# Upper Cretaceous European theropod palaeobiodiversity, palaeobiogeography and the intra-Maastrichtian faunal turnover: new contributions from the Iberian fossil site of Laño

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**Abstract:** A total of 227 theropod teeth have so far been recovered from the upper Campanian Laño site (northern Iberian Peninsula). The teeth were studied for their qualitative and quantitative features. From the theropod sample found at Laño, seven morphotypes attributed to five taxa are identified: a medium to large abelisaurid (*Arcovenator* sp.) and four small coelurosaurians (Dromaeosauridae indet., Paraves indet., cf. *Paronychodon* sp. and cf. *Richardoestesia* sp.) Together with the ground bird *Gargantuavis* and a possible ornithomimosaur, the theropod fauna of Laño might be composed of two medium–large-sized non-avian theropods, four small-bodied non-avian theropods and a large terrestrial bird. This makes the Laño site the richest and most diverse latest Cretaceous theropod site in Europe. Furthermore, the Laño site and the Upper Cretaceous localities of Europe that have yielded theropod remains suggest that the medium–large-sized theropods were abelisaurids or indeterminate theropods. The small theropods are more abundant, diverse and represented by different dromaeosaurids, *Paronychodon*, *Richardoestesia* or related forms, troodontids and, probably, by other paravians. Of the birds, enantiornithines, gargantuaviids and ornithurines are also common in the European Upper Cretaceous sites. The theropod assemblage of Laño, together with the taxa of other Upper Cretaceous sites, supports the idea that several theropod dispersal events took place during the Cretaceous. This resulted in a mixture of European endemic, Asiamerican and Gondwanan forms. This study also supports the hypothesis that the intra-Maastrichtian faunal turnover that occurred in the Ibero-Armorican landmass seems to have had no apparent effect on theropods.

**Key words:** Theropoda, teeth, Late Cretaceous, Europe, palaeobiodiversity, palaeobiogeography.

Aside from Asia and North America, the latest Cretaceous dinosaur sites of Europe have the largest and most complete samples and have, therefore, been studied in detail (Csiki-Sava *et al.* 2015; Vila *et al.* 2016). The rigorous and systematic sampling of European Upper Cretaceous continental deposits has led to the discovery of hundreds of dinosaur sites (Pereda-Suberbiola 2009; Riera *et al.* 2009; Csiki-Sava *et al.* 2015; Canudo *et al.* 2016; Fondevilla *et al.* 2019). Indeed, around 500 dinosaur-bearing sites from the Campanian and Maastrichtian have been documented in the Ibero-Armorican domain (Vila *et al.* 2016), which are mainly distributed in the Iberian basins (Spain and Portugal), the Pyrenees region, and the Provence and Languedoc regions (southern France) (Vila *et al.* 2016; Fondevilla *et al.* 2019).

The Laño site is one of the most important Upper Cretaceous dinosaur sites of Europe. Laño has yielded a wide range of large and small-sized vertebrate taxa (nearly 40 species of continental vertebrates) (Pereda-Suberbiola *et al.* 2015). This continental vertebrate association consists of actinopterygian fish, chelonians, crocodilians, dinosaurs, lissamphibians, mammals, pterosaurs and squamates (Astibia *et al.* 1999a; Pereda-Suberbiola *et al.*

2015). The dinosaur assemblage is represented by the ankylosaur *Struthiosaurus* (Pereda-Suberbiola 1999), an indeterminate hadrosaurid (Pereda-Suberbiola *et al.* 2003), the ornithopod *Rhabdodon* (Pereda-Suberbiola & Sanz 1999), the titanosaurian sauropod *Lirainosaurus astibiae* (Díez Díaz *et al.* 2011, 2012, 2013*a*, *b*), and a diverse theropod assemblage.

The theropod fauna of Laño is composed of an unnamed abelisaurid that has been compared with *Tarascosaurus* (Le Loeuff & Buffetaut 1991; Le Loeuff 1992), two coelurosaurians identified as Coelurosauria indet. and ?*Richardoestesia* sp., two dromaeosaurids referred to ?Dromaeosauridae indet. and ?*Pyroraptor olympius* (Torices *et al.* 2015), and the large ground bird *Gargantuavis philoinos* (Angst *et al.* 2017). Most of the theropod taxa have been identified on the basis of isolated teeth, which are the most abundant elements (Torices *et al.* 2015). Torices *et al.* (2015) have studied 120 teeth found at the Laño site. To date, 227 theropod teeth have been recovered from the site, making Laño the richest theropod site in Iberia and from the Upper Cretaceous of Europe.

The aim of this article is to revise the isolated theropod teeth found at the Laño site and to describe new material found in the collections. Furthermore, statistical analysis has been used in the study of the theropod teeth to refine the existing palaeobiodiversity of theropod dinosaurs at the site. Along with this, the Turonian–Maastrichtian theropod fossil record of Europe is reviewed, and the palaeobiodiversity and palaeobiogeographical relationships and affinities of the theropod association are evaluated. Finally, the impact of the intra-Maastrichtian faunal turnover on non-avian theropods of the Ibero-Armorican domain is discussed.

## GEOGRAPHICAL AND GEOLOGICAL SETTING

The material studied in the present paper was found at the Laño vertebrate site. It is situated *c.* 30 km south of the city of Vitoria-Gasteiz in an abandoned sand quarry (the Laño quarry) between the towns of Laño and Albaina (Condado de Treviño), in the northern region of the Iberian Peninsula (Fig. 1). The quarry extends *c.* 1.5 km in an east–west direction, and has a *c.* 70-m-thick stratigraphic section of continental and marine exposures. The continental vertebrate-bearing beds L1 and L2 are located at the base of the quarry (Astibia *et al.* 1999*b*; Corral *et al.* 2016). Precise locality details are recorded with all reposited specimens.

In the Late Cretaceous, Europe was an extensive archipelago largely covered by shallow epicontinental seas (e.g. Haq 2014; Csiki-Sava *et al.* 2015), and the Ibero-Armorican domain was the largest landmass in southern Europe. In this context, three main basins developed, called the Iberian Basin (central Spain), the Provence Basin (south-eastern France) and the Pyrenees Basin (north-eastern Spain and southern France) (Vila *et al.* 2016). Another smaller basin found in west-central Portugal is called the Lusitanian Basin.

The Laño site is geologically in the Basque–Cantabrian Basin, specifically on the southern margin of the Miranda–Treviño syncline (Pereda-Suberbiola *et al.* 2015; Corral *et al.* 2016), where the Sub-Cantabrian Synclinorium developed (Fig. 1). This synclinorial structure is mainly composed of Upper Cretaceous and Palaeogene deposits (Baceta *et al.* 1999). The sedimentary series deposited in the basin from the late Albian to the Maastrichtian consists of five megasequences (Floquet 1998; Gräfe *et al.* 2002).

Floquet *et al.* (1982) defined the Sedano Formation as having a lower unit with marine marls and clays and an upper unit with silty quartzarenites with interbedded limestone layers. In the Laño quarry the equivalent materials to the Sedano Formation crop out and are 22 m thick (Berreteaga 2008; Corral *et al.* 2016). Two units have been recognized in the area (Astibia *et al.* 1999*a*; Pereda-Suberbiola *et al.* 2000). One unit contains a silty and clayey vertebrate-bearing bed, named L2 (Corral *et al.* 2016). In the second unit two vertebrate-rich beds are located, known as L1A and L1B (Astibia *et al.* 1999*a*; Pereda-Suberbiola *et al.* 2000). Pereda-Suberbiola *et al.* (2000) considered level L2 to be the equivalent of level L1A further northwards.

The Sedano Formation represents a littoral environment, with a siliciclastic sequence in the upper part, formed due to the deltaic aggradation in the subtidal and intertidal areas, before the delta plain prograded (Corral *et al.* 2016; Martín-Chivelet *et al.* 2019). Astibia *et al.* (1990) and Pereda-Suberbiola *et al.* (2000) suggested that it was a braided river system, where channels, sandbars and pools developed. The vertebrate bones of Laño are typically covered with iron oxides; the diagenetic processes that led to their development could have been the consequence of a hydromorphic process due to seasonal variations in the phreatic water level. This suggests a climate with variations in rainfall associated with dry and wet seasons (Elorza *et al.* 1999). The presence of pelomedusoid turtles and crocodyliforms indicates an intertropical warm climate (Pereda-Suberbiola *et al.* 2015).

The Sedano Formation was previously dated as early Maastrichtian (Floquet 1998; Berreteaga 2008). Combining lithostratigraphic and magnetostratigraphic analyses, however, Corral *et al.* (2016) dated the continental vertebrate site of Laño as late Campanian in age (chron C32n, 72–73.5 Ma).
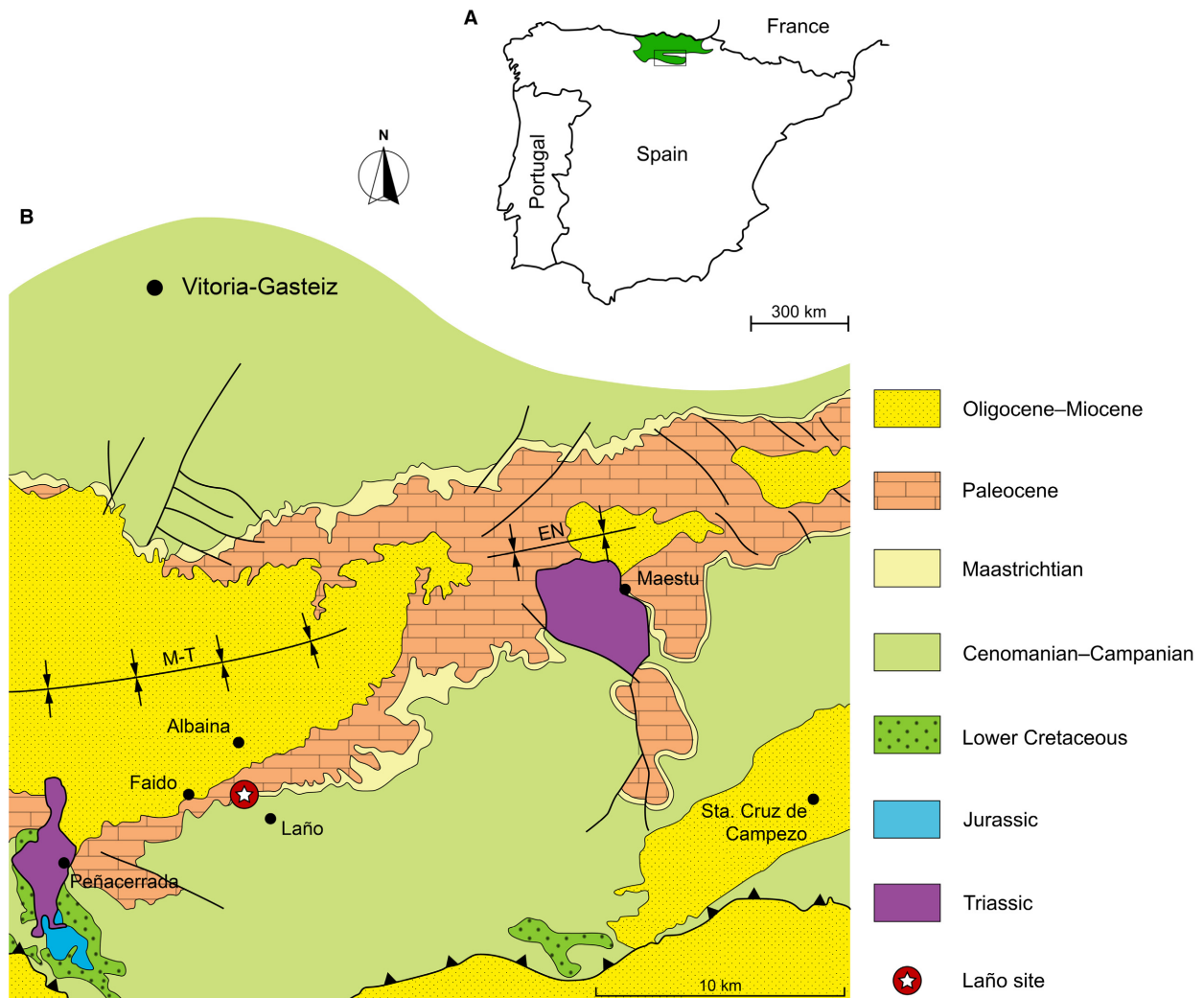
**FIG. 1.** Geological setting of the Laño site. A, geographical map of the Iberian Peninsula. B, geological map of the Miranda–Treviño and Entzia synclines. The Cenozoic material crops out in the inner part of the synclines whereas the flanks are mainly composed of Cretaceous material. *Abbreviations*: EN, Entzia Syncline; M-T, Miranda–Treviño Syncline. (Modified from Corral *et al.* 2016).

## MATERIAL AND METHOD

The present material consists of four teeth associated with dentary fragments and 223 isolated theropod teeth. Most of the teeth were recovered from screen-washing sediments from the fossiliferous level L1A during excavations in the 1990s (Astibia *et al.* 1999a). The largest teeth were collected from all three levels. The material is curated at the Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa (Vitoria-Gasteiz, Basque Country).

The theropod teeth from Laño were mainly studied under a stereo microscope (Olympus SZ-STS) and a digital microscope (Celestron 44308). The largest teeth were measured with a digital calliper (Mitutoyo Digimatic Series no. 500). The measurements of the small teeth and denticles were taken with the Imagej program.

The nomenclature used in this work regarding dental anatomy follows the one proposed by Hendrickx *et al.* (2015) and references therein. The qualitative and quantitative characters of the teeth were studied in accordance with the methodology proposed by Currie *et al.* (1990), Smith *et al.* (2005) and Hendrickx *et al.* (2015). The qualitative characters are: crown shape, type and cross-section, position of the carinae, presence or absence of denticles, morphology and position of the denticles, and crown ornamentation. Furthermore, the crown measurements taken are: crown height (CH), crown base length (CBL), crown base width (CBW), crown base ratio (CBR; defined as CBW/CBL), crown height ratio (CHR; defined as CH/CBL), mesial denticle density (MDD), distal denticle density (DDD), denticle size density index (DSDI; defined as MDD/DDD), mesial denticle height (MDH),

mesial denticle length (MDL), mesial denticle width (MDW), distal denticle height (DDH), distal denticle length (DDL), and distal denticle width (DDW) (Fig. 2). In the largest teeth, denticle density was measured per 5 mm at the base, mid-crown and apex. Nevertheless, in most teeth, due to their small size and the state of preservation, the denticle density could be measured only per millimetre. Afterwards, before performing the statistical analysis, the denticle density in the small specimens was multiplied by 5 in order to normalize the data. In the biggest teeth, the mid-crown denticle density was used for statistical analysis. When the teeth were almost complete, some of the measurements were inferred following the line of the tooth, if possible.

