Arenysuchus*),

and probably *Allodaposuchus palustris*, whose characteristic teeth have been found up to chron C29r [122,148]. In addition, Blanco et al. (2020) [122] described *Allodaposuchus* sp. 2 on the basis of a dentary from the Fontllonga-6 site (C30r), which seems to be different from the allodaposuchids previously described and could represent a new taxon. Finally, there are plenty of isolated teeth of allodaposuchids [64,121,148,159] that due to their conical generalist shape are difficult to ascribe to specific taxa.

Gavialoidea is represented by a skull and other associated remains from the site of Cassagnau (Haute-Garonne, southern France). These have been ascribed to *Thoracosaurus neocesariensis* [160]. This assignment has been debated, as the remains could belong to a new taxon [161]. In addition, more teeth referred to cf. *Thoracosaurus* have been found in the Spanish Pyrenees, including the record of the Western Tresp Syncline [64,122].

The diversity of hylaeochampsids, “atoposaurids”, and notosuchians during the late Maastrichtian is difficult to determine, since most of their fossils are isolated teeth. There are several teeth referred to cf. *Acynodon* from France [162,163] and the Spanish Pyrenees, including the Western Tresp Syncline [122]. “Atoposaurids” are represented by teeth identified as cf. *Theriosuchus*; these are from the Spanish Pyrenees [122,148] but not the Western Tresp Syncline. “Atoposauridae” is here written in quotes, since Tennant et al. (2016) [164] have argued that some taxa assigned to this clade, such as “*Theriosuchus*” *ibericus* and “*Theriosuchus*” *sympiestodon*, belong to Paralligatoridae and have accordingly grouped these taxa under the new genus *Sabresuchus*. There are also some teeth from the Spanish Pyrenees identified as the notosuchian cf. *Doratodon* [122,148]. It should further be noted that plenty of undetermined eusuchian and crocodylomorph remains have been discovered in the French and Spanish Pyrenees (see [23] and references therein), as well as fossil tracks of crocodylomorphs [125], but due to their limited diagnostic value, it is difficult to ascertain their taxonomic status more precisely. There are also indeterminate eusuchian remains from La Solana (Valencia) [132] and Quecedo de Valdivielso (Burgos, NW Spain) [165,166]. Thus, Ibero-Armorican crocodylomorphs are represented during the late Maastrichtian by a minimum of eight taxa (Table 1, Figures 7 and 9).

The record of testudines during the late Maastrichtian of the Ibero-Armorican island is poorer than during the early Maastrichtian. In the Pyrenees, pleurodiran turtles are represented by the bothremydid *Elochelys convenarum* Laurent, Tong, Claude [167] from southern France and another bothremydid turtle from Isona. This represents the species *Polysternon isonae* Marmi, Luján, Riera, Gaete, Oms, Galobart [168], although Pérez-García [169] considers this a *nomen dubium*, lacking enough diagnostic characters for a new species, and classifies the remains as *Foxemydina* indet. Isolated remains of indeterminate bothremydidids are also present in other sites in the Pyrenees [128,170] and in the northwestern Spanish sites of Urria and Quecedo de Valdivielso (Burgos) [165,166]. In the fossil site of Albaina, there is a plate identified as cf. *Polysternon atlanticum* [144]. Pan-cryptodirans are represented by the remains of solemydid turtles from the Pyrenees, from the sites of Blasi and Fontllonga-6 [128,170], and from La Solana (Valencia) [132,133]. Pereda-Suberbiola et al. (2015) [144] describe a plate from a putative pan-cryptodiran that differs from solemydidids. This makes a minimum of three pan-pleurodirans and two pan-cryptodirans in the Ibero-Armorican island during the late Maastrichtian (Table 1, Figures 7 and 9).

Small-sized upper Maastrichtian tetrapods from the Ibero-Armorican island are represented only by amphibians and squamates from the Spanish and French Pyrenees [129,134,152,171] and from Valencia [172] (Figure 10). The first group consists of albanerpetontids, with at least one taxon present, identified in Blasi 2 as *Albanerpeton* aff. *nexuosum* [129], plus several albanerpetontid remains from the L’Espinau and Serrat del Rostiar 1 sites (Lleida, Catalonia, NE Spain) [171], Cassagnau 1 (Haute-Garonne, southern France) [134,152], and La Solana [172]. In La Solana, the presence of a salamandrid is also documented [172]. Anurans may be represented by at least four different groups with one discoglossid and one palaeobatrachid recognized at Blasi 2, L’Espinau, and Serrat del Rostiar [129,171], and an alytid and a putative pelobatid or gobiatid at L’Espinau [171].

It is noteworthy that there are remains of a palaeobatrachid from Valencia [172] that shows differences from the Blasi 2 taxon and could represent another taxon.

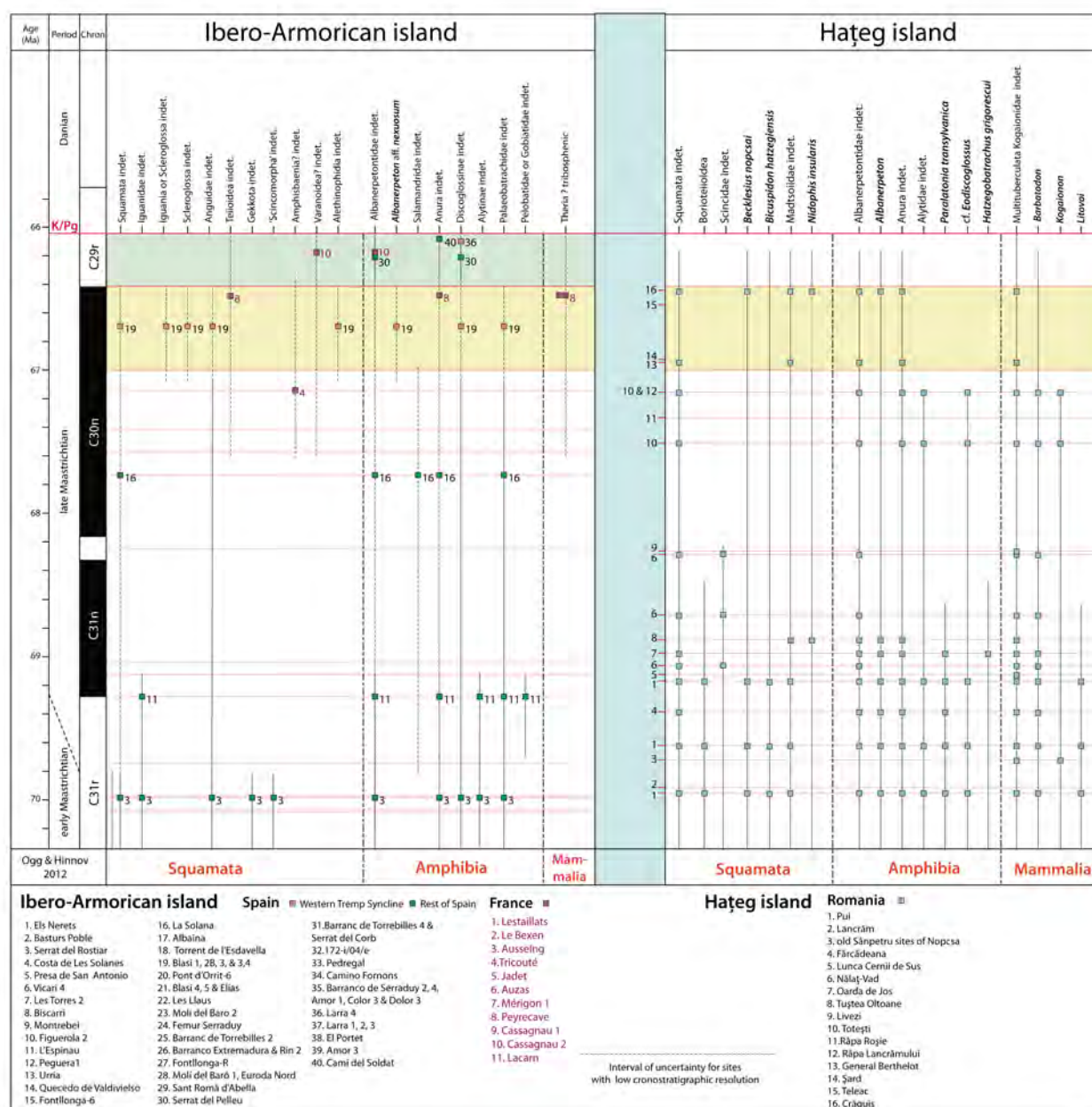


Figure 10. Squamate, amphibian and mammal groups and species occurrences in the Ibero-Armorican island and Hațeg island during the late Maastrichtian. Hațeg island data based on [32] with updated information. The yellow band marks the temporal interval used for comparison, whereas the green band marks the last ~350 ka of the Maastrichtian, with a record only in the Ibero-Armorican island. Magnetochronostratigraphic scale based on [153] and calibration for the K-Pg boundary based on [28].