Different morphotypes and taxa were established using the data obtained. In addition, a principal component analysis (PCA) and a discriminant analysis (DA) were carried out using SPSS 26 (IBM SPSS Statistics for Windows, v. 26.0, release 2020). In the statistical analysis, a total of 758 teeth, represented by 692 from the database and 66 complete or virtually complete teeth from Laño, were analysed (Isasmendi *et al.* 2021a, appendix A). For

the database, mainly theropod taxa recovered from uppermost Cretaceous deposits were chosen with the aim of introducing as little noise as possible into the statistical analysis. The approximately temporally equivalent teeth added in the database belong to the following genera: *Arcovenator*, *Dromaeosaurus*, *Majungasaurus*, *Paronychodon*, *Pyroraptor*, *Richardoestesia*, *Saurornitholestes*, *Troodon*, *Tyrannosaurus* and *Velociraptor*, all from the Campanian–Maastrichtian. Due to the scarcity of taxa with unserrated teeth available for building the database, the theropod *Buitreraptor* from the Cenomanian was included in the analysis. Furthermore, because the teeth of *Falcarius* from the Early Cretaceous show a large number of denticles, it was added to the database. Not all the variables from the Laño sample were used when performing the statistical analysis because not all of these measurements were taken in the comparative database. The variables considered for the statistical analysis were: CBL, CBW, CH, DDD and MDD. The theropod teeth measurements used for comparison were taken from Farlow *et al.* (1991), Sankey (2001, 2008), Sankey *et al.* (2002, 2005), Currie & Varricchio (2004), Smith *et al.* (2005); Larson
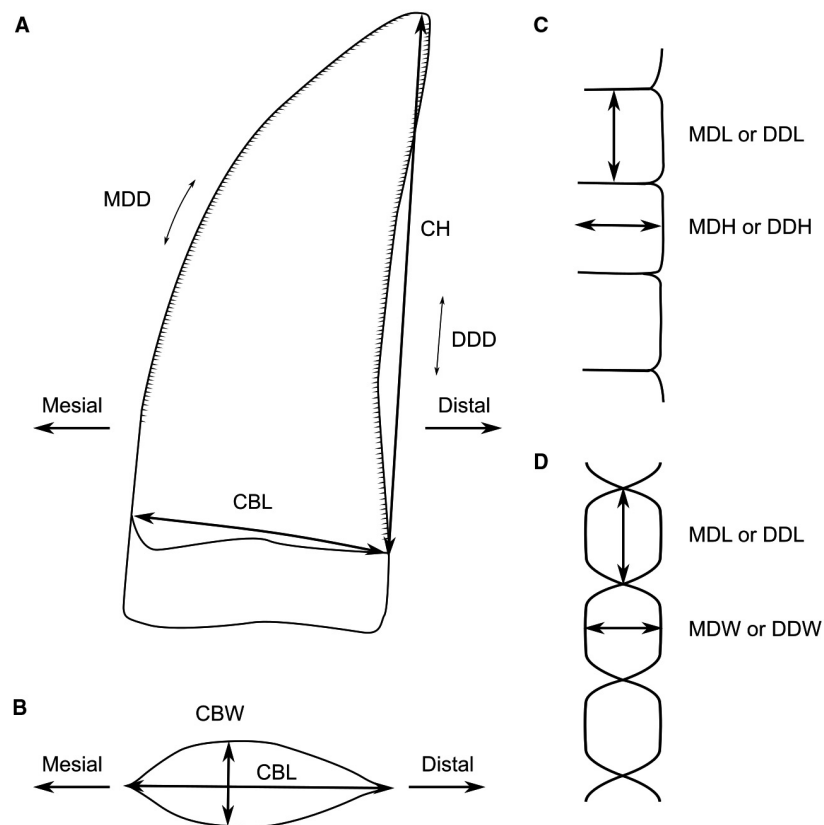


**FIG. 2.** Morphometric terminology used for the Laño teeth. A, theropod tooth in lateral or lingual view. B, theropod tooth in basal view. C, denticles in labial or lingual view. D, denticles in mesial or distal view. *Abbreviations*: CBL, crown base length; CBW, crown base width; CH, crown height; DDD, distal denticle density; DDH, distal denticle height; DDL, distal denticle length; DDW, distal denticle width; MDD, mesial denticle density; MDH, mesial denticle height; MDL, mesial denticle length; MDW, mesial denticle width.

(2008), Longrich (2008), Gianechini *et al.* (2011), Larson & Currie (2013), Tortosa *et al.* (2014), Williamson & Brusatte (2014), Hendrickx *et al.* (2015), Pérez-García *et al.* (2016), and Young *et al.* (2019). Before performing the statistical analysis, the data were normalized using Log $(x + 1)$, so that the data with zero values could be used in the analysis. For the DA, only the specimens from the database were grouped in the genera to which they were previously assigned, and the teeth from the Laño sample were not grouped before conducting the analysis. Moreover, given that it was not possible to create groups of the same size, the prior probabilities of group membership was set to be equal.

*Institutional abbreviations.* MCNA, Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Basque Country; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; ZIN PH, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

## SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAURIDAE Bonaparte & Novas, 1985
ARCOVENATOR Tortosa et al., 2014
*Arcovenator* sp.
Figure 3

*Material.* 12 teeth (MCNA 1852, 1853, 2205, 8589, 8600, 10082, 14067, 14520–14522, 16863 and 16864) and 20 tooth fragments (MCNA 1855, 2206, 14073, 14074, 16756–16764, 16808–16813, 16862).

*Description.* Most of the *Arcovenator* sp. teeth show wear facets at the apex, and eroded denticles, especially near the apex. The teeth MCNA 1852, 2205, 8589, 10082, 14520 and 14521 are elongated with a high CHR as compared with the CBR (Fig. 3B–D, F–H), but MCNA 1853, 1855, 2206, 8600, 14073, 14067, 14522, 16863 and 16864 are more flattened (Fig. 3O–Q). All of the teeth have a blade-like shape (ziphodont crowns) and are labiolingually compressed. The lingual side is flat or convex whereas the labial side is always convex. The mesial margins of the teeth are convex and the distal margins are concave (Fig. 3G, P) or almost straight (Fig. 3C). The cross-section of the basalmost part of the tooth, at the level of the cervix, varies with the tooth, and can be elliptical, oval or lanceolate (Fig. 3I, K). The tooth MCNA 14520 has a figure-eight cross-section (Fig. 3J) due to an apicobasally oriented groove on both the lingual and labial surfaces from the cervix up to the middle part of the crown (Fig. 3G).

The teeth belonging to the *Arcovenator* sp. morphotype are medium to large in size. CH varies between 20.42 and 62.57 mm, and CBL between 12.78 and 21.58 mm. The CBW ranges from 5.89 to 10.48 mm, being approximately half of the CBL, with CBR varying from 0.42 to 0.68.

Most of the teeth have very subtle transverse undulations that can be either evenly marked throughout the crown or more pronounced apically. Furthermore, they are usually more obvious adjacent to the carinae, especially near the distal one (Fig. 3M). Nevertheless, no marginal undulation is observed. The texture of all of the teeth is irregular and non-oriented (Fig. 3L).

The mesial carina extends apicobasally from the apex down to the mid-crown (Fig. 3B, F, O), whereas the distal carina reaches the cervix (Fig. 3D, H, Q). The mesial carina is displaced towards the lingual side basally (Fig. 3B, F, O). By contrast, the distal carina is labially displaced adjacent to the cervix (Fig. 3D, H). The most flattened teeth show a straight distal carina (Fig. 3Q).

All of the teeth have denticles along both carinae, unless these are eroded (Fig. 3B, D, F, H, O, Q). The denticle shape is subrectangular or subquadrangular and there are no interdenticular sulci (Fig. 3A, E, M, N, R). The denticle density varies between the two carinae (from 11 to 21 denticles per 5 mm on the mesial carina and between 11 and 19 per 5 mm on the distal one), and even on the same carina, with higher densities in the basal part and at mid-crown. Nonetheless, the size of the denticles decreases close to the apex. The denticles are usually bigger on the distal carina in both length and height (DSDI, 0.91–1.41). The MDH ranges from 0.19 to 0.24 mm, and the MDL from 0.17 to 0.26 mm. The DDH varies between 0.21 and 0.39 mm, and the DDL between 0.19 and 0.26 mm. The denticle width in the fragments ranges between 0.24 and 0.53 mm.

*Remarks.* Most of the European abelisaurid material consists of fragmentary elements (Tortosa *et al.* 2014), although several taxa have been described in southern France: *Genusaurus sisteronis* (Accarie *et al.* 1995), *Tarascosaurus salluvicus* (Le Loeuff & Buffetaut 1991) and *Arcovenator escotae* (Tortosa *et al.* 2014). Moreover, *Betasuchus bredai* is known from the Maastrichtian of Limburg in the Netherlands, and is considered to be related to *Tarascosaurus* (Huene 1932; Le Loeuff & Buffetaut 1991; Carrano & Sampson 2008).

Isolated abelisaurid teeth are quite abundant in the latest Cretaceous European sites (e.g. Csiki-Sava *et al.* 2015; Pérez-García *et al.* 2016). Furthermore, there are some isolated theropod teeth that might belong to abelisaurids, such as some of those assigned to dromaeosaurids by Chanthasit & Buffetaut (2009), and some of those referred to Theropoda indet. by Torices *et al.* (2015) and by Puértolas-Pascual *et al.* (2018).

Some abelisaurid taxa have low lateral teeth, but others have elongate lateral crowns (Hendrickx *et al.* 2020). Smith (2007) considered a straight or slightly curved distal profile to be a synapomorphy of Abelisauridae, but this is not observable in all abelisaurids (Hendrickx *et al.* 2020). Indeed, Hendrickx *et al.* (2020) noted that most abelisaurids have slightly convex, straight or weakly concave distal margins, but some teeth of *Arcovenator* are more distally curved, similar to the teeth of this morphotype from Laño. In Abelisauroidea (Bonaparte 1991), a concave surface adjacent to the carinae in the mesial teeth can be seen, as in other tetanurans such as *Allosaurus* or coelurosaurians like tyrannosauroids (Hendrickx 2015; Hendrickx *et al.* 2020). Usually, the mesial carina reaches the cervix in abelisauroids, but this is not the case in *Arcovenator* (Tortosa *et al.* 2014) and *Masiakasaurus* (Hendrickx 2015). However, the distal carinae are

**FIG. 3.** *Arcovenator* sp. morphotype teeth from the upper Campanian Laño site. A–E, MCNA 1852, mesial carina, crown in mesial, lingual and distal views, and distal carina. F–H, MCNA 14520, crown in mesial, lingual and distal views. I–K, basal cross-sections of MCNA 1852, 14520 and 16863, respectively. L, enamel texture of MCNA 1852. M, transverse undulation on MCNA 16864. N–R, MCNA 16863, mesial carina, crown in mesial, labial and distal views, and distal carina. Scale bars represent: 5 mm (A, E, L–N, R); 1 cm (B–D, F–H, I–K, O–Q).

centrally positioned or slightly labially displaced in the whole dentitions of these theropod taxa (Hendrickx 2015; Hendrickx *et al.* 2020). The denticles can be hooked in abelisauroids such as in *Abelisaurus*, *Majungasaurus*, *Masiakasaurus* and *Rugops*, or symmetrical to slightly asymmetrical, as in *Arcovenator* and *Skorpiovenator* (Hendrickx 2015; Hendrickx *et al.* 2020). Furthermore, the teeth of all abelisaurids examined by Hendrickx *et al.* (2020) possessed non-oriented and irregular enamel textures.

Figure-eight crown cross-sections seem not to occur in ceratosaurian theropods (Hendrickx & Mateus 2014*a*), but the tooth MCNA 14520 has this feature. Nevertheless, this may be due to a growth abnormality that formed the apicobasally oriented grooves causing this cross-section. Hendrickx *et al.* (2020) did also observe this cross-section in the root of some abelisaurid teeth.

A number of isolated teeth found at the upper Campanian Armuña site have been referred to cf. *Arcovenator* (Pérez-García *et al.* 2016). The teeth of the holotype of *A. escotae* are high (30–55 mm), with a CHR greater than 2.3 and a CBR of 0.48–0.58 (Hendrickx *et al.* 2020). The distal carinae of *Arcovenator* teeth are straight but labially displaced, whereas the mesial carinae are lingually displaced towards the cervix. Furthermore, the DSDI can exceed 1.2. The denticles of *Arcovenator* are subrectangular and mesiodistally elongate in the distal carinae, and apicobasally lengthened and subquadrangular in the mesial carinae (Hendrickx *et al.* 2020). The mesial denticles are present only from the apex to mid-crown (Tortosa *et al.* 2014; Hendrickx *et al.* 2020). Their denticle density varies between 14 and 21 denticles per 5 mm on the mesial carinae whereas on the distal carinae it ranges between 12.5 and 18 denticles per 5 mm (Tortosa *et al.* 2014). The teeth from Laño are similar in shape, height, basal length and width to those of *A. escotae*. Furthermore, both carinae follow a similar course and extension to those observed in *A. escotae* and have an almost identical enamel texture, denticle density, DSDI and denticle shape. Therefore, the teeth from Laño strongly resemble those of *Arcovenator* and could be attributed to *Arcovenator* sp.

There is a wide range of shape variability in the *Arcovenator* sp. morphotype from Laño. Nevertheless, all the teeth share some diagnostic characters, such as denticle density, a subquadrangular denticle shape and the fact that the mesial carina does not reach the cervix. Furthermore, the PCA shows a close relationship between the teeth of *Arcovenator escotae*, the cf. *Arcovenator* teeth from Armuña and the *Arcovenator* sp. morphotype from Laño (see Statistical Analysis). The DA grouped all of these teeth as *Arcovenator*, except MCNA 1853 and 14521, which were classified as *Majungasaurus* (Isasmendi *et al.* 2021*a*, appendix A). Nevertheless, the extension and disposition of the carinae support the assignment of these two specimens to *Arcovenator* sp.

In the light of these similarities, six teeth from Laño (MCNA 1852, 1853, 2205 and 14520–14522) previously attributed to Theropoda indet. by Torices *et al.* (2015) and 26 additional specimens are now assigned to *Arcovenator* sp., pending the discovery of more material that could undoubtedly indicate that these teeth belong to *Arcovenator escotae* or to another species.

Heterodonty is known in some theropods (Currie *et al.* 1990; Carrano *et al.* 2002; Rauhut *et al.* 2010). The mesial teeth of most abelisaurid theropods have a salinon- to J-shaped or a D-shaped to lanceolate cross-section (Hendrickx *et al.* 2020 and references therein). No mesial teeth are known that belong to *Arcovenator*. The cross-section of lateral teeth of abelisaurids is lenticular or lanceolate (Hendrickx *et al.* 2020). Therefore, the position of the teeth of this morphotype in the tooth row is unknown.

The isolated theropod teeth from Chera, grouped in 'Morfotipo A' (Company 2005) or referred to ?Neoceratosauria indet. (Company *et al.* 2009), share the following features with the teeth of *A. escotae* and the *Arcovenator* morphotype from Laño: denticle density, denticle shape, the position and extent of the distal and mesial carinae, and the crown shape (see Company 2005 for a more detailed description). These crowns show the same shape variability found in the Laño specimens. Therefore, it is probable that these teeth belong to cf. *Arcovenator*. Teeth assigned to cf. *Arcovenator* are undoubtedly represented in three Iberian sites. The teeth studied by Torices *et al.* (2015) from the Maastrichtian Montrebei and Blasi sites were statistically classified into the same morphogroup (Morphotype 1) as the Laño specimens (*Arcovenator* sp. of this study), and therefore could belong to *Arcovenator* or another indeterminate abelisaurid. Pérez-García *et al.* (2016) already assigned the isolated theropod teeth from the southern Pyrenees to this taxon. However, this is mainly based on a statistical analysis in which *Arcovenator* is the only medium–large-sized theropod from the database. In fact, no characteristic features of this taxon were noted in the description of Theropoda indet. morphotypes from the southern Pyrenees in Torices *et al.* (2015) and in Pérez-García *et al.* (2016). Therefore, this assignment seems doubtful, and a more detailed revision of these specimens is required. Puértolas-Pascual *et al.* (2018) also mentioned the similarities between an isolated crown of a medium–large theropod (MPZ 2017/804 from the upper Maastrichtian 172-i/04/e site) and the teeth of Morphotype 1 of the indeterminate theropod of Torices *et al.* (2015) (*Arcovenator* sp. of this study). However, it is not possible to determine if the crown belongs to the same theropod or to a different taxon because its mesial carina is not complete (Puértolas-Pascual *et al.* 2018, fig. 11F). Nevertheless, it is highly likely that this tooth belongs to an abelisaurid.

TETANURAE Gauthier, 1986
COELUROSAURIA Marsh, 1884
FAMILY INDET.
PARONYCHODON Cope, 1876
cf. *Paronychodon* sp.
Figure 4K–P

*Material.* 6 isolated teeth (MCNA 14547, 14562–14565, 16755).