Upper Maastrichtian squamates are represented by the previously described fossils from Blasi 2 [129], with two undetermined lizards, one anguid lizard, and an alethinophid snake. Additionally, in the Pyrenees, the site of Serrat del Rostiar 1 (Lleida, Catalonia) has yielded several squamate remains [171] including geckos, anguid, and “scincomorph” lizards, and an indeterminate iguanid. An indeterminate iguanid can also be found at L’Espinau. The Serrat del Rostiar 1 site is dated to within chron C31r in the early Maastrichtian, but due to its stratigraphic position, it lies very close to the boundary with

the late Maastrichtian, so we have extended its faunal assemblage to the lower part of the late Maastrichtian (Figure 10). In the French Pyrenees, there is also evidence of a large varanoid, “scincomorph” lizards, and other indeterminate squamates [134,152]. Outside the Pyrenees, there are also undetermined squamate remains at the La Solana site [132].

It is interesting to note that during the late Maastrichtian, there is almost no evidence of mammals in the Spanish record of the Ibero-Armorican island, despite the fact that their presence is documented during the early Maastrichtian [173–175] and the earliest Paleocene [176,177]. The only evidence of mammals during the late Maastrichtian is some tribosphenic teeth from the Peyrecave site, in the Petites Pyrénées (Haute-Garonne, southern France). These would have belonged to a therian mammal [152,178].

4. Discussion

4.1. Comparison with the Upper Maastrichtian Vertebrate Assemblage from the Hațeg Island

To assess the composition of the dinosaur communities of the European Archipelago at the end of the Cretaceous and thus how they faced the K-Pg extinction event, we performed a faunal comparison between the inferred communities of Ibero-Armorican tetrapods and those of Hațeg island, which is another European landmass with a well-known Maastrichtian tetrapod assemblage (Table 1, Figures 7 and 8). The Hațeg island encompasses part of present-day Transylvania (western Romania) [179]. During the Late Cretaceous, it was inhabited by an unusual community of vertebrates, with several groups showing dwarfism and other peculiar adaptations to insularity [30,180]. The upper Maastrichtian vertebrate fossils of Hațeg island are recovered mainly from the Sînpetru, Densuș-Ciula and Sebeș formations, which range from the Santonian-Campanian to the upper Maastrichtian (see [32] for a detailed chronostratigraphic framework). In the late Maastrichtian, the dinosaur assemblage consisted of rhabdodontids, hadrosauroids, titanosaurian sauropods and nodosaurid ankylosaurs, similar to the early Maastrichtian assemblages of the region; this presumably indicates that a major dinosaur turnover did not occur during the early–late Maastrichtian transition. This represents a remarkable difference with respect to the replacement pattern observed in the Ibero-Armorican island [33]. Here, we summarize the tetrapod assemblages of Hațeg island present in tiers 3 and 4 of Csiki-Sava et al. (2016) [32], which is equivalent to the uppermost part of the lower Maastrichtian (C31r) and to the upper Maastrichtian (C31n, C30n, C30r, but not chron C29r) (Figures 8–10). In order to focus on the youngest time interval in the latest Maastrichtian in which contemporary tetrapod communities are preserved in both islands, we thus select the last 800–850 ky of the Maastrichtian, which comprises the upper part of chron C30n (yellow fringe in Figures 8–10) and the Maastrichtian part of chron C29r (green fringe in Figures 8–10). As can be observed, there are C29r vertebrate sites only in the Ibero-Armorican island (Figures 8–10).

4.1.1. Dinosauria

Despite both islands having very similar assemblages of dinosaurs during the early Maastrichtian, this dramatically changed in the late Maastrichtian due to the aforementioned faunal turnover on the Ibero-Armorican island. Regarding herbivorous dinosaurs, in the last 800 ky prior to the K-Pg event (during the upper part of chron C30n and lower part of C29r), the communities of the Ibero-Armorican island were dominated by lambeosaurine hadrosaurids and titanosaurian sauropods (Table 1, Figures 7 and 8). The lambeosaurines were represented by at least four medium-sized taxa (*Arenysaurus*, *Blasisaurus*, *Canardia*, and *Pararhabdodon*), which was probably a small-sized hadrosaurid that had undergone insular dwarfism [79], and a non-hadrosaurid hadrosauroid [75]. Titanosaurs have not yet been documented in chron C30n, but they are present in C29r (Figure 8), and it is reasonable to assume that those forms present in C29r would be present in the upper part of C30n. These correspond to a large and a small–medium form [71]. In Hațeg island, by contrast, the herbivorous communities show a higher clade diversity, with rhabdodontids, hadrosauroids, nodosaurian ankylosaurs, and titanosaurs.

The small-sized rhabdodontids were represented by two species of the genus *Zalmoxes*, *Z. robustus* and *Z. shqiperorum* [32,181,182], although the latter seems not to have reached the upper part of chron C30n (Figure 8). Hadrosauroids are represented only by the small-sized non-hadrosaurid hadrosauroid *Telmatosaurus* [32,183]. However, the latter could be a wastebasket taxon, and hadrosauroid diversity in the latest Maastrichtian could be higher [184]. Ankylosaurs also reached the latest Maastrichtian, although only isolated teeth and fragmentary fossils have been found [32,185–187]. However, the holotype of *Struthiosaurus transylvanicus* [188] might be situated in the basal part of the upper Maastrichtian (tier 3, [32]). Titanosaurs are represented by dwarf and medium-sized forms, which cohabited the island during the late Maastrichtian [189–192], although their record is absent in the lower part of C29r. At least three taxa are recognized, including *Paludititan* and *Magyarosaurus* (Table 1, Figure 8), but most of the recovered material is indeterminate and is in review [193], so the diversity of sauropods remains uncertain [32].

These differences between the two islands are clearly caused by the reorganization of the ecosystems after the arrival of lambeosaurines and new titanosaur faunas on the Ibero-Armorican island [33,34]. This group of hadrosaurids arrived on the island around the mid-part of chron C31r, in the late early Maastrichtian [33]. This arrival apparently occurred in several waves, but it was all of Asian origin [80,83,84], and it represented a complete shift in the herbivorous dinosaur assemblages of the island. Hadrosaurids have been recognized as very efficient plant-eaters mainly on account of the advantages of their dental battery and feeding strategies [194–196]. Although they coexisted for some time with rhabdodontids and ankylosaurs, rhabdodontids seem to have been unable to compete and did not reach the upper part of the late Maastrichtian, disappearing from the island around the C31r–C31n boundary, followed by the nodosaurid ankylosaurians in chron C30n [33] (Figure 8). By contrast, it seems that lambeosaurine hadrosaurids did not reach Hațeg island, and the Hațeg herbivorous assemblage remained stable until the K–Pg boundary. Consequently, in Hațeg island, there is no evidence of herbivore turnover due to ecosystem reorganization after the arrival of newcomers.

As regards non-avian theropods, the fossil record in both islands is composed mainly of isolated teeth, making it difficult to assess their diversity. Both islands were inhabited by several taxa of small to medium-sized maniraptoran theropods: at least three in the Ibero-Armorican island (*Richardoestesia*, *Paronychodon*, and a dromaeosaurid morphotype) and (historically) at least five morphotypes in Hațeg, including *Richardoestesia*, *Paronychodon*, *Euronychodon*, a “troodontid”, and a “velociraptorine dromaeosaurid” [32,185,197] (Table 1; Figure 8). However, new research simplifies the teeth from Hațeg to within three morphospaces: Dromaeosauridae, *Richardoestesia* and *Euronychodon* [198]. The recent discovery of the troodontid *Tamarro* in the Ibero-Armorican island [149] represents the fourth maniraptoran theropod of the island and the first not described based on isolated teeth. It implies that troodontids were then present in both islands. However, significant differences between the islands exist regarding the medium to big-sized theropods. In the Ibero-Armorican island, there was at least one abelisaurid (cf. *Arcovenator*) during chron C30n, which would be the main predator. In the Hațeg island, there is no record of this kind of theropod, nor of any kind of medium to big-sized theropod (Figure 8). Nor is there any evidence of the enigmatic theropods *Balaur* [199,200] and *Elopteryx* [32] in the latest Maastrichtian of Hațeg island, although they are present in the lower part of the upper Maastrichtian (Figure 8). Finally, some small teeth have been found in the Ibero-Armorican island in the upper part of chron C30n; these have been referred to indeterminate small coelurosaurians (Figure 8).

Avialae are not recorded during C30n in either of the two islands (Figure 8), but in the Ibero-Armorican island, a putative enantiornithine [152] and a large ornithuromorph [110] are present during chron C29r, so their presence could be inferred in the upper part of chron C30n. In Hațeg island, enantiornithine birds [201] and gargantuaviids [202] have been recognized, but just in the lower part of the upper Maastrichtian (C31n–C30r; Figure 8).

These faunal differences between the islands indicate that the Ibero-Armorican land-mass, despite its insular condition, allowed the dispersal of faunas at some points in time. This is supported by the presence of ‘Ibero-Armorican’ groups outside the island (arenysaurins and titanosaurs in Africa; [84,203]) and by the arrival of Gondwanan theropods (abelisaurids; [204]) or Laurasian hadrosaurids (lambeosaurines; [139]). By contrast, the immigrants arriving at Hațeg island at the Campanian–Maastrichtian boundary did not include Asian lambeosaurines but distinct velociraptorines and possibly alvarezsaurids [30] that probably followed different migratory routes. The arrival of such newcomers seems not to have significantly altered the evolution of its “primitive” dinosaur faunas or their ecological roles, and some of them became smaller in size as a consequence of “insular dwarfism” ([180]) whereas others showed peculiar ecological adaptations (e.g., aberrant theropods [200]).