*Description.* The state of preservation of the teeth assigned to cf. *Paronychodon* sp. is variable; therefore not every anatomical feature could be studied in every tooth. The teeth are elongate and have a somewhat conidont or ziphodont crown type (Fig. 4K–M). The tooth MCNA 14547 is much more robust than the others
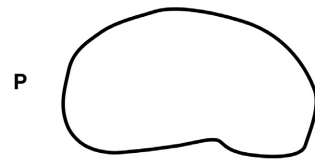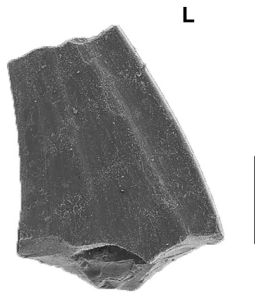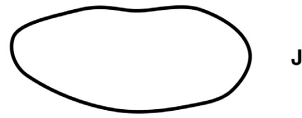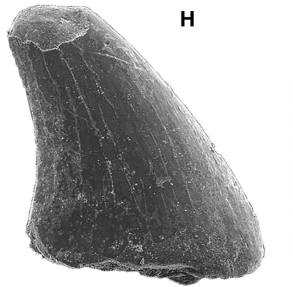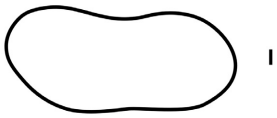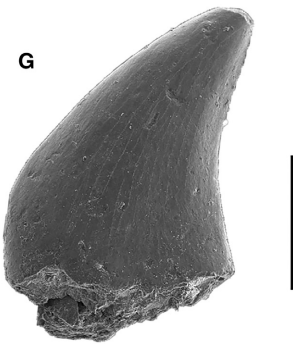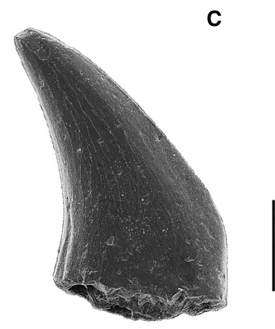
**FIG. 4.** Theropod teeth from the upper Campanian Laño site. A–F, Paraves indet. A morphotype. A, D, MCNA 14524 in lingual view and the basal cross-section scheme. B, E, MCNA 14526 in labial view and the basal cross-section scheme. C, F, MCNA 14538 in lingual view and the basal cross-section scheme. G–J, Paraves indet. B morphotype: G, I, MCNA 14541 in lingual view and the basal cross-section scheme; H, J, MCNA 14532 in labial view and the basal cross-section scheme. K–P, cf. *Paronychodon* sp. morphotype: K, N, MCNA 14563 in lingual view and the basal cross-section scheme; L, O, MCNA 14562 in lingual view and the basal cross-section scheme; M, P, MCNA 14547 in lingual view and the basal cross-section scheme. All scale bars represent 1 mm.

(Fig. 4M). The crown cross-section of the teeth varies between elliptical and reniform (Fig. 4N–P). The lingual side of most of the teeth is straight and planar whereas the labial side is straight or slightly convex. In MCNA 16755 the lingual side is concave, with the apex facing lingually. The mesial margin of the teeth is convex and the distal margin is concave. The teeth have a distally displaced apex (Fig. 4K–M). They have an irregular texture on the enamel and have no transverse or marginal undulations.

These teeth are small in size. CH ranges between 2.43 and 8.29 mm, and CBL varies between 1.83 and 4.85 mm. CBW ranges from 0.93 to 2.38 mm, therefore the basal width of the teeth is almost half of the basal length. All of the specimens have mesial and distal carinae. The mesial carina is not well defined, but it is straight and lingually displaced. The distal carina is also straight and lingually displaced. MCNA 14562 is the only specimen with centred carinae. MCNA 16755 preserves only the mesial carina, which seems to have subtle crenulations. Both carinae seem to reach the cervix or nearly so in all of the teeth. None of the teeth is serrated.

Longitudinal ridges are common on both labial and lingual surfaces. These ridges are apicobasally oriented and extend almost from the apex to the cervix on the lingual surface and usually to mid-crown on the labial side. Longitudinal ridges are more abundant on the labial side with three to seven ridges, whereas on the lingual surface they vary between three and four in number.

*Remarks. Paronychodon* is a genus of theropod dinosaur reported from Asia, Europe and North America (e.g. Currie *et al.* 1990; Sankey *et al.* 2002; Sues & Averianov 2013; Torices *et al.* 2015; Marmi *et al.* 2016). The position of *Paronychodon* in Theropoda is still undetermined. Several authors have tentatively attributed this genus to different theropod clades such as Coelurosauria, Paraves, Dromaeosauridae and Troodontidae, but there is no consensus among specialists (Currie *et al.* 1990; Antunes & Sigogneau-Russell 1991; Makovicky & Norell 2004; Larson 2008; Sues & Averianov 2013; Torices *et al.* 2015). Teeth belonging to *Paronychodon* have even been associated with growth abnormalities caused by the prolonged contact of the tooth with the medial wall of the alveolus (Currie *et al.* 1990). Although there is no fossil material to support this hypothesis, it has also been proposed that *Paronychodon* may be another tooth form of *Richardoestesia* due to the heterodonty found in the jaws (Longrich 2008).

Teeth attributed to *Paronychodon* show wide variability. Most of them lack denticles, but others have serrations on the distal carina, or even on both carinae (Currie *et al.* 1990). However, they all have a plane lingual side with three or more longitudinal ridges and a convex labial side that may also bear longitudinal ridges (Currie *et al.* 1990; Canudo & Ruiz-Omeñaca 2003).

Some North American *Paronychodon* teeth with denticles overlap morphologically with teeth identified as *Zapsalis*, which have now been shown to be premaxillary teeth of dromaeosaurids such as *Bambiraptor* and *Sauronitholestes* (Currie & Evans 2020). The Laño teeth belonging to this morphotype cannot be regarded as dromaeosaurid premaxillary teeth because they are unserrated, unlike those of *Bambiraptor* or *Saurornitholestes*. Indeed, the cf. *Paronychodon* teeth from Laño are more similar to those unserrated teeth with longitudinal grooves from North America.

Several tooth morphotypes recovered from the Cenomanian–Turonian of Uzbekistan have been regarded as *Paronychodon asiaticus* (Nessov 1995; Sues & Averianov 2013). These teeth can be serrated, but most of them lack denticles (Sues & Averianov 2013), similar to the Laño teeth. These teeth can have up to 20 ridges on both sides (Sues & Averianov 2013), thus differing from the Laño sample. In contrast, the teeth classified as morphotype IV have fewer grooves (Sues & Averianov 2013). Although the tooth ZIN PH 1071/16 has a similar number of grooves to the teeth from Laño, it has denticles and overall a different crown morphology (see morphotype III of Sues & Averianov 2013).

Although teeth similar to the North American *Paronychodon* have been classified as *Euronychodon* in southern Europe (Antunes & Sigogneau-Russell 1991), they are indistinguishable from each other (Torices *et al.* 2015), so they could be considered synonyms (Rauhut 2002; Sues & Averianov 2013).

*Paronychodon* or cf. *Paronychodon* teeth have been described from the Upper Cretaceous of the European sites (e.g. Pol *et al.* 1992; Garcia *et al.* 2000; Codrea *et al.* 2002; Vasile & Csiki-Sava 2011; Vasile *et al.* 2012; Ortega *et al.* 2015; Torices *et al.* 2015; Marmi *et al.* 2016; Ősi *et al.* 2019). However, some teeth referred to *Paronychodon* from the Maastrichtian of Transylvania probably represent derived paravian theropods (Csiki-Sava *et al.* 2015). Two specimens from the teeth included in cf. Coeluridae by Antunes & Sigogneau-Russell (1992) from the Maastrichtian Taveiro locality are unserrated, ziphodont and seem to show those characteristic longitudinal ridges of *Paronychodon* (Antunes & Sigogneau-Russell 1992, pl. 1, fig. 8, pl. 2, fig. 3).

Most of the teeth referred to *Paronychodon* found in the Upper Cretaceous European sites have a D-shaped cross-section with a flat lingual surface, unserrated carinae and grooves on the lingual side (e.g. Ősi *et al.* 2019) or on both the lingual and labial surfaces (e.g. Antunes & Sigogneau-Russell 1991; Vasile *et al.* 2012; Ortega *et al.* 2015; Torices *et al.* 2015). The teeth from Laño are similar to those from these European sites in that they have unserrated carinae, grooved lingual and labial sides, and in the number of grooves and in their cross-section. The Laño teeth have a reniform cross-section that hardly differs from the D-shaped cross-

section observed in other European teeth referred to *Paronychodon*. Therefore, the teeth belonging to this morphotype are nearly identical to other *Paronychodon* teeth from Europe.

The teeth from La Neuve described by García *et al.* (2000) as cf. *Paronychodon* sp. do not have the characteristic ridges and may not belong to this taxon. The teeth of cf. *Paronychodon* found in the locality of Quintanilla del Coco seem to have serrated distal carinae (Pol *et al.* 1992). Therefore, they differ from those studied here.

The PCA shows an overlap between the teeth of the Laño morphotypes cf. *Paronychodon* sp. and Paraves indet. because they lack denticles and are similar in size (see Statistical Analysis). Nevertheless, the teeth of the morphotype cf. *Paronychodon* sp. from Laño can be distinguished by the presence of longitudinal ridges. Moreover, the DA classified correctly all of the specimens from Laño as *Paronychodon* (Isasmendi *et al.* 2021*a*, appendix A).

The presence and number of grooves in the labial and lingual sides, the lack of denticles on the carinae and the basal cross-section make the teeth of this morphotype from Laño nearly identical to those of *Paronychodon* from Europe. Nevertheless, the lack of fossil material other than teeth in the fossil record does not enable clarification of whether all of the teeth of this morphotype belong to the same genus or not. Hence, five teeth (MCNA 14547, 14562–14565) assigned to Coelurosauria indet. by Torices *et al.* (2015) and a new specimen (MCNA 16755) are here attributed to cf. *Paronychodon* sp.

Family INDET.
RICHARDOESTESIA Currie *et al.*, 1990
cf. *Richardoestesia*
Figure 5

*Remarks.* 2 cf. *Richardoestesia* sp. morphotypes (A and B) have been distinguished in the Laño sample.

cf. Richardoestesia sp. A
Figure 5A–AB

*Material.* 35 isolated teeth and 59 fragments (MCNA 14566–14610, 14612–14622, 16768, 16779, 16780, 16786–16788, 16790, 16803, 16804, 16816–16823, 16825–16830, 16832, 16833, 16837, 16841, 16846–16849, 16851, 16852, 16857–16861).

*Description.* The teeth included in the cf. *Richardoestesia* sp. A morphotype are flattened, labiolingually compressed and blade-like (ziphodont crowns) (Fig. 5A–AB). Most of the teeth have a planar surface on both the labial and lingual sides (Fig. 5C, E, K, M, U, V). Their cross-section can be elliptical, oval, lanceolate or even slightly lenticular (Fig. 5G–I, R, S, Z–AB). The position of the apex varies with the tooth, and can be either more mesial or more distal in position. Sometimes the apex points sharply backwards (Fig. 5E, K, V).

All of the teeth have convex mesial and concave distal margins. The degree of concavity and convexity is related to the curvature of the tooth (Fig. 5A, C, E, K, M, P, U, V, X). The labial

surface is straight or convex whereas the lingual side is flat, convex or concave.

These specimens are small-sized theropod teeth. The CH varies between 1.37 and 6.82 mm. The CBL ranges between 1.14 and 6.5 mm, and the CBW between 0.45 and 2.14 mm. The carinae are apicobasally oriented, always extending along the mesial and distal margins. The distal carina extends from the apex to the cervix. By contrast, the mesial carina extends from the apex to the mid-crown, but can also almost reach the cervix (Fig. 5A, C, E, K, M, P, U, V, X). The distal carina can be straight or somewhat twisted, with the apical part of it displaced labially and the part adjacent to the cervix displaced lingually. However, in most of the teeth the distal carina is centred. The mesial carina is always straight, but it can be centred or slightly lingually displaced.

All of the teeth have serrated distal carinae. In contrast, the mesial carinae may or not be serrated (Fig. 5A, C, E, K, M, P, U, V, X). The denticles are small, subrectangular and rounded. Their orientations can vary in the carinae, being perpendicular to it or slightly apically inclined (Fig. 5B, D, F, J, L, N, O, Q, T, W, Y). They usually get smaller towards the apex, and sometimes also towards the cervix (Fig. 5A, C, E, K, M, P, U, V, X). The denticles are much smaller on the mesial margin (Fig. 5L, Q). No interdenticular sulcus is distinguished in the teeth. The denticle density varies between 6 and 15 denticles/mm on the mesial side and between 5 and 15 denticles/mm on the distal edge. Of the specimens with mesial serrated carinae, the DSDI ranges from 1 to 1.86. The MDH varies between 0.03 and 0.04 mm and the MDL between 0.09 and 0.13 mm, whereas the DDH ranges from 0.01 to 0.1 mm and the DDL from 0.03 to 0.15 mm.

No ornamentation has been identified on the cf. *Richardoestesia* sp. teeth, but sometimes they have subtle apicobasally oriented flutes. The teeth may be polished, but the texture of the enamel seems to be irregular. This is not very pronounced, with the result that the surface is almost smooth.

cf. Richardoestesia sp. B
Figure 5AC–AL

*Material.* 18 almost complete isolated teeth and 35 fragments (MCNA 16765–16767, 16769–16778, 16781–16785, 16789, 16791–16802, 16805–16807, 16814, 16815, 16824, 16831, 16834–16836, 16838–16840, 16842–16845, 16850, 16853–16856).

*Description.* Most of the teeth of cf. *Richardoestesia* sp. B are incomplete, but they retain enough features to describe the morphotype. Although these teeth are ziphodont, compared with those teeth from the cf. *Richardoestesia* sp. A morphotype they are labiolingually less compressed. The teeth classified as cf. *Richardoestesia* sp. B morphotype are elongate and quite straight (Fig. 5AC, AF, AI). Their cross-section can have an oval, figure-eight or subcircular outline (Fig. 5AK, AL). The crowns of some teeth are quite subsymmetrical, which hinders the differentiation between the mesial and distal margins (Fig. 5AI). Their mesial edge is convex, but the distal side can be convex, concave or almost straight (Fig. 5AC, AF, AI). The labial surface is flat or
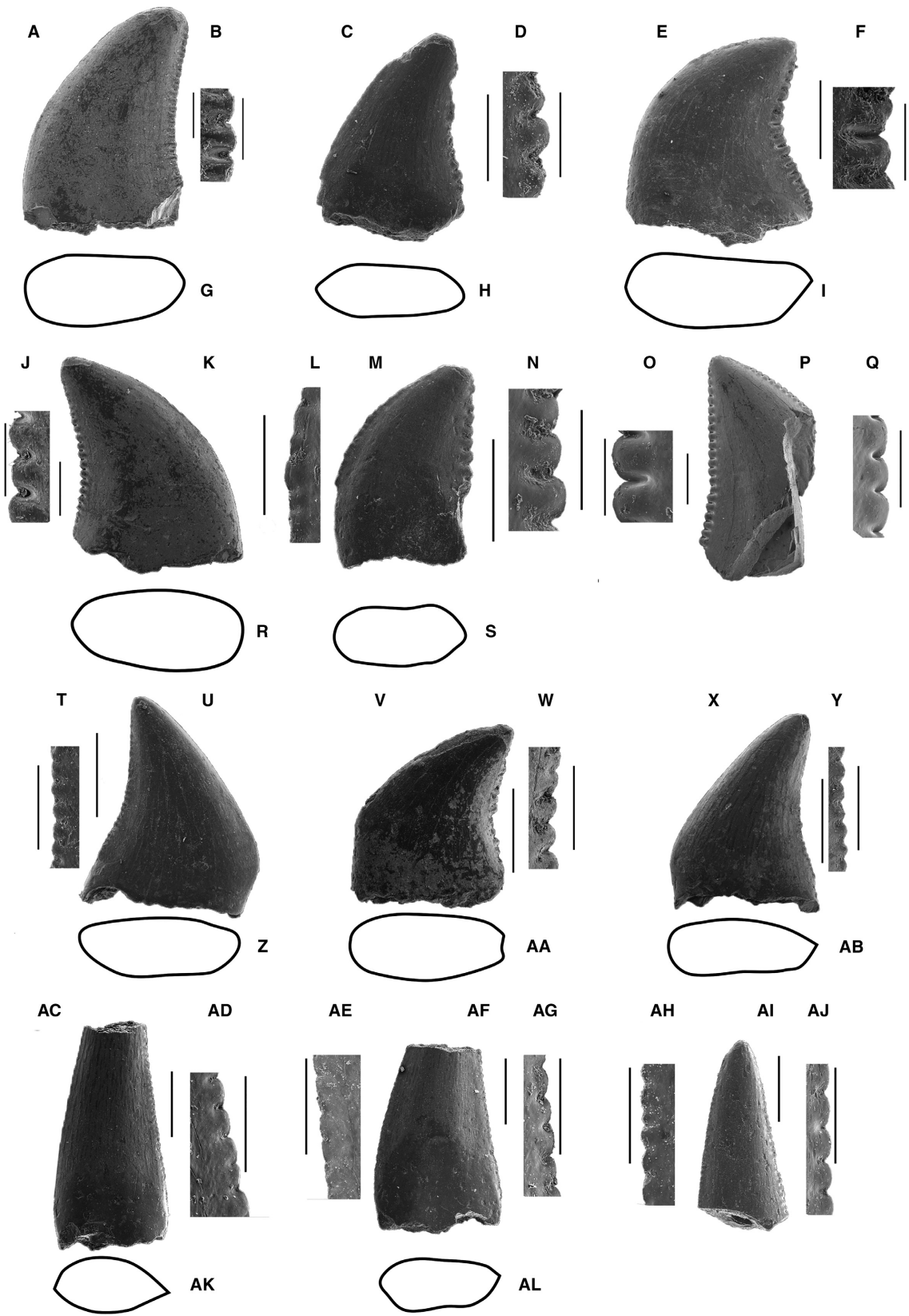
**FIG. 5.** Cf. *Richardoestesia* sp. morphotype teeth from the upper Campanian Laño site. A–AB, cf. *Richardoestesia* sp. A morphotype: A–B, G, MCNA 14606, crown, distal denticles and basal cross-section scheme; C–D, H, MCNA 14577, crown, distal denticles and basal cross-section scheme; E–F, I, MCNA 14608, crown, distal denticles and basal cross-section scheme; J–K, R, MCNA 14607, distal denticles, crown and basal cross-section scheme; L–N, S, MCNA 14588, mesial denticles, crown, distal denticles and basal cross-section scheme; O–Q, MCNA 16832, distal denticles, crown and mesial denticles; T–U, Z, MCNA 14571, distal denticles, crown and basal cross-section scheme; V–W, AA, MCNA 14609, crown, distal denticles and basal cross-section scheme; X–Y, AB, MCNA 14580, crown, distal denticles and basal cross-section scheme. AC–AL, cf. *Richardoestesia* sp. B morphotype: AC–AD, AK, MCNA 16797, crown, distal denticles and basal cross-section scheme; AE–AG, AL, MCNA 16792, mesial denticles, crown, distal denticles and basal cross-section scheme; AH–AJ, MCNA 16796, mesial denticles, crown and distal denticles. Scale bars represent: 1 mm (A, C, E, G–I, K, M, P, R, S, U, V, X, Z, AA–AC, AF, AI, AK, AL); 0.3 mm (B, D, F, J, L, N, O, Q, T, W, Y, AD, AE, AG, AH, AJ).

convex whereas the lingual margin is flat or concave. Due to the fact that no complete tooth is preserved, only the measurements of four crowns have been possible, with CH between 2.27 and 3.34 mm. The CBL ranges between 1.19 and 3.47 mm and the CBW varies between 0.54 and 1.8 mm.

Both carinae reach the cervix, or nearly so. The distal carina is almost straight and centred along the sagittal midline, but it may be displaced labially adjacent to the cervix. The mesial carina is straight and centred. The carinae are usually serrated, but some of the teeth lack mesial denticles. The denticles are also subrectangular or subquadrangular, having rounded tips. Sometimes they are tilted towards the apex (Fig. 5AD, AE, AG, AH, AJ). Overall, the denticles are smaller in this morphotype than in cf. *Richardoestesia* sp. A on both the mesial and distal carinae. They may be minute on the mesial carina, and are always smaller on this carina (Fig. 5AD, AE, AG, AH, AJ). Nevertheless, not all mesial carinae are serrated. The distal carinae can show a decrease in the size of the denticles towards the apex or the cervix. The teeth do not show interdenticular sulci. The denticle density ranges between 7 and 15 denticles/mm on the mesial carinae and between 5 and 17 denticles/mm on the distal carinae. The teeth with the highest denticle density on the distal carina are those that lack denticles on the mesial side. The DSDI varies between 1.09 and 1.57. Regarding the denticle size, the MDH ranges between 0.01 and 0.03 mm and the MDL between 0.03 and 0.04 mm. The DDH varies between 0.03 and 0.04 mm and the DDL between 0.08 and 0.1 mm.

These teeth also seem to have a very irregular enamel texture that can be almost smooth and not very well marked. The enamel does not have transverse or marginal undulations, nor ornamentation.

*Remarks. Richardoestesia gilmorei* was erected on the basis of a pair of dentaries with erupted and unerupted teeth from the Judith River Formation of Canada (Currie *et al.* 1990). No more remains assigned to this taxon have been found except isolated teeth. Teeth assigned to *Richardoestesia* have been found in Asia, Europe and North America (e.g. Currie *et al.* 1990; Sankey *et al.* 2002; Sues & Averianov 2013; Torices *et al.* 2015). These teeth are characterized by their small-sized denticles and by a density greater than 5 denticles/mm on the distal carinae (Currie *et al.* 1990). Indeed, *Richardoestesia* denticles are the smallest of all Late Cretaceous theropods (Torices *et al.* 2015). Usually, the mesial carina is unserrated, but if denticles are present, they are smaller than the distal ones (Torices *et al.* 2015).

The teeth of *Richardoestesia* show wide variability in shape and size (Currie *et al.* 1990; Torices *et al.* 2015). Two different morphologies have been observed (Currie *et al.* 1990; Baszio 1997; Sankey *et al.* 2002): flattened and curved versus elongate and straight or slightly recurved crowns. Currie *et al.* (1990) proposed that each morphotype could represent a different species of *Richardoestesia*, but they did also note the possibility that these morphological variations may be due to heterodonty. Baszio (1997) considered that they belong to different species and provisionally referred the elongate teeth as *Richardoestesia* sp. Finally, Sankey (2001) renamed them *Richardoestesia isosceles*.

Sankey *et al.* (2002) noted that the distal denticles of *R. isosceles* were smaller and more subquadrangular than those of *R. gilmorei*. *Richardoestesia isosceles* also lacks interdenticular slits (Sankey *et al.* 2002). Unlike *R. gilmorei*, *R. isosceles* usually has mesial denticles (Sankey *et al.* 2002).

Even though the two species are considered to be two different morphotypes, an overlap is present in the measurements, meaning that they are not distinguishable in terms of CH and CBL (Sankey *et al.* 2002; Torices *et al.* 2015). Indeed, Currie *et al.* (1990) noted the variability both in shape and size in the jaws of *R. gilmorei*. Heterodonty is also known in other theropods (e.g. Currie *et al.* 1990; Carrano *et al.* 2002; Rauhut *et al.* 2010), therefore the differences between these two species are very slight, and the validity of *R. isosceles* is still doubtful (Torices *et al.* 2015). Furthermore, it is probable that *Richardoestesia* teeth may represent more than one taxon (Williamson & Brusatte 2014).

The North American *Richardoestesia* genus differs from the Laño sample in having a distal carina strongly deflected labially and sporadic variation in the denticle size (Currie *et al.* 1990; Hendrickx *et al.* 2019). In contrast, the cf. *Richardoestesia* sp. teeth from Laño have almost centred distal carinae and no sporadic denticle size variation.

Isolated teeth from different European sites have been referred to *Richardoestesia*. There are teeth from the Upper Jurassic of Portugal (Zinke 1998; Hendrickx & Mateus 2014*a*) and the Lower Cretaceous of Spain (Rauhut 2002), which are identified as *Richardoestesia* aff. *R. gilmorei* and cf. *Richardoestesia* sp., respectively, as well as teeth from the Upper Cretaceous formations of Romania (Codrea *et al.* 2002; Vasile 2008; Vasile & Csiki-Sava 2011; Vasile *et al.* 2012; Csiki-Sava *et al.* 2016) and the Ibero-Armorican domain (Prieto-Márquez *et al.* 2000; Valentin *et al.* 2012; Ortega *et al.* 2015; Torices *et al.* 2015; Marmi *et al.* 2016). There are some teeth that, although they closely resemble those of *Richardoestesia*, have not been assigned to this taxon. According

to the illustrations and descriptions provided by Buffetaut *et al.* (1986), the isolated crowns found in Champ-Garimond, La Neuve, Serviers and Villeveyrac are very small (CH < 3.5 mm), with DDD between 8 and 15 denticles/mm and higher MDD if the mesial denticles are conserved (Buffetaut *et al.* 1986). Furthermore, in the figure (drawings), the denticles become much smaller towards the apex of the crown. On the whole, these features make these teeth similar to those of cf. *Richardoestesia*. Torices *et al.* (2015) noted that the measurements and morphologies of the teeth and denticles from Romania and those from the Iberian Peninsula correspond to one another.

The teeth assigned to *Richardoestesia* from Europe (e.g. Valentin *et al.* 2012; Vasile *et al.* 2012; Ortega *et al.* 2015; Marmi *et al.* 2016) show a wide range of variability in crown shape, presence and absence of mesial denticles, and degree of curvature. However, the *Richardoestesia* teeth always have small crowns, minute denticles and DSDI greater than or equal to 1, if the mesial carina is serrated. The teeth from Laño have a different curvature and crown shape, but all of them share the features of this taxon.

In Laño two cf. *Richardoestesia* sp. morphotypes have been recognized in the sample. On the one hand, the teeth of the cf. *Richardoestesia* sp. A morphotype are similar to those of *R. gilmorei*, being flattened, curved and more blade-like. On the other hand, the teeth of the cf. *Richardoestesia* sp. B morphotype are similar to *R. isosceles*, because the crowns are more elongate, straight and conical, and have smaller denticles than those of *Richardoestesia gilmorei* and the cf. *Richardoestesia* sp. A morphotype. Furthermore, the teeth of the cf. *Richardoestesia* sp. B morphotype from Laño highly resemble the teeth morphotypes A and C of *Richardoestesia asiatica* studied by Averianov & Sues (2019). Nonetheless, the teeth of the cf. *Richardoestesia* sp. A morphotype from Laño curve more strongly backwards than those of the Asian taxon.

In the PCA, the sample of cf. *Richardoestesia* sp. morphotypes from Laño falls in the morphospace of the smallest teeth of the North American *Richardoestesia*, including *R. gilmorei* and *R. isosceles*. There is an important overlap between the teeth of *Richardoestesia*, *R. gilmorei*, *R. isosceles* and the cf. *Richardoestesia* sp. morphotypes from Laño. Furthermore, in all of the morphospaces of *Richardoestesia*, the teeth are separated by the presence or absence of mesial denticles. Furthermore, the two morphotypes of cf. *Richardoestesia* sp. identified in the Laño sample overlap, therefore it is not statistically possible to distinguish the teeth of each of the morphotypes (see Statistical Analysis). The DA correctly identifies most of the specimens attributed to cf. *Richardoestesia* sp. as *Richardoestesia*. Five teeth (MCNA 14573, 14610, 16798, 16800 and 16832) were attributed to *Falcarius* and one specimen (MCNA 14608) was assigned to *Velociraptor* (Isasmendi *et al.* 2021a, appendix A). Nevertheless, the mesial teeth of *Falcarius* are incisiform and unserrated while the distal teeth have basal constrictions (Zanno 2010; Hendrickx *et al.* 2019), thus differing from the Laño sample. Furthermore, the MCNA 14608 tooth does not have any crown ornamentation unlike those of *Velociraptor* (Hendrickx *et al.* 2019).

Despite the similarities of the Laño sample and isolated teeth of *Richardoestesia*, the lack of fossil material other than teeth in the European fossil record does not lead to the safe attribution of these teeth to any species of *Richardoestesia* or even to this genus. Therefore, in the light of these considerations, 64 teeth from Laño referred to ?*Richardoestesia* sp. by Torices *et al.* (2015), as well as another 83 teeth from Laño, are here assigned to cf. *Richardoestesia* sp. Furthermore, the MCNA 14622 specimen is here attributed to cf. *Richardoestesia* sp. A because its denticle shape and density are similar to those of the cf. *Richardoestesia* sp. A morphotype (instead of to ?Dromaeosauridae indet., *contra* Torices *et al.* 2015).

MANIRAPTORA Gauthier, 1986
PENNARAPTORA Foth *et al.*, 2014
PARAVES Sereno, 1997
PARAVES INDET.
Figure 4A–J

*Remarks.* Two tooth morphotypes (A and B) pertaining to indeterminate paravians have been differentiated at Laño.

Paraves indet. A
Figure 4A–F

*Material.* 7 isolated teeth (MCNA 14523–14529).

*Description.* Most of the teeth are complete but some of them lack apices. The teeth are highly elongate, curved backwards, and are moderately labiolingually compressed. Usually the crowns are conidont, although some are ziphodont (Fig. 4A–C). Their cross-section is elliptical or slightly reniform at the level of the cervix, where no constriction can be distinguished (Fig. 4D–F). The teeth lack marginal and transverse undulations or any ornamentation (Fig. 4A–C), and seem to have a very subtle irregular enamel texture.

The mesial edge is convex whereas the distal side is concave (Fig. 4A–C). The labial face is convex and the lingual face varies between convex and almost straight. In some of the teeth the middle part of the lingual side shows a pronounced planar area (Fig. 4A, C).

This morphotype consists of small-sized theropod teeth. The CH varies between 1.43 and 5.22 mm, and the CBL between 0.94 and 2.38 mm. The CBW ranges from 0.61 to 1.46 mm, being slightly more than half of the CBL. Indeed, the CBR ranges from 0.53 to 0.71 whereas the CHR varies between 1.52 and 2.73.

The teeth have unserrated distal and mesial carinae. Both carinae reach the cervix or nearly so. The mesial carina is straight, but it is slightly lingually displaced. In contrast, the distal carina is centred along the midline in most of the teeth.

Paraves indet. B
Figure 4G–J

*Material.* 31 specimens including isolated teeth and fragments (MCNA 14530–14546, 14548–14561).

*Description.* The teeth of Paraves indet. B are quite similar to the Paraves indet. A. Nevertheless, they are flattened, ziphodont, labiolingually more compressed and their apices are more displaced backwards (Fig. 4G, H). The cross-section is generally elliptical or reniform, but is sometimes even close to being D-shaped (Fig. 4I, J). They are relatively straight in the basal part of the crown, but before reaching the mid-crown both mesial and distal faces curve backwards significantly (Fig. 4G). No constriction is seen at the level of the cervix. The enamel has a slightly irregular texture and does not show marginal or transverse undulations.

The mesial margin is convex whereas the distal one is concave. The labial face is convex whereas the lingual surface is flat or convex. According to the measurements, the CH ranges between 1.26 and 4.55 mm, the CBL varies between 0.93 and 2.82 mm, and the CBW between 0.5 and 1.4 mm. The CBR ranges from 0.36 to 0.72 whereas the CHR varies between 1.11 and 1.88.

All the teeth belonging to Paraves indet. B have both mesial and distal unserrated carinae, which reach, or almost reach, the cervix (Fig. 4G, H). The mesial carina is straight, but it is slightly lingually displaced in some teeth. The distal carina is usually centrally positioned, although it is labially or lingually displaced in some teeth.

*Remarks.* The teeth here classified as the Paraves indet. A and B morphotypes were previously assigned to Coelurosauria indet. by Torices *et al.* (2015), because it seems that the loss of serrations on the carinae is a convergent character in several coelurosaurian clades. These include ornithomimosaurs such as *Pelecanimimus* (Pérez-Moreno *et al.* 1994), some troodontids (Hendrickx *et al.* 2019 and references therein), the maniraptor *Fukuivenator* (Azuma *et al.* 2016), and alvarezsaurids such as *Shuvuuia* (Suzuki *et al.* 2002).

Compsognathids have ziphodont dentition with teeth smaller than 1 cm in CH (Hendrickx *et al.* 2019). The anteriormost teeth of compsognathids may have either serrated or unserrated carinae, but their lateral teeth have mesial denticles (e.g. Dal Sasso & Maganuco 2011; Hendrickx & Mateus 2014*a*). However, the Laño sample shows a wide morphological variability, suggesting that there might also be lateral unserrated teeth.

Derived ornithomimosaurs are edentulous, but this is not the case for *Pelecanimimus*, *Harpymimus*, *Shenzhosaurus* (Makovicky *et al.* 2004) and *Nqwebasaurus* (Choiniere *et al.* 2012). The teeth of these basal ornithomimosaurs have no denticles, like the teeth from Laño. However, *Pelecanimimus* teeth show basal constrictions between the roots and the crowns (Pérez-Moreno *et al.* 1994), and *Shenzhosaurus* and *Nqwebasaurus* teeth lack carinae (Ji *et al.* 2003; Choiniere *et al.* 2012). Furthermore, the presence of a subsymmetrical conidont dentition is a synapomorphy for Ornithomimosauria but not for *Pelecanimimus* (Hendrickx *et al.* 2019). The Laño teeth belonging to these morphotypes are asymmetrical and do not show any constriction at the base of the crown.

Alvarezsauroids have a CH less than 1 cm, unserrated mesial carinae and subsymmetrical teeth (Hendrickx *et al.* 2019). Although the teeth from Laño are less than 1 cm and unserrated, the teeth are asymmetrical. Non-alvarezsaurid alvarezsauroids such as *Shuvuuia* and *Mononykus* have ziphodont dentition. Their teeth do not have serrated carinae and have basal constrictions (Perle *et al.* 1994; Chiappe *et al.* 1998; Suzuki *et al.* 2002; Hendrickx 2015). The basal constriction thus distinguishes them from the Laño teeth. *Haplocheirus* has anterior unserrated and posterior serrated teeth (Choiniere *et al.* 2014). Nonetheless, the morphological variation in the Laño teeth suggests the possibility of anterior and lateral unserrated teeth in the sample.