4.1.2. Pterosauria

Pterosaurs are represented by large azhdarchids during the late Maastrichtian of both islands, although the record in Ibero-Armorica is scarcer and more fragmentary [114,154,157]. In Hațeg, during the late Maastrichtian, at least two different taxa of giant azhdarchids (*Hatzegopteryx* [191,205,206] and *Albadraco* [207]) (Table 1) coexisted, despite there being no record of them in the upper part of C30n and C29r. However, it seems plausible that they were present since there are remains of indeterminate azhdarchids in that interval (Figure 9). It has been suggested that in Hațeg island, these giant azhdarchids would have occupied the role of large predators due to the absence of large theropods in the island [206]. Their ecological role in the Ibero-Armorican island is more difficult to determine, since there were medium–large theropods (abelisaurids) dwelling on the island.

4.1.3. Crocodylomorpha

The main clades of Crocodylomorpha present in the latest Cretaceous of Europe already inhabited the continent millions of years before the extinction at the K-Pg boundary. The most common clade is Allodaposuchidae, whose earliest record is from the Santonian of Hungary [208]. Subsequently, these basal eusuchians became the dominant crocodylomorphs during the Campanian and Maastrichtian of Europe. During the late Maastrichtian of the Ibero-Armorican island, indeterminate allodaposuchids (mostly isolated teeth) are present in most stratigraphic levels up to the uppermost part of the Maastrichtian part of chron C29r (Figure 9). Many of these teeth may fall within C29r and belong to *Arenysuchus gascabadiolorum*, *Agaresuchus subjuniperus*, or other unknown species, but their generalist morphology does not allow a more specific assignment. Other remains with a more peculiar morphology may belong to the lower Maastrichtian species *Al. palustris*, and thus, its record would cover almost the entire Maastrichtian [122]. In addition, remains very similar to a specimen that Blanco et al. (2020) [122] assigned to *Allodaposuchus* sp. 2 are present throughout the upper Maastrichtian. Therefore, during the late Maastrichtian and up to the K-Pg boundary, there was a great abundance of defined species of allodaposuchids in the Ibero-Armorican island, with at least three species and a fourth possible new species. This contrasts with the allodaposuchid situation observed in Hațeg island during this time interval, where only remains assigned to *Allodaposuchus* sp. have been described (e.g., [32]). Whether these remains belong to the Romanian species *Al. precedens* or to other taxa is difficult to establish, since most occurrences are based on undiagnostic postcranial material or isolated teeth with generalist morphologies typical of several contemporary European taxa such as *Arenysuchus* and *Agaresuchus*. Another difference between the allodaposuchids of the two islands is that the last record in Hațeg occurs in the middle part of chron C30n. Whether their absence during the last million years before the K-Pg boundary is real or due to some kind of bias cannot be determined in the present work. However, it should be noted that in most Maastrichtian microvertebrate sites in Europe, the conical teeth of Allodaposuchidae are among the most common remains, appearing in a wide variety

of sedimentary environments [122]. Consequently, the hypothesis that the clade truly disappeared at the end of the Maastrichtian, and that this disappearance is not merely an artifact of biases, must be considered.

Another common clade of basal eusuchians during the late Maastrichtian of Europe is Hylaeochampsidae, specifically the genus *Acynodon*. This genus is known from the Campanian to the late Maastrichtian of Europe (e.g., [23]). Most of the late Maastrichtian remains assigned to this taxon are isolated teeth with a peculiar button-like (molariform, tribodont) morphology associated with durophagy. Although this dental morphology is present in several lineages among Crocodylomorpha (e.g., *Bernissartia*), so far, the only European Late Cretaceous taxon with this morphology is *Acynodon*. For this reason, these teeth are usually assigned to cf. *Acynodon*. In contrast to the allodaposuchids, there is a similar record of the clade on both islands, covering most of the late Maastrichtian. The last record of cf. *Acynodon* (and the last record of Crocodylomorpha in Hațeg) occurs at the end of chron C30n. This last appearance is based on an isolated blunt tooth recovered in Crăguș, which is a very rich area for microvertebrates ([32]). However, the presence of *Acynodon* and other vertebrates in Hațeg island during chron C29r cannot be ascertained, as there is no sedimentary record for this period [32] (Figure 9).