Oviraptorosaurs have larger mesial teeth compared with the lateral ones (Hendrickx *et al.* 2019). Mesial teeth belonging to these theropods are conical in shape and unserrated (Hendrickx *et al.* 2019). Moreover, basal oviraptorosaurs such as *Caudipteryx* (Osmólska *et al.* 2004) and *Protarchaeopteryx* (Senter *et al.* 2004) have unserrated teeth, but these teeth, together with those of *Incisivosaurus*, have basal constrictions (Ji *et al.* 1998; Osmólska *et al.* 2004; Balanoff *et al.* 2009; Hendrickx 2015). Furthermore, the lateral teeth of *Incisivosaurus* and *Similicaudipteryx* are folidont (Hendrickx *et al.* 2019). Both morphotypes found in Laño differ from oviraptorosaur teeth in the lack of basal constrictions and folidont crown shapes. As aforementioned, the variability shown by both morphotypes may suggest the presence of lateral and anterior teeth in the sample.

Moreover, the teeth of all ornithomimosaurs, therizinosaurs, alvarezsaurids and apparently *Caudipteryx* have CBRs greater than 0.75 (Hendrickx *et al.* 2019). This is not the case for the unserrated teeth of Laño, which do not exceed that value.

As defined, Paraves comprises dromaeosaurids, troodontids and birds (Sereno 1997). However, some phylogenetic analyses have included Scansoriopterygidae inside this clade (e.g. Lefevre *et al.* 2017). Paravians have a wide range of dentition types (e.g. Currie *et al.* 1990; Sankey *et al.* 2002; Hendrickx 2015; Hendrickx *et al.* 2015, 2019; Torices *et al.* 2015). Unserrated teeth are common in paravians. Based on Senter *et al.* (2004), Hendrickx (2015) proposed that this condition is synapomorphic for Pennaraptora, and thus plesiomorphic for Paraves. The troodontids *Byronosaurus*, *Gobivenator*, *Urbacodon* and *Xixiasaurus* (Hendrickx *et al.* 2019 and references therein), unenlagiines such as *Austroraptor* and *Buitreraptor* (Novas *et al.* 2008; Gianechini *et al.* 2011), and some crowns of microraptorine dromaeosaurids (Hendrickx *et al.* 2019) have unserrated teeth. Halszkaraptorines and unenlagiines have strongly recurved ziphodont teeth with no denticles, but not *Austroraptor*, and an irregular enamel texture (Hendrickx *et al.* 2019). Unenlagiinae theropods seem to have ridged or fluted lateral teeth (Hendrickx *et al.* 2019). Nevertheless, if *Pyroraptor* is an unenlagiine, as suggested by Hartman *et al.* (2019), not all unenlagiines would have unserrated and fluted crowns. Furthermore, *Halszkaraptor* and possibly halszkaraptorines have D-shaped mesial teeth (Hendrickx *et al.* 2019). The Laño morphotypes differ from those of troodontids in their overall crown morphology. Indeed, most troodontids have folidont dentitions, but not some basal forms, which have heterodont lateral dentitions with folidont and ziphodont crowns (Hendrickx *et al.* 2019). Most of jinfengopterygines have small unserrated crowns and folidont dentition, but not all of the teeth are unconstricted in *Jinfengopteryx* (Hendrickx *et al.* 2019). The teeth found in Laño resemble those of halszkaraptorines and unenlagiines in the dentition type, tooth curvature,

texture and lack of denticulate carinae. Moreover, some teeth belonging to these morphotypes have an almost D-shaped cross-section such as *Halszkaraptor* and possibly halszkaraptorines (Hendrickx *et al.* 2019). Nevertheless, these teeth lack the characteristic flutes or ridges of unenlagiines. The ziphodont teeth of *Jinfengopteryx* are also similar to those of Paraves indet. from Laño in the dentition type, tooth curvature and unserrated crowns.

Based on skeletal remains, the paravian record from the uppermost Cretaceous of Europe is rather scarce, consisting of the dromaeosaurids *Balaur bondoc*, *Pyroraptor olympius* and *Variraptor mechinorum* (Le Loeuff & Buffetaut 1998; Allain & Taquet 2000; Csiki *et al.* 2010; Csiki-Sava *et al.* 2015) and the possible jinfengopterygine troodontid *Tamarro insperatus* (Sellés *et al.* 2021). Nevertheless, *V. mechinorum* has been regarded as a *nomen dubium* because of the lack of dromaeosaurid features (Allain & Taquet 2000; Turner *et al.* 2012). Isolated teeth have also been described and attributed to dromaeosaurines and velociraptorines (e.g. Baiano *et al.* 2014; Ortega *et al.* 2015; Marmi *et al.* 2016). Furthermore, isolated teeth have also been regarded as belonging to troodontids (e.g. Antunes & Sigogneau-Russell 1992). Most of these paravian teeth, when preserved, have denticulate carinae. Furthermore, the teeth of *Paronychodon* have fluted crowns (Currie *et al.* 1990).

The paravian teeth from Laño are classified into two morphotypes. The teeth included in the Paraves indet. A morphotype are elongate and mostly conidont, whereas the teeth belonging to the Paraves indet. B morphotype are flattened and ziphodont, with the apex more displaced backwards. Both morphotypes preserve carinae on both the mesial and distal margins. Moreover, the PCA shows an overlap between these morphotypes, therefore it is not possible to statistically determine whether they belong to two different taxa (see Statistical Analysis, below). Instead, they are likely to represent the dental variation within a single taxon. Most of the teeth belonging to Paraves indet. from Laño were classified as *Paronychodon* or *Buitreraptor* by the DA (Isasmendi *et al.* 2021*a*, appendix A). Nonetheless, the teeth of Paraves indet. morphotypes from Laño do not show grooves or ridges on their crowns, thus differing from the dentition of the American genera.

The studied teeth do not have the characteristics of alvarezsauroids, compsognathids, ornithomimosaurs, oviraptorosaurs or therizinosaurs, and share more features with some paravians. Given that the knowledge of European theropods is still limited, the most conservative option is therefore to assign these teeth from Laño to Paraves indet.

There are isolated theropod teeth from other Ibero-Armorican sites that resemble those of the Paraves indet. morphotypes from Laño. The theropod teeth studied by Torices *et al.* (2015) from the Maastrichtian Blasi, Montrebei and Vicari 4 localities have the same features as these teeth and, thus, may be attributed to Paraves indet. The teeth assigned to Theropoda indet. by Sigé *et al.* (1997) from the middle–upper Campanian Fons-Champ-Garimond locality, the coeval cf. *Paronychodon* tooth from the La Neuve site described by Garcia *et al.* (2000), the Coelurosauria indet. teeth studied by Company *et al.* (2009) found at the upper Campanian Chera site, and by Puértolas-Pascual *et al.* (2018) from the latest

Maastrichtian Larra 4 site do also show similar features. Therefore, they might belong to a single taxon or to closely related taxa. There are also isolated theropod teeth in Portugal that have the same features as those of these morphotypes found in the Laño site. Most of the teeth described as cf. Coeluridae by Antunes & Sigogneau-Russell (1992) are ziphodont and have both distal and mesial carinae with no denticles (Antunes & Sigogneau-Russell 1992, pl. 2, figs 1, 2, 4–8, pl. 3, figs 5–7). Hence, they share these features with those of Paraves indet. from Laño.

## DROMAEOSAURIDAE Matthew & Brown, 1922
## DROMAEOSAURIDAE INDET.
### Figure 6

*Material.* 4 teeth (MCNA 14623–14626).

*Description.* The teeth assigned to Dromaeosauridae indet. are associated with dentary fragments. The interdental plates, located on the lingual surface of the dentary, are fused together (Fig. 6C, G). Two of the teeth are complete crowns (MCNA 14623 and 14624), but the other two lack apices (Fig. 6C, G). The teeth show a ziphodont crown morphology. Moreover, the apex points sharply backwards (Fig. 6C, G). No marginal or transverse undulations or ornamentation can be identified on the crowns. Their cross-sections are figure-eight or oval in outline (Fig. 6I, J). The lingual side is flat whereas the labial side is convex or flat. The mesial margins of the teeth are convex and the distal edges are concave (Fig. 6C, G). The enamel texture of the teeth belonging to this morphotype is braided (Fig. 6K).

The specimens grouped in this morphotype are small-sized theropod teeth. The CH varies between 5.66 and 6.62 mm in the complete teeth, but the teeth lacking the apical parts seem to be shorter. The CBL ranges between 3.5 and 5.29 mm and the CBW between 1.6 and 4.32 mm.

Both carinae are straight. Whereas the distal carina runs apicobasally from the apex to the cervix (Fig. 6C, D, G), the mesial carina does not reach the cervix and ends approximately two-thirds of the way along the crown from the apex (Fig. 6B, C, F, G). Both carinae have serrations along their entire extension. The denticles are chisel-shaped, subquadrangular or slightly subrectangular in shape, symmetrical, and perpendicular to the carina (Fig. 6A, E, H). The denticle density varies between 8 and 9 denticles/mm on the mesial margin and there are 6 denticles/mm on the distal edge, therefore the mesial denticles are smaller than the distal ones, with DSDI ranging from 1.33 to 1.5.

*Remarks.* Fused interdental plates are a common feature of dromaeosaurids such as *Deinonychus*, *Dromaeosaurus* and *Saurornitholestes* (Currie *et al.* 1990; Currie 1995; Torices *et al.* 2015; Currie & Evans 2020). This feature has also been observed in other theropods such as abelisaurids, most allosauroids or some megalosauroids such as *Torvosaurus* (Currie 1995; Sampson & Witmer 2007; Brusatte *et al.* 2008; Carrano *et al.* 2012; Hendrickx & Mateus 2014*b*). Furthermore, the braided enamel
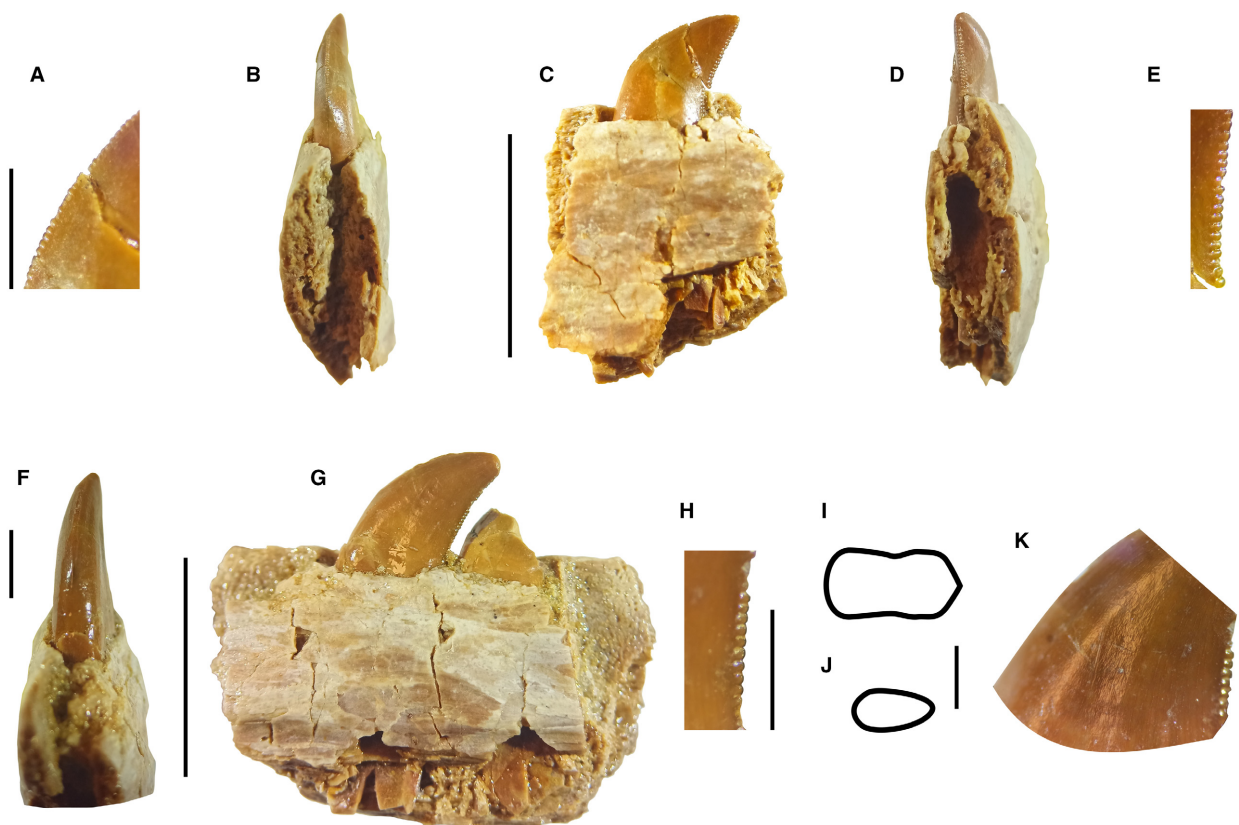
**FIG. 6.** Dromaeosauridae indet. morphotype teeth from the upper Campanian Laño site. A–E, MCNA 14623, mesial denticles, crown and dentary fragment in mesial, lingual and distal views, and distal denticles. F, MCNA 14624, mesial view. G, MCNA 14624 and 14625, lingual view. H, MCNA 14624, distal denticles. I, MCNA 14623, basal cross-section scheme. J, MCNA 14626, basal cross-section scheme. K, MCNA 14624, enamel texture. Scale bars represent: 2 mm (A, E, F, H–K); 1 cm (B–D, G).

texture seems to be present in a variety of theropods such as *Atrociraptor*, *Bambiraptor*, *Deinonychus*, *Saurornitholestes* and some mesial teeth of *Dromaeosaurus* (Hendrickx *et al.* 2019). Therefore, at least some dromaeosaurids share these features with the teeth from this Laño morphotype.

Dromaeosaurid teeth have small crowns with serrations on both carinae but which are smaller on the mesial carina (Hendrickx 2015; Alonso *et al.* 2017). Hendrickx *et al.* (2019) also indicated the following synapomorphies for some dromaeosaurine teeth: ziphodont dentition with denticles in the mesial and distal carina in the lateral teeth and DSDI greater than 1.2. Nevertheless, the teeth of *Dromaeosaurus* have a lower DSDI or lack mesial denticles. The teeth from Laño have ziphodont crowns, serrated mesial and distal carinae, and a DSDI greater than 1.2.

The denticle shape of dromaeosaurid theropods is an important character. These are often subrectangular and chisel-like in morphology (Currie *et al.* 1990; Torices *et al.* 2015), although the denticles of *Atrociraptor* and *Saurornitholestes* are hooked (Hendrickx *et al.* 2019). Most dromaeosaurines and velociraptorines, and all microraptorines have symmetrically to asymmetrically convex denticles (Hendrickx *et al.* 2019). The Laño teeth have subrectangular, chisel-like and symmetrical denticles, as in other dromaeosaurids.

A number of dromaeosaurid teeth have been reported from the Upper Cretaceous formations of the Ibero-Armorican domain (e.g. Ortega *et al.* 2015; Torices *et al.* 2015; Marmi *et al.* 2016). The teeth show similarities to the dromaeosaurid teeth described by Alonso *et al.* (2017) from the Lower Cretaceous Castrillo de la Reina Formation of Burgos. These teeth from the Ibero-Armorican domain have a similar crown cross-section, denticle morphology and DSDI to the teeth from Burgos. The dromaeosaurine teeth studied by Ortega *et al.* (2015) from the Upper Cretaceous Lo Hueco site also have a similar cross-section and denticle morphology, but lower denticle densities. The cf. Dromaeosauridae teeth from Blasi, Figuerola 2 and Fontllonga 6 (Torices *et al.* 2015) have a lower MDD and DDD than those of Laño, and straight distal edges in lateral view.

*Pyroraptor olympius* was defined on the basis of the material found in the Begudian deposits (middle Campanian; Cojan & Moreau 2006; Tortosa *et al.* 2014) of Provence (Allain & Taquet 2000). In the Iberian Peninsula, the localities of Chera (Chera 0 and Chera 2) from the upper Campanian and Montrebei from the lower Maastrichtian have yielded isolated teeth attributed to cf. *Pyroraptor* and ?*Pyroraptor olympius*, respectively (Company *et al.* 2009; Torices *et al.* 2015). The teeth of the holotype of *P. olympius* are laterally compressed, tapered and curved backwards (Allain & Taquet 2000). The mesial margin has a higher denticle density

than the distal carina (MDD, 8–9 denticles/mm; DDD, 6 denticles/mm) (Allain & Taquet 2000). In *P. olympius* the mesial denticles are restricted to the basal half of the mesial carina. However, the apicalmost denticles could have been eroded.

The teeth belonging to the Dromaeosauridae indet. morphotype from Laño were previously assigned to ?*Pyroraptor olympius* by Torices *et al.* (2015). However, the Laño teeth differ from those of *P. olympius* in the overall shape of the crown, the curvature and the extension of the mesial denticles. Indeed, the Laño teeth have apices that are more recurved, and mesial carinae that do not reach the cervices. Instead, the teeth of the holotype of *P. olympius* are not as recurved as the Laño teeth, and regardless of whether the teeth lack the apical mesial denticles or whether they were lost to erosion, the teeth of *P. olympius* seem to bear denticles that reach the basal part of the crown (Allain & Taquet 2000).

The PCA places the teeth belonging to this morphotype closest to the teeth of *Richardoestesia isosceles*, *Saurornitholestes* and *Velociraptor*, and not as close to *Dromaeosaurus* and *P. olympius* (Fig. 7). The DA misidentified two teeth attributed to the Dromaeosauridae indet. morphotype. MCNA 14623 was classified as *Richardoestesia* whereas MCNA 14624 was assigned to *Falcarius* by the DA. MCNA 14623 cannot be assigned to *Richardoestesia* due to the more centred distal carina and the absence of sporadic variation of denticle size. Furthermore, the serrated teeth of *Falcarius* show basal constrictions (Zanno 2010; Hendrickx *et al.* 2019), unlike MCNA 14624. Therefore, the classification made by the DA cannot be taken into consideration.

Only two badly preserved teeth are known from the holotype of *P. olympius* and only one seems to be complete. Although they have identical denticle densities, this tooth is larger and has a different denticle disposition to those of the Dromaeosauridae indet. morphotype from Laño. Therefore, the teeth previously attributed to ?*Pyroraptor olympius* by Torices *et al.* (2015) are here assigned to Dromaeosauridae indet.

Furthermore, one tooth from Montrebei classified as ?*Pyroraptor olympius* by Torices *et al.* (2015) lacks mesial denticles due to erosion (Torices *et al.* 2015, fig. 3A). Company *et al.* (2009) also assigned two small isolated teeth from Chera to cf. *Pyroraptor* ('Morfotipo B' of Company 2005). Similar to the teeth of *P. olympius*, the distal edges of the specimens are almost straight, but, unlike the holotype, these crowns have crenulations in the basal third of the mesial carinae instead of denticles (see Company 2005 for a detailed description). These teeth are similar to those teeth classified as Dromaeosauridae indet. morphotype from Laño in the denticle shape, denticle density and position of the denticles on both carinae. Nevertheless, the Laño specimens are more distally recurved. Hence, it is not possible to assign the tooth from Montrebei to ?*Pyroraptor olympius*, and the specimens from Chera may belong to an indeterminate dromaeosaurid, but not to cf. *Pyroraptor*.

## STATISTICAL ANALYSIS

In the PCA, the two principal components (PCs) explain most of the variation between the teeth. PC-1 describes 63.95% of the variance, with the main loading being the size of the teeth (CH, CBL and CBW). PC-2 explains 22.59% of the variance, with the main loading being the denticle densities (MDD and DDD), especially DDD.

Three main groups are formed in the PCA: the taxa with unserrated teeth, the taxa with serrated small crowns, and the taxa with large serrated teeth. The taxa with unserrated teeth (*Buitreraptor*, *Paronychodon* and *Paronychodon lacustris*), the Paraves indet. morphotypes from Laño and the cf. *Paronychodon* sp. morphotype from Laño fall in the third quadrant, whereas the teeth with denticulate carinae fall in all four quadrants. Of the serrated teeth, two groups can be distinguished, with the largest specimens being located on the right side of the graph and the smallest teeth being situated on the centre or on the left side (Fig. 7).

There is a strong overlap among the taxa with the smallest teeth (*Dromaeosaurus*, the Dromaeosauridae indet. morphotype from Laño, *Falcarius*, *Pyroraptor olympius*, *Richardoestesia*, *Richardoestesia gilmorei*, *Richardoestesia isosceles*, the cf. *Richardoestesia* sp. morphotypes from Laño, *Saurornitholestes*, *Troodon* and *Velociraptor*). Nonetheless, the teeth of *Richardoestesia*, *R. gilmorei*, *R. isosceles* and the cf. *Richardoestesia* sp. morphotypes from Laño are usually smaller and therefore on the left side of the graph, whereas the teeth of the other taxa are more central or shifted to the right (Fig. 7).

Among the largest teeth of the sample there is a minimum overlap. The teeth of abelisaurids and the smallest teeth of *Tyrannosaurus* are similar in size, but they differ in the number of denticles, in that the teeth of *Arcovenator escotae*, the cf. *Arcovenator* morphotype from Armuña and the *Arcovenator* sp. morphotype from Laño have the highest densities. Overall, most of the teeth of the *Tyrannosaurus* sample are bigger than those of abelisaurids (Fig. 7).

Due to the lack of denticles, the unserrated teeth are shown in a line, and differ only in size. The large variability of the teeth of *Paronychodon lacustris* creates a considerable overlap between the teeth. Nevertheless, the teeth of *Buitreraptor* and the Paraves indet. morphotype are smaller and thus are located on the left side of the graph. Instead, the teeth of *Paronychodon*, the cf. *Paronychodon* sp. morphotype from Laño and most of the sample of *P. lacustris* are positioned on the right side (Fig. 7).

The results of the DA are quite good, with 85.5% of the previously grouped cases correctly classified. From the Laño large-sized tooth sample, six teeth were classified as *Arcovenator* and two as *Majungasaurus*. In regards to the smaller teeth with serrations, six teeth were assigned to *Falcarius*, 23 to *Richardoestesia* and one to *Velociraptor*. Finally, only two Laño teeth were classified as *Buitreraptor* whereas 26 were identified as *Paronychodon* (Isasmendi *et al.* 2021*a*, appendix A). The canonical discriminant
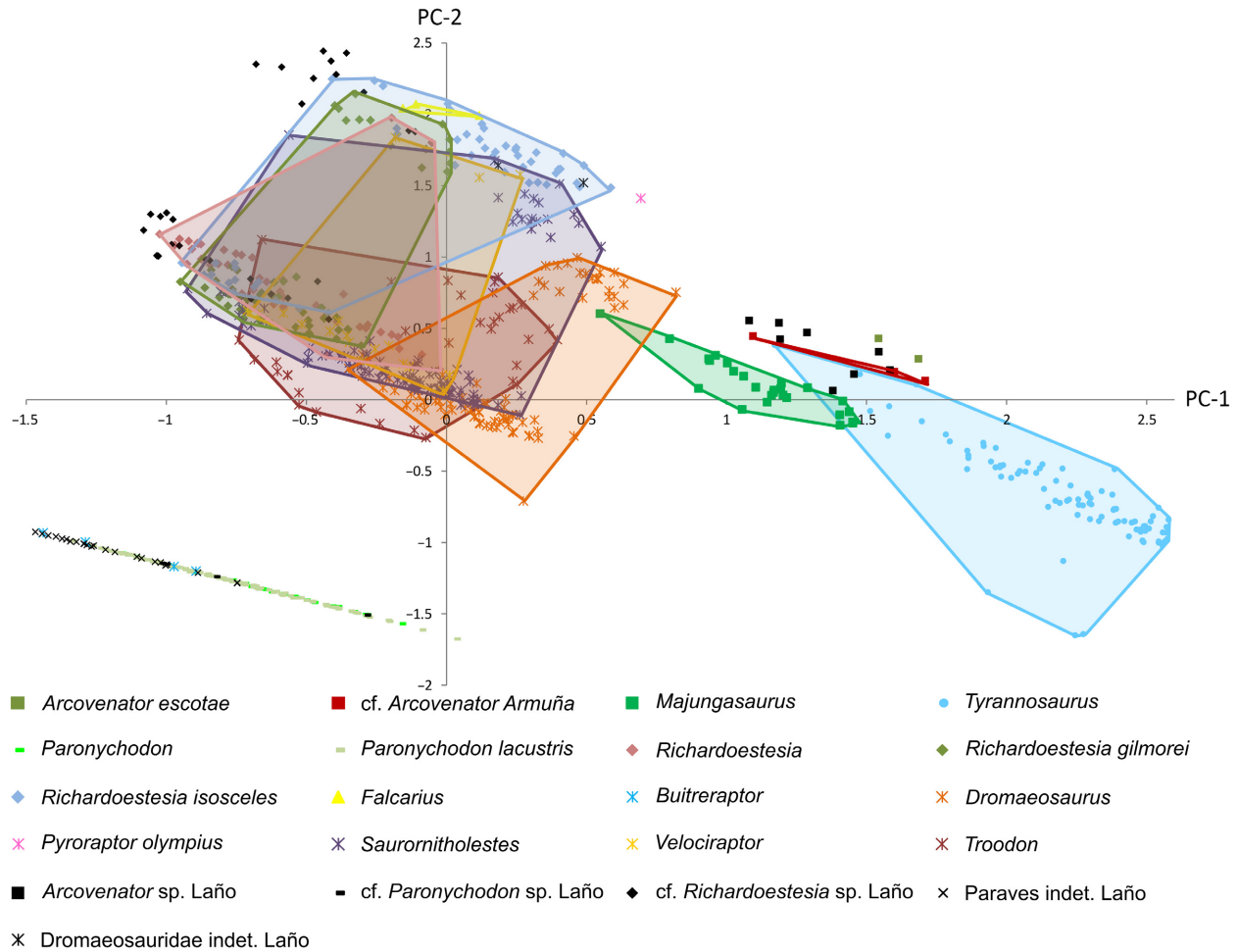
**FIG. 7.** Principal component analysis of the tooth sample from Laño and the database (Isasmendi *et al.* 2021*a*, appendix A).

functions (Fig. 8) show a strong overlap among the smaller teeth from the sample and database. Nevertheless, for the large-sized teeth in the theropod sample the overlap is minimal. The teeth attributed to *Arcovenator* sp. from Laño fall between the teeth of *Arcovenator* and *Majungasaurus*, especially near those of the first genus, because of the similar size and denticle densities. The MCNA 14623 specimen of Dromaeosauridae indet. is located closest to *Pyroraptor olympius* and the largest teeth of *Richardoestesia* and *Saurornitholestes*. In contrast, MCNA 14624 is separated from the other teeth because it is similar to the size of *Dromaeosaurus* teeth, but with similar denticle densities to *Pyroraptor olympius* and *Richardoestesia*. The teeth of Paraves indet. and cf. *Paronychodon* sp. from Laño are grouped with the teeth of *Buitreraptor* and *Paronychodon*, and are positioned mostly closest to the teeth of *Buitreraptor* and the smallest teeth of *Paronychodon* (Fig. 8), given that they are unserrated and small in size. Finally, the teeth of cf. *Richardoestesia* sp. from Laño fall near the smaller teeth of *Saurornitholestes*, *Velociraptor* and, especially,

*Richardoestesia*, due to the small size of the teeth and high denticle densities (Fig. 8).

## DIVERSITY OF THE LAÑO THEROPOD ASSOCIATION

Several studies of the theropod material have been carried out in the Laño site since it was discovered. Astibia *et al.* (1990) referred a pair of femora to Abelisauridae? and around 50 isolated teeth to Theropoda indet. The femora were compared with that of *Tarascosaurus* (Le Loeuff & Buffetaut 1991; Le Loeuff 1992). Furthermore, isolated teeth from Laño were attributed to cf. *Euronychodon* and three dromaeosaurid morphotypes (Pereda-Suberbiola *et al.* 2000). A pedal ungual was also assigned to Ornithomimosauria (Pereda-Suberbiola *et al.* 2000).

The revision and study of new isolated theropod teeth identified four small theropods (Coelurosauria indet., ?Dromaeosauridae indet., ?*Pyroraptor olympius* and ?*Richardoestesia* sp.) and two morphotypes of a larger-
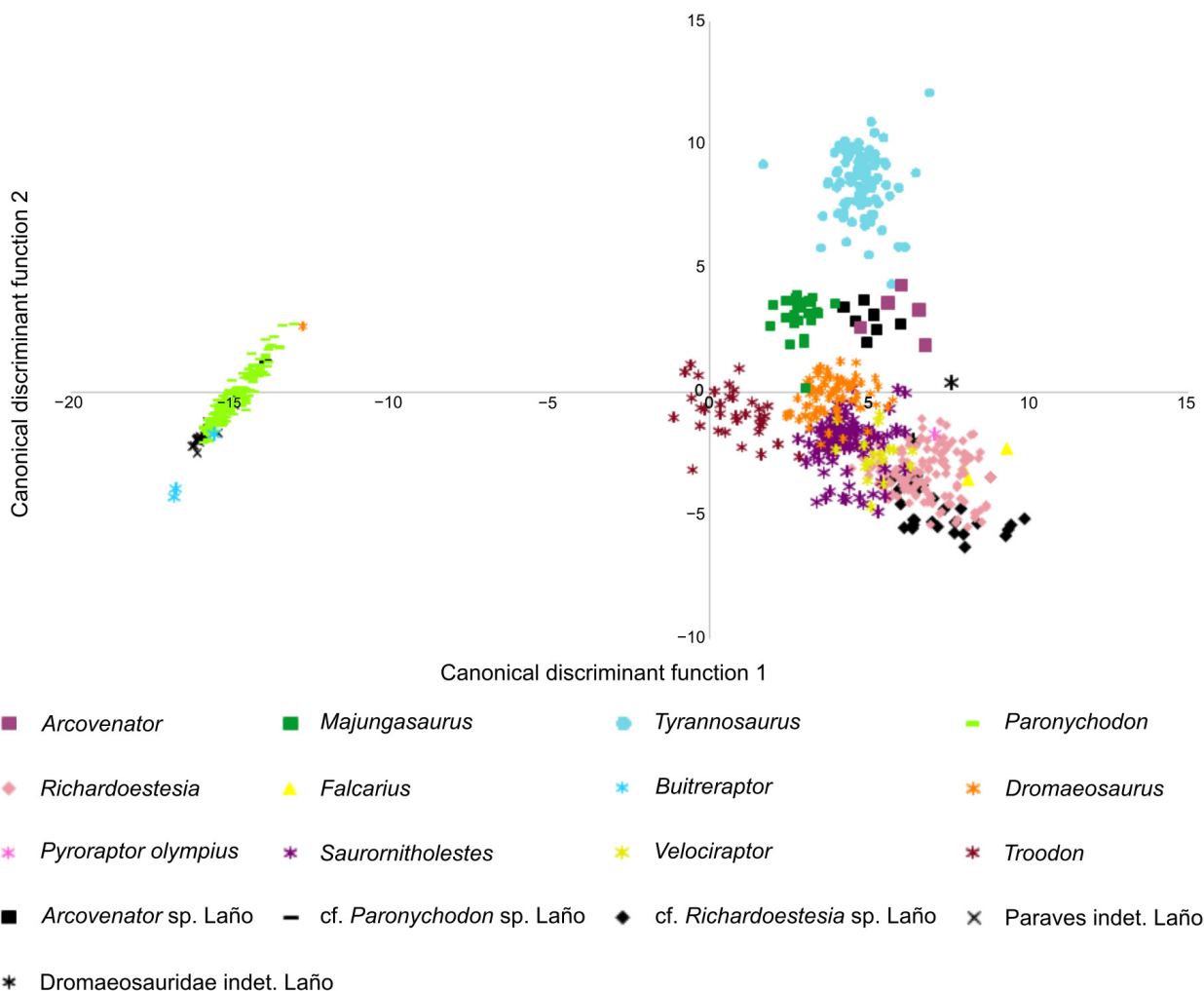
**FIG. 8.** Discriminant analysis of the tooth sample from Laño and the database (Isasmendi *et al.* 2021*a*, appendix A).

sized indeterminate theropod (Torices *et al.* 2015). Pereda-Suberbiola *et al.* (2015) also noted the presence of a small maniraptoran on the basis of isolated teeth. The presence of the giant ground bird *Gargantuavis philoinos* has also been recognized at the site (Angst *et al.* 2017). An isolated tibiotarsus from Laño (MCNA 1813; preserved length 201 mm) has bird-like features. It is unlike the tibiotarsi of enantiornithines, and may belong either to a fairly large primitive bird or to a bird-like non-avian theropod (E. Buffetaut unpub. data 2006). However, a more detailed study of the specimen is needed.