During the late Maastrichtian, the only clade whose presence is recorded in the Ibero-Armorican island but not in Hațeg is Crocodylia, with a single representative, the genus *Thoracosaurus*. The presence of this genus is based on an almost complete skull, teeth, osteoderms, and vertebrae recovered within chron C29r of Cassagnau 1 and 2 (Haute-Garonne, France) [134,160]. In addition, isolated slender conical teeth tentatively assigned to cf. *Thoracosaurus* have been recovered from deposits of the lower and upper part of the upper Maastrichtian of the Tremp Basin in Spain [122]. The scarce representatives of the crown group Crocodylia during the Late Cretaceous of Europe, and the fact that most of the *Thoracosaurus* remains have been recovered in marine and coastal paleoenvironments (e.g., [23,122,160,161]), could explain the scarcity of remains in the continental deposits of the Ibero-Armorican island and their absence in Hațeg. Interestingly, *Thoracosaurus* is the only European crocodylomorph that has been recovered below and above the K-Pg boundary.

Only two clades of non-eusuchian crocodylomorphs have been found in the Maastrichtian of Europe, “Atoposauridae” and Notosuchia. Most of the “atoposaurid” record in the Upper Cretaceous of Europe is based on isolated teeth similar to those present in *Sabresuchus* (= *Theriosuchus*) *sympiestodon* [209], whose type material was found in the lower Maastrichtian of the Densuș-Ciula Fm but also reported from upper Maastrichtian sites on Hațeg island, although it does not reach the upper part of the upper Maastrichtian [32,210] (Figure 9). Remains assigned to this taxon are also present throughout the upper Maastrichtian of the Ibero-Armorican island [23,148]. As regards Notosuchia, many ziphodont teeth similar to *Doratodon carcharidens* from the Campanian of Austria and the Santonian of Hungary [211] have been found in the Maastrichtian of the Ibero-Armorican island and Hațeg (e.g., [32,122]). As happens with other crocodylomorphs, there is a record of both clades throughout the upper Maastrichtian of the Ibero-Armorican island, but they disappear at the top of chron C30n in Hațeg.

As we have already pointed out, the most striking difference between the Crocodylomorpha record of the Ibero-Armorican island and Hațeg is the almost complete absence of crocodylomorphs from the top of chron C30n in Hațeg island. Several factors could explain this, such as geological and sampling biases. However, the abundance of microfossil sites from the top of chron C30n in Hațeg, together with the fact that crocodylomorphs are usually among the most abundant remains found in this kind of site [32], make it difficult to justify their absence by biases alone. Further studies are needed to clarify this question.

Therefore, the crocodylomorph fossil assemblage of Europe during the Maastrichtian is mostly composed of endemic European taxa such as Allodaposuchidae, Hylaeochampsidae, and *Sabresuchus*. This would imply sporadic connections and faunal exchanges between the two islands, probably via the Adriatic–Australpine domain [116], and subse-

quent isolation processes that allowed endemism and differentiation at species and even the genus level. Isolated cases of intercontinental faunal exchange are explained by the presence of taxa with Gondwanan affinities such as *Notosuchia* (*Doratodon*) in the Maastrichtian of both islands, and the presence of taxa with North American affinities such as *Crocodylia* (*Thoracosaurus*) in the late Maastrichtian of the Ibero-Armorican island. The presence of *Doratodon* is explained by several episodic Cretaceous faunal and geographical links between Africa and Europe [211], such as a Turonian–Coniacian immigration wave that connected eastern Europe and northern Africa [30,212]. The presence of *Thoracosaurus*, a common taxon in North America, could be explained by the more aquatic and cosmopolitan nature of this taxon, which was able to move great distances across the ocean or, for example, via the Thulean Land Bridge [115].

4.1.4. Testudines

The record of turtles in the two islands shows a certain contrast. The diversity of testudines in the Ibero-Armorican island appears to be greater than in Hațeg, with three freshwater taxa of bothremydid pleurodirans (*Elochelys*, *Polysternon isonae?* and *Polysternon atlanticum*) reaching the C29r (Figure 9), and at least one taxon of a solemydid cryptodiran and an indeterminate pan-cryptodiran. By contrast, in Hațeg, there are no cryptodiran turtles.

Hațeg turtles are represented only by two main groups that span the whole Maastrichtian: the basal turtle (stem Testudines) *Kallokibotion*, and the dortokids, which are stem pleurodirans and are present during the upper part of chron C30r [32,213,214] (Table 1, Figure 9).