The present study has led to the identification of at least seven tooth morphotypes and five theropod taxa: one medium–large-sized abelisaurid (*Arcovenator* sp.) and four small theropods (Dromaeosauridae indet., cf. *Paronychodon* sp., Paraves indet. and cf. *Richardoestesia* sp.).

Of the tooth sample recovered in the fossiliferous level L1A, *Arcovenator* sp. represents 12.95% of the specimens,

Dromaeosauridae indet. 1.79%, Paraves indet. 16.96%, cf. *Paronychodon* sp. 2.68% and cf. *Richardoestesia* sp. 65.62%. Hence, cf. *Richardoestesia* sp. is by far the most abundant Laño theropod in the number of teeth.

In addition, *Gargantuavis philoinos* (Angst *et al.* 2017) and a possible ornithomimosaur (Astibia *et al.* 1990; Pereda-Suberbiola *et al.* 2000) increase the number of theropod taxa to six, or even to seven if the presence of the latter at the site is confirmed. The Laño site is therefore the uppermost Cretaceous locality with the greatest theropod diversity and the richest abundance of teeth in Europe.

Isasmendi *et al.* (2021*b*) tentatively assigned a caudal vertebra from Laño to a medium–large-sized abelisaurid. However, the relationship of the abelisaurid postcranial remains at the site to other European taxa is yet to be established, and it is not clear whether they belong to a theropod similar to *Arcovenator*. Alternatively more than one abelisaurid taxon might be present in Laño.
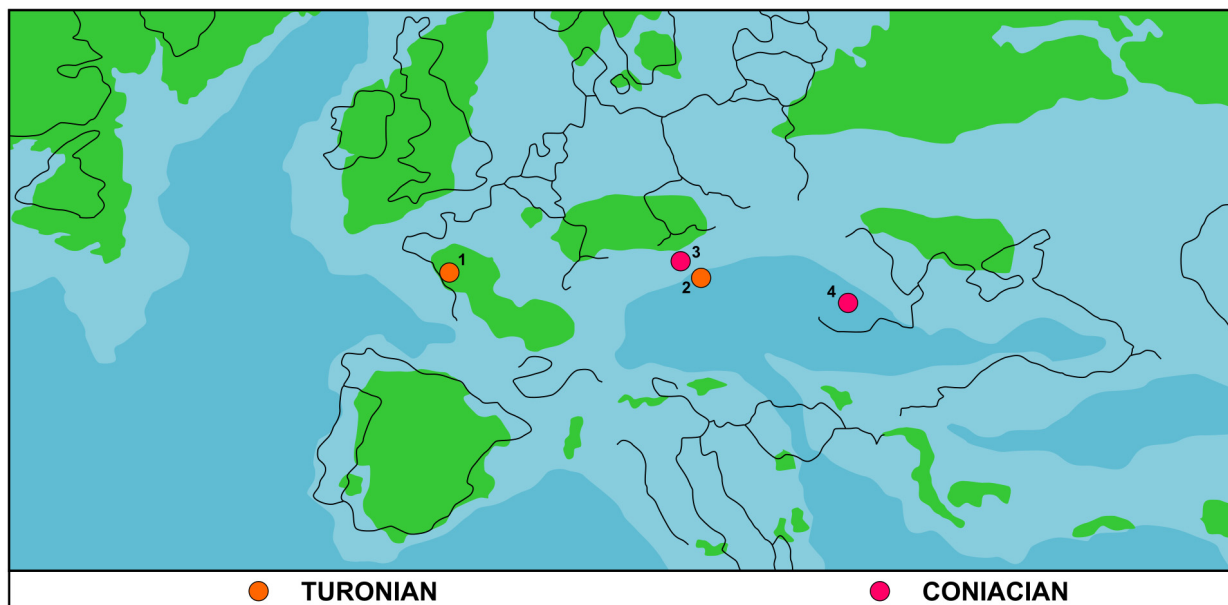
**FIG. 9.** Palaeogeographic map of Europe with the distribution of fossil sites that yielded theropod remains from the early Late Cretaceous (Turonian–Coniacian) (base map for Turonian, modified from Scotese 2014). *Localities*: 1, Châteauneuf-Raillères site (Vendée, France); 2, Gams locality (Gams, Austria); 3, Tiefengraben locality (Salzkammergut, Austria); 4, Borod (Bihor County, Romania). See Isasmendi *et al.* (2021a, appendix B, C) for further information.

## THE UPPER CRETACEOUS THEROPOD FOSSIL RECORD IN EUROPE

Upper Cretaceous (Turonian–Maastrichtian) theropod sites in the European archipelago are mainly located in central and eastern Europe (Austria, Bulgaria, Hungary, Romania and the European part of Russia) and the Ibero-Armorican domain (France, Spain and Portugal). Other theropod sites are known in Belgium, the Netherlands, Slovenia and Sweden (Csiki-Sava *et al.* 2015) (Figs 9, 10 and Isasmendi *et al.* 2021a, appendix B and C).

In the upper Turonian Gams area (Schönleiten Formation) of Austria (Fig. 9, loc. 2), two theropod taxa have been documented: cf. *Paronychodon* and an indeterminate theropod (Ősi *et al.* 2019). Teeth of indeterminate theropods are also known in the late? Turonian Raillères site ('Grès calcaires') of western France (Buffetaut *et al.* 1991; Buffetaut & Pouit 1994) (Fig. 9, loc. 1).

In the early Coniacian strata of the Gosau Group (Austria), the Tiefengraben locality (Fig. 9, loc. 3) has yielded isolated theropod teeth referred to an indeterminate tetanuran and two maniraptoran morphotypes (Ősi *et al.* 2021). Isolated teeth of a small theropod ('*Megalosaurus hungaricus*' of Nopcsa 1902) from the Coniacian to ?lower Santonian 'Gosau facies' (Csiki & Grigorescu 1998; Csiki-Sava *et al.* 2015) of Borod in Romania (Fig. 9, loc. 4) are recognized as an indeterminate theropod possibly related to either tyrannosauroids or dromaeosaurids (Carrano *et al.* 2012). A manual ungual phalanx ('*Megalosaurus lonzeensis*' of Dollo 1883) from the ?Coniacian–Santonian Lonzée Formation (former 'Glauconie argileuse') of Namur in Belgium (Fig. 10, loc. 2) is considered to belong to an indeterminate coelurosaur (Carrano *et al.* 2012).

The Santonian locality of Iharkút in the Csehbánya Formation (Hungary) (Fig. 10, loc. 3) has yielded a wide theropod biodiversity, with an abelisaurid, the paravian *Pneumatoraptor fodori*, an indeterminate tetanuran (Ősi *et al.* 2010; Ősi & Buffetaut 2011), indeterminate paravian teeth that may belong to *Pneumatoraptor*, an indeterminate theropod (Ősi *et al.* 2010, 2012), the enantiornithine *Bauxitornis* and indeterminate birds (Ősi 2008; Dyke & Ősi 2010). Teeth of cf. *Paronychodon* sp. are also present at Iharkút (Ősi *et al.* 2019). The contemporaneous 'lignite-bearing clayey–sandy deposits' of Notre-Dame-de-Riez (Fig. 10, loc. 1) have also yielded indeterminate theropod teeth (Buffetaut *et al.* 1991; Buffetaut & Pouit 1994).

Buffetaut *et al.* (2002) described a fossil feather belonging to a bird or a non-avian dinosaur from the Tomaj Limestone dated as late Santonian to early Campanian of the Lipica Formation (Tyler & Križnar 2013) at Križ (Slovenia) (Fig. 10, loc. 4). In the coetaneous Tran site located in the Rezhantsi Formation of the western Srednogorie (Bulgaria) (Fig. 10, loc. 5), Nikolov *et al.* (2018) mentioned the possible presence of a theropod.

The early Campanian theropod record of Austria consists of isolated tetanuran teeth ('*Megalosaurus*
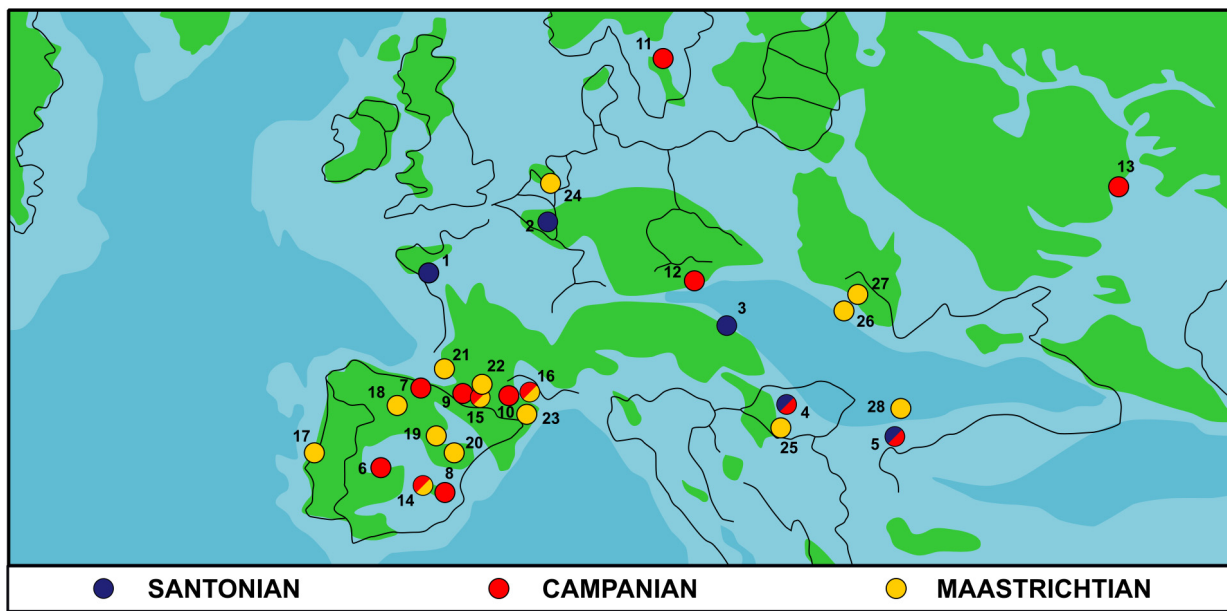
**FIG. 10.** Palaeogeographic map of Europe with the distribution of fossil sites that yielded theropod remains from the late Late Cretaceous (Santonian–Maastrichtian) (base map for Maastrichtian, modified from Scotese 2014). Localities: 1, Notre-Dame-de-Riez (Vendée, France); 2, Lonzée (Namur, Belgium); 3, Iharkút site (Iharkút, Hungary); 4, Križ near Tomaj (Kras, Slovenia); 5, Tran site (western Srednogorie, Bulgaria); 6, Armuña site (Segovia, Spain); 7, Laño site (Treviño, Spain); 8, Chera locality (Valencia, Spain); 9, Villeveyrac and Fons 0 or Champ-Garimond site (Hérault and Gard departments in Languedoc, France); 10, Fox-Amphoux, La Neuve, Lambeau du Beausset, Pourrières-Jas Neuf, Trets-La Boucharde and Velaux-Bastide Neuve (Bouches-Du-Rhône and Var departments in Provence, France); 11, Ivö Klack and Ugnsmunnarna localities (Scania, Sweden); 12, Muthmannsdorf locality (Niederösterreich, Austria); 13, Bereslavka, Karyakino, Malaya Rybka, Polunino Farm and Rychkovo localities (Saratov and Volvograd regions, Eastern Russia); 14, Fuentes-Lo Hueco site (Cuenca, Spain); 15, Cruzy and Villespassans-Combebelle (Hérault department in Languedoc, France); 16, Pourcieux and Roques-Hautes (Bouches-du-Rhône and Var departments in Provence, France); 17, Aveiro, Taveiro and Viso (Beira Litoral, Portugal); 18, Quintanilla del Coco locality (Burgos, Spain); 19, Blasi, Camino de Rin 1, Camino de Rin 2, Camino de Fornons 1, Dolor 2 or 3, Figuerola 2, Fontllonga 6, Fornons 3, Larra 4, Molí de Baró 1, Montrebei, L'Abeller, Sant Romà d'Abella, Vicari 4 and 172-i/04/e site (Lleida and Huesca, Spain); 20, Peguera 1 (Barcelona, Spain); 21, Lestaillats, Marignac-Laspeyres-Cassagnau, Marsoulas and other sites (Haute-Garonne department in Petites Pyrénées, France); 22, Campagne-sur-Aude and Fonjoncouse-Le Bexen (Aude department in Languedoc, France); 23, Vitrolles-La Plaine (Bouches-du-Rhône department in Provence, France); 24, Maastricht Tuff, CBR-Romontbos Quarry and Marnebel Quarry (Limburg, Belgium and the Netherlands); 25, Kozina (Kras, Slovenia); 26, Burudone, site from Fărcădeana Brook Valley, Gârjobel, locality near Lunca Cernii de Sus, Nălaţ-Vad, Sinpetru, Toteşti-baraj, Tustea and Vălioara (Rusca Montană Basin and Haţeg Basin, Romania); 27, Sebeş-Glod and Oarda de Jos (southwestern Transylvanian Basin, Romania); 28, 'The Dinosaur' sinkhole (Vratsa district, Bulgaria). See Isasmendi *et al.* (2021*a*, appendix B, C) for further information.

*pannoniensis*' of Seeley 1881) found in the Gosau Beds of Muthmannsdorf (Ősi *et al.* 2010) (Fig. 10, loc. 12). In the coeval lignite-bearing grey clays ('Fuvelian' continental local stage; chron C33.1r, Benammi *et al.* 2006) of Languedoc (France) (Fig. 10, loc. 9), teeth found in the L'Olivet site of Villeveyrac (Hérault Department) have been assigned to Dromaeosauridae indet. (cf. *Richardoestesia* in this study) (Buffetaut *et al.* 1986; Garcia *et al.* 2015). In the lower Campanian 'Fuvelian' grey limestone (upper part of Chron C33r; Fondevilla *et al.* 2016) of Lambeau du Beausset (Var Department) in Provence (France), the abelisaurid *Tarascosaurus salluvicus* has been described (Le Loeuff & Buffetaut 1991; Tortosa *et al.* 2014) (Fig. 10, loc. 10).

In Scania (Sweden) (Fig. 10, loc. 11), an indeterminate theropod has been found in the uppermost lower Campanian Ugnsmunnarna locality of the Kristianstad Basin (Poropat *et al.* 2015). Furthermore, hesperornithiform skeletal elements have been described in the uppermost lower Campanian Ivö Klack quarry of the same basin (Nessov & Prizemlin 1991; Lambrecht 1933; Rees & Lindgren 2005), including material of *Baptornis* sp., *Hesperornis* sp. (Rees & Lindgren 2005) and *Hesperornis rossicus* (Nessov & Yarkov 1993).

Three localities called Karyakino, Malaya Rybka (lower Campanian) from the Rybushka Formation and Rychkovo (lowermost Campanian, Rybushka Formation?), situated in the Saratov and Volvograd regions (European

part of Russia) (Fig. 10, loc. 13), have yielded avian remains, with *Hesperornis* sp. in the three sites and *H. rossicus* in Karyakino and Rychkovo (Nessov & Yarkov 1993; Panteleyev *et al.* 2004; Zelenkov *et al.* 2017). In the Paleocene Bereslavka locality (Fig. 10, loc. 13) of the Volgograd Region (European Russia), redeposited late Campanian fossils of an indeterminate theropod and a dromaeosaurid have been found (Averianov & Yarkov 2004; Zelenkov *et al.* 2017). Furthermore, avians are represented by ?*Asiahesperornis* (Zelenkov *et al.* 2017) or *H. rossicus* according to Panteleyev *et al.* (2004). At the upper Campanian Polunino Farm site (Averianov & Yarkov 2004) (Campanian–Maastrichtian according to Nessov 1995) only an indeterminate theropod has been identified (Nessov 1995) (Fig. 10, loc. 13).