4.1.5. Amphibia and Squamata

The upper Maastrichtian assemblages of amphibians in the Ibero-Armorican island (upper part of chron C30n) consist of albanerpetontids, discoglossid anurans, palaeobatrachids, and probably salamandrids (Figure 10). In Hațeg island, the assemblages are dominated by albanerpetontids and alytid anurans [32,215], the latter represented by two taxa (*Paralatonina transylvanica* and cf. *Eodiscoglossus*). However, there is no direct evidence of these two taxa in the upper part of C30n (Figure 10). Moreover, the presence of the bombinatorid *Hatzegobatrachus* is documented in the lower part of the upper Maastrichtian [215]. The absence of palaeobatrachids in Hațeg island is also noteworthy.

The squamate assemblages of both islands are diverse and have some groups in common (anguimorph and “scincomorph” lizards, teioids) but also show some differences (Table 1, Figure 10). In Hațeg island, there are borioteioid lizards (*Bicuspidon hatzeiensis*) and paramacellodids, which are represented by *Becklesius nopcsai* [32,216–218]. Snakes are represented by the madtsoiid *Nidophis insularis* [219,220], which shows Gondwanan affinities. This clade of snakes has no record in the upper Maastrichtian deposits of the Ibero-Armorican island but is present in the lower Maastrichtian [30,221]. In the Ibero-Armorican island, there are certain groups that do not appear in Hațeg, such as varanoids and iguanids (Table 1, Figure 10).

4.1.6. Mammalia

During the late Maastrichtian, mammals were part of the communities of both islands, but there is almost no information about those of the Ibero-Armorican island, except the alleged therian teeth from Peyrecave [152,178], which is situated in the upper part of the upper Maastrichtian. By contrast, mammals from Hațeg island are well known, with at least three taxa of kogaionid multituberculate mammals: *Barbatodon*, *Kogaionon*, and *Litovoi* [32,222–224] (Table 1) (Figures 7 and 10). Kogaionids were a group of multituberculates endemic to Hațeg island that survived up to the top of the Maastrichtian and made it to the Paleocene, diversifying and dispersing through Europe [225].

4.2. Evaluation of the Tetrapod Diversity of the Ibero-Armorican Island and Its Biases

Despite the high number of fossiliferous localities that are known in the last million years of the Cretaceous in the Tremp Basin (over 50, see Figure 2), the fossil record of tetrapods is certainly limited by a series of factors including geological history, rock outcrop area, taphonomy, and study and sampling biases [226–229], as well as uncertainties in the taxonomic identification of specimens and the dating of the fossil-bearing deposits. Such biases (resulting, for example, from variations in the fossilization potential of vertebrate remains, interruptions in deposition in continental environments, anagenetic evolutionary lineages, syn-sedimentary and post-sedimentary erosion, etc.) strongly influence the measurement of diversity (i.e., taxonomic richness over a given time period). Some of them are shared with the coeval fossil records of continental to transitional fossiliferous deposits [230,231], but others are specific to the Ibero-Armorican island.

As far as geological and rock outcrop area biases are concerned, the available outcrops of the uppermost Maastrichtian beds are limited by the following factors: the geological history of the basin, the outcrop area, and the number of exposures. The relatively extensive Ibero-Armorican island has reduced potential for fossiliferous outcrops, due to its geological history. In the Pyrenean region, the Alpine orogeny has had an important impact on the availability of outcrops and localities. Thus, a significant reduction in outcrops occurred due to a series of thrusts that caused a shortening of circa 120 km [232]. Second, highly erosive fluvial and glacial valleys generated during and after the last glaciation have eroded Mesozoic formations for thousands of years, further limiting potential outcrops. The number of exposures (i.e., sedimentary bedrock that is visibly exposed at the surface) is constrained by the Pyrenean climate, which favors a high level of vegetation cover. However, in general terms, the southern Pyrenean regions are less forested than the northern foothills, and this enhances the number of available exposures.

As regards taphonomic biases, it is worth mentioning that because of the fragmentary character of the fossil remains commonly found in the Lower Red Garumnian of the Tremp Basin (channel-lag bone accumulations from fluvial-deltaic channelized sandstones, modes 1 and 2 of [233]), major uncertainties exist in the taxonomy of most of the collected specimens. Consequently, their taxonomic assignment is usually to what is commonly held to be a family rank (e.g., Azhdarchidae, Bothremydidae, Titanosauridae, Rhabdodontidae, Solemydidae) or a superfamily rank (Hadrosauroidea, Varanoidea) (Figures 8–10). A similar scenario has been observed in the Hațeg Basin [32]. This reveals that our understanding of the real taxonomic diversity in both regions is preliminary, and diversity comparisons between the regions at lower taxonomic levels (genus or species level) are still not possible. Furthermore, we concur with previous authors [234,235] that the diversity of dinosaurs varies in different paleobioprovinces because of climatic, environmental, or biotic conditions that caused differences in dinosaur evolution. Therefore, endemism or variations in speciation due to the particularities of insular ecosystems are assumed.

With respect to study and sampling biases, the accessibility of sedimentary rock exposures and variations in the efforts of paleontologists in the region are the two main factors affecting the fossil record. First, the complex relief of the Western Tremp Basin reduces accessibility to some of the outcrops (Figure 3), hindering the collection of large macroremains or representative amounts of bulk rock for sieving. Sampling efforts made by paleontologists are unequal as well. Indeed, there are microvertebrate fossil assemblages present in the Maastrichtian outcrops of the Tremp Basin that have not been sampled. One exception is the great effort made by some teams in the 1990s in their pursuit of mammal microfossils [177]. This otherwise unsuccessful survey resulted in the discovery of important localities such as Blasi 2 and Fontllonga 6 [129,151]. Prospecting efforts are currently being carried out in selected localities—L’Espinau, Veracruz 1 [43,57,171]—but an extensive microfossil sampling campaign is lacking. Regarding macrovertebrates, the greater amount of hadrosaur and crocodylomorph fossils—probably because their osteological remains are both more resilient and more easily identifiable compared with other vertebrate clades—produced a clear study bias in the faunal diversity of the Tremp

Formation. These two clades of vertebrates have been the subject of further studies probably because their fossils are more informative or better preserved and thus allow greater taxonomic resolution. By contrast, other groups such as pterosaurs, turtles, sauropods, and theropods have a more fragmentary and less diagnostic fossil record that makes assessment of their abundance more difficult.

Finally, however, one of the key strengths of the fossil record in the Tresp Basin is the dating of the fossil-bearing deposits. In this context, detailed correlations of stratigraphic successions and magnetochrons coupled with accurate age constraints provided by planktic foraminifera [56,60,64] provide a solid chronostratigraphic framework.

By all these reasons, interpreting if there was or not a decline in the diversity of some groups of tetrapods before the K-Pg boundary in the islands of the European archipelago is difficult. However, the discovery during the last years of new taxa whose presence was not known in the islands (e.g., the troodontid *Tamarro* [149], the ornithomorph from Beranuy [110], or the azhdarchid *Albadraco* [207]) points that the late Maastrichtian tetrapod ecosystems were in fact more diverse than what the studied fossil record had pointed up to the day. By this reason, it seems plausible to think that diversity was far from declining prior to the extinction, but this would perhaps be a daredevil judgment, since a higher resolution of the Maastrichtian fossil record (in number of specimens and age constraints) is needed in the Maastrichtian to observe differences and clear trends in the evolution of diversity.

5. Conclusions

The vertebrate record of the Western Tresp Syncline comprises some of the youngest sedimentary deposits with vertebrate fossils in the late Maastrichtian of Europe, with a continuous succession from the upper part of chron C30r to chron C29r (≈ 67 – 66.052 Ma). Among the upper Maastrichtian outcrops of the Tresp and Arén Sandstone formations in this area, more than 50 fossil sites have been recognized. Fossils have been recovered belonging to hadrosauroid ornithomorphs, including the holotypes of *Arenysaurus* and *Blasisaurus*, titanosaurian sauropods, abelisaurid and maniraptoran theropods, a large avialan ornithomorph, pterosaurs, non-eusuchian and eusuchian crocodylomorphs, including the holotypes *Arenysuchus* and *Agaresuchus subjuniperus*, pleurodiran and cryptodiran turtles, squamates, and amphibians. This record is augmented by a relatively diverse oological record, albeit one in need of further study, and ichnites of both dinosaurs (*Hadrosauropodus*) and crocodylomorphs (*Characichnos* and cf. *Crocodylopodus*).

A first attempt at comparing Late Cretaceous European regions indicates that the Ibero-Armorican island and Hačeg island show diverse and thriving communities of vertebrates during the late Maastrichtian, with certain differences in the faunas probably caused by their different paleobiogeographic evolution. Despite these differences, it seems that both European islands flourished during the late Maastrichtian. The rich record of the Ibero-Armorican island and its chronostratigraphic framework indicate that its tetrapod assemblages were thriving just a few hundred thousand years before the K-Pg extinction, and some groups even just tens of thousands of years before.

Despite its small size and relatively inaccessible outcrops, the Western Tresp Syncline is a privileged area when it comes to studying the last Mesozoic ecological communities of tetrapods in Europe, and it is key to understanding how they were affected by the K-Pg extinction event. Further research in this area would help to unveil missing taxa and shed light on these communities and the environment in which they lived.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/geosciences11040162/s1>, Table S1: Arén and Tresp Fm Aragonese sites.

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