The middle–late Campanian theropod record of Europe is mainly found in the Ibero-Armorican domain. In France, theropod remains have been recovered in Languedoc and Provence. Sigé *et al.* (1997) found isolated theropod teeth that were identified as ?Dromaeosauridae indet. and Theropoda indet. (the second may belong to Paraves indet.) in the middle–upper Campanian deposits of Fons-Champ-Garimond (Gard Department) (Fig. 10, loc. 9). The Bouches-du-Rhône Department has yielded several theropod localities (Fig. 10, loc. 10). In La Neuve, isolated theropod teeth assigned to Dromaeosauridae indet. (cf. *Richardoestesia* according to this study) (Buffetaut *et al.* 1986; Garcia *et al.* 2000) and cf. *Paronychodon* sp. (Garcia *et al.* 2000) that may belong to Paraves indet. have been described. In the middle Campanian 'Begudian' fluvio-lacustrine sandstones (Allain & Taquet 2000) of Trets-La Boucharde (Fig. 10, loc. 10), *Pyroraptor olympius* (Allain & Taquet 2000) and an indeterminate abelisaurid have been described (Allain & Pereda-Suberbiola 2003; Tortosa *et al.* 2014). In the upper Campanian 'Begudian' sandstones (Garcia *et al.* 2010; Cincotta *et al.* 2015) of Velaux-Bastide Neuve (Fig. 10, loc. 10), abelisaurid remains have been recovered (Tortosa *et al.* 2014). The middle–upper Campanian (to lower Maastrichtian?) sites of Fox Amphoux (Var Department) (Fig. 10, loc. 10) have provided remains of Abelisauridae indet. (Tortosa *et al.* 2014), Dromaeosauridae indet. (Chanthasit & Buffetaut 2009), Enantiornithes indet. (Buffetaut *et al.* 2000), *Gargantuavis philoinos* (Buffetaut *et al.* 2015; Buffetaut & Angst 2016) and *Variraptor mechinorum* (Le Loeuff & Buffetaut 1998). At the upper Campanian Jas Neuf Sud locality from the lower 'Argiles rutilantes' Formation, remains of *Arcovenator escotae* have been found (Buffetaut *et al.* 1988; Tortosa *et al.* 2014).

In the Iberian Peninsula, remains of cf. *Arcovenator* and an indeterminate theropod have been reported from the Vegas de Matute Formation in the Armuña site (Pérez-García *et al.* 2016) (Fig. 10, loc. 6). The Laño (Fig. 10, loc. 7) theropod assemblage is represented by *Arcovenator* sp., Dromaeosauridae indet., *Gargantuavis philoinos*, Paraves indet., cf. *Paronychodon* sp. and cf. *Richardoestesia* sp. (Angst *et al.* 2017; this study). Furthermore, an ornithomimosaur and a bird-like theropod (Pereda-Suberbiola *et al.* 2000; E. Buffetaut unpub. data 2006) could also be present in the site. At the upper Campanian Chera site (Company *et al.* 2005) from the Sierra Perenchiza Formation of Valencia (Fig. 10, loc. 8), theropod remains belong to cf. *Arcovenator*, Dromaeosauridae indet., Paraves indet. and to an indeterminate theropod (Company 2005; this study).

In the upper Campanian to lower Maastrichtian Villalba de la Sierra Formation of Lo Hueco (Cuenca, Spain) (Fig. 10, loc. 14), five theropod morphotypes have been identified: a medium–large-sized indeterminate theropod and four small coelurosaurs (Dromaeosaurinae indet., cf. *Paronychodon*, cf. *Richardoestesia* and Velociraptorinae indet.) (Ortega *et al.* 2015).

In southern France, Languedoc has yielded a number of upper Campanian to lower Maastrichtian localities (Fig. 10, loc. 15). In the red beds of the 'Grès à reptiles' of several sites of Cruzy, such as Massecaps, Montplô-Nord and Plô Saint-Pons (Hérault Department), the following theropods have been identified: Abelisauridae indet. (Buffetaut *et al.* 1999; Buffetaut 2005; Tortosa *et al.* 2014), Dromaeosauridae indet. (Chanthasit & Buffetaut 2009), Enantiornithes indet. (Buffetaut 1998), *Gargantuavis philoinos* (Buffetaut & Le Loeuff 1998; Buffetaut & Angst 2013, 2016, 2019), the enantiornithine *Martinavis cruzyensis* (Walker *et al.* 2007) and the dromaeosaurid *Variraptor mechinorum* (Chanthasit & Buffetaut 2009). Furthermore, in the same beds of Villespassans-Combebelle, remains have been assigned to Dromaeosauridae indet. (Chanthasit & Buffetaut 2009) and *Gargantuavis philoinos* (Buffetaut & Le Loeuff 1998; Buffetaut & Angst 2016). In the coeval 'Rognacian' coarse sandstone of the Les Tuillières site in Pourcieux (Var Department), theropod remains (the Pourcieux specimen) have been attributed to ?*Arcovenator* sp. (Buffetaut *et al.* 1988; Tortosa *et al.* 2014). In Provence, in the upper Campanian to lower Maastrichtian 'Grès à reptiles' deposits of Roques-Hautes (Bouches-du-Rhône Department) (Fig. 10, loc. 16), remains of *Variraptor mechinorum* have been identified (Le Loeuff *et al.* 1992; Le Loeuff & Buffetaut 1998).

In the Iberian Peninsula, the South Pyrenean Basin contains the most latest Cretaceous dinosaur fossil sites (Vila *et al.* 2016) (Fig. 10, loc. 19). In Lleida, the lower Maastrichtian Montrebei locality has yielded four theropod taxa (Paraves indet., ?*Pyroraptor olympius*, ?*Richardoestesia* sp. and possibly Abelisauridae indet.) (Torices *et al.* 2015; this study), and the Vicari 4 site, two taxa (Paraves indet. and ?*Richardoestesia* sp.). Moreover, a *Richardoestesia*-like tooth has been reported from the L'Abeller site in the Arén Sandstone Formation (Prieto-

Márquez et al. 2000; Fondevilla et al. 2019). The Figuerola 2 site of the Figuerola Formation (Tremp Group; lower–?upper Maastrichtian according to Fondevilla et al. 2019) has also produced an isolated ?Dromaeosauridae indet. tooth (Torices et al. 2015). Finally, in the upper(?) Maastrichtian Quintanilla del Coco site (Burgos) (Fig. 10, loc. 18) teeth of ?Dromaeosauridae indet and cf. Paronychodon sp. have been identified by Pol et al. (1992).

In southern France, teeth found in the lower Maastrichtian Bellevue site of Campagne-sur-Aude (Aude Department, France) (Fig. 10, loc. 22) have been assigned to Dromaeosauridae indet. (Laurent et al. 2001). Remains belonging to Gargantuavis philoinos have also been reported (Buffetaut & Le Loeuff 1998; Buffetaut & Angst 2016).

The upper Maastrichtian sites of the southern Pyrenees are rich in isolated theropod teeth (Fig. 10, loc. 19). In Huesca, the Blasi sites found at the top of the Arén Sandstone and the lower part of the Tremp Group have yielded five taxa: Paraves indet., ?Dromaeosauridae indet., ?Paronychodon sp., ?Richardoestesia sp. and probably Abelisauridae indet. (Torices et al. 2015; this study). In the lower upper Maastrichtian (C30r; Fondevilla et al. 2019) of Fontllonga 6 (Lleida) in the Tremp Group, a tooth has been attributed to ?Dromaeosauridae indet. by Torices et al. (2015). Five theropod taxa have been identified in the latest Maastrichtian Molí de Baró 1 site: cf. Dromaeosauridae, aff. Paronychodon, cf. ?Richardoestesia and two Theropoda indet. morphotypes (Marmi et al. 2016). An ornithuromorph, an indeterminate paravian and probably an abelisaurid have been recognized in several localities of the Tremp Group of the Serraduy area in Huesca (Puértolas-Pascual et al. 2018; Pérez-Pueyo et al. 2021; this study). The basal troodontid Tamarro insperatus from the latest Maastrichtian locality of Sant Romà d'Abella (Lleida) was recently described by Sellés et al. (2021). A single tooth from the Peguera 1 site of Barcelona (Fig. 10, loc. 20) was attributed to Velociraptorinae indet. (Baiano et al. 2014).

In southern France, the upper Maastrichtian sites with theropod remains are concentrated in Gascony and Languedoc. The sites located in the Petites Pyrénées have yielded a wide range of theropod taxa (Fig. 10, loc. 21). Marignac-Laspeyres-Cassagnau and other sites from the Auzas Marls Formation (Haute-Garonne Department) have produced isolated theropod teeth identified as Dromaeosauridae indet. (Laurent et al. 2002; Laurent 2003) and Theropoda indet., some of which could belong to abelisaurids (Laurent 2003; Csiki-Sava et al. 2015). Other indeterminate theropod remains have been reported in the Lestaillats Marls of Lestaillats (Haute-Garonne Department) (Gheerbrant et al. 1997; Laurent et al. 1999; Laurent 2003). A tooth from the Auzas Marls Formation of Marsoulas (Haute-Garonne Department) could belong to an indeterminate paravian (Csiki-Sava et al. 2015). In

Fonjoncouse-Le Bexen (Aude Department) (Fig. 10, loc. 22), an indeterminate theropod was identified by Laurent (2003). In the late? Maastrichtian Vitrolles-La Plaine site (Bouches-du-Rhône Department) (Fig. 10, loc. 23), remains of an abelisaurid and, possibly, indeterminate paravians have been described (Valentin et al. 2012; Csiki-Sava et al. 2015).

From the Upper Cretaceous lignite beds of Serviers (Gard Department) Buffetaut et al. (1986) described an isolated theropod tooth that may belong to cf. Richardoestesia (this study).

The ceratosaurian Betasuchus bredai was found in the Maastricht Formation of Limburg (the Netherlands) (Huene 1932; Carrano & Sampson 2008) (Fig. 10, loc. 24). Birds are abundant in the Belgian upper Maastrichtian Maastricht Formation, with Enantiornithes remains found in the Marnebel Quarry (Dyke et al. 2002, 2008), and Ornithurae fossils (Dyke et al. 2008) and Asteriornis (Field et al. 2020), both from the CBR-Romontbos Quarry (Fig. 10, loc. 24).

In Portugal, the latest Cretaceous Aveiro, Taveiro and Viso localities near Coimbra have yielded a wide range of theropod taxa (Fig. 10, loc. 17). Antunes & Sigogneau-Russell (1991) described isolated theropod teeth similar to Paronychodon in the Taveiro locality (this study). This site has also yielded isolated theropod teeth identified as cf. Coeluridae (Paraves indet. and cf. Paronychodon, this study), cf. Dromaeosauridae, aff. Megalosauridae (Tetanurae indet. according to Carrano et al. 2012), Theropoda indet. and cf. Troodontidae (Antunes & Sigogneau-Russell 1992). Similar tooth morphotypes were reported in the coeval Aveiro locality by Antunes & Sigogneau-Russell (1992). The Viso locality remains have been referred to Carnosauria incertae sedis, Theropoda indet., Maniraptora and aff. Megalosauridae (Antunes & Sigogneau-Russell 1992, 1996; Galton 1996). The attribution of some teeth to cf. Troodontidae is rather doubtful due to the fragmentary nature of the specimens (Antunes & Sigogneau-Russell 1992, pl. 1, figs 9–11). Other teeth show similarities to those of cf. Richardoestesia or dromaeosaurid morphotypes from the Ibero-Armorican landmass. Therefore, it would be convenient to revise this material.

Theropod remains found in upper Maastrichtian fissure fillings of Kozina (south-west Slovenia) (Fig. 10, loc. 25) comprise teeth that may belong to dromaeosaurids or that are troodontid-like (Debeljak et al. 2002). At the upper Maastrichtian 'The Dinosaur' sinkhole site of Vratsa district (Bulgaria) (Fig. 10, loc. 28), a fragment of humerus has been tentatively assigned to an ornithomimosaur (Mateus et al. 2010).

The Maastrichtian deposits of the Hațeg, Rusca Montană and the southwestern Transylvanian basins in Romania have produced plenty of theropod remains (Csiki-Sava et al. 2015). In the Hațeg Basin several sites have

yielded theropod remains (Fig. 10, loc. 26). In the lower Maastrichtian Nălaţ-Vad of the Sînpetru Formation, non-avian theropod remains have been described as cf. *Elopteryx*, *Paronychodon*, Theropoda indet., troodontid-like and Velociraptorinae (Smith *et al.* 2002; Csiki-Sava *et al.* 2016). Avialans are represented by Enantiornithes (Wang *et al.* 2011*a*) and an indeterminate gargantuaviid (Mayr *et al.* 2020*a*). Csiki-Sava *et al.* (2016) assigned isolated theropod remains from the coeval 'Pui Swamp' locality of the 'Pui beds' to *Euronychodon* sp. (= *Paronychodon* sp.), and assigned the material from the La Scoabă site of the Sînpetru Formation to *Richardoestesia* sp. Csiki-Sava *et al.* (2016) did also identify theropod teeth of *Richardoestesia* sp., 'Troodontid' and Velociraptorinae indet. at the upper Maastrichtian Crăguiş locality. *Richardoestesia* sp. remains are also known in the coeval Pui site as well as an ungual phalanx attributed to Theropoda *incertae sedis* (Codrea *et al.* 2013).

In the same basin, but with lower temporal resolution, other Maastrichtian localities are known. Weishampel & Jianu (1996) described a dromaeosaurid skull roof from Gârobel (Sînpetru Formation) that could be closely related to *Saurornitholestes*; Weishampel *et al.* (2010) noted the presence of an indeterminate theropod but this locality is not indicated. The coeval sites of Sînpetru (Sînpetru Formation) have yielded isolated theropod teeth regarded as cf. *Euronychodon* (Csiki & Grigorescu 1998) (here assigned to cf. *Paronychodon*), troodontid-like (Csiki & Grigorescu 1998) and Velociraptorinae (Csiki & Grigorescu 1998; Grigorescu *et al.* 1999). Furthermore, the taxa *Elopteryx nopcsai* (Andrews 1913), *Bradycneme draculae* and *Heptasteornis andrewsi* (Harrison & Walker 1975) have been described in the area. In the Vălioara sites of the Densuş-Ciula Formation, the theropod assemblage includes velociraptorine (Csiki & Grigorescu 1998; Grigorescu *et al.* 1999; Vasile 2008), troodontid-like (Csiki & Grigorescu 1998), Theropoda indet. (Csiki & Grigorescu 1998), *Richardoestesia* (Vasile 2008) and *Euronychodon* (= *Paronychodon*) (Vasile 2008) tooth morphotypes. Furthermore, Wang *et al.* (2011*b*) reported the presence of ornithurine birds in Vălioara. In the Nvs site in Pârâul Ogradiilor, Botfalvai *et al.* (2021) reported a fragmentary tibiotartus referred to a paravian theropod. As in other Romanian sites, isolated theropod teeth are also the most common elements in the Toteşti-baraj sites of the Sînpetru Formation. Codrea *et al.* (2002) distinguished the following morphotypes: *Euronychodon* (= *Paronychodon*), *Paronychodon*, *Richardoestesia*, a troodontid-like taxon and Velociraptorinae. Finally, the theropod remains in the Tuştea and Budurone localities from the Densuş-Ciula Formation have been identified as velociraptorines (Csiki & Grigorescu 1998; Grigorescu *et al.* 1999) and *Euronychodon* (Csiki *et al.* 2008) (= *Paronychodon*), respectively.

Theropod teeth are scarce in the Rusca Montanâ Basin (Fig. 10, loc. 26). In the Maastrichtian locality near Lunca Cernii de Sus, Codrea *et al.* (2012) noted the presence of troodontid-like and Velociraptorinae morphotypes (Theropoda indet. of Vasile & Csiki-Sava 2011), and in the coeval site of Negoiu from Fărcădeana Brook Valley only isolated theropod teeth were found, and these were assigned to *Paronychodon* and *Richardoestesia* (Vasile & Csiki-Sava 2011; Vasile *et al.* 2012).

The south-western Transylvanian Basin (Fig. 10, loc. 27) lacks the diversity of Maastrichtian theropods found in the other Romanian basins. In the Oarda de Jos site (Sebeş Formation), isolated theropod teeth have been identified as Velociraptorinae or Theropoda *incertae sedis* and an ungual phalanx as Dromaeosauridae indet. (Codrea *et al.* 2010*a*, 2013). Avialans are represented by enantiornithine remains (Dyke *et al.* 2012; Codrea *et al.* 2013). The dromaeosaurid *Balaur bondoc* was described in the upper lower Maastrichtian Sebeş-Glod locality (Sebeş Formation) (Csiki *et al.* 2010; Brusatte *et al.* 2013). In the Metaliferi area, Codrea *et al.* (2010*b*) noted the presence of isolated theropod teeth that were assigned to Theropoda *incertae sedis* and Velociraptorinae indet.

# DIVERSITY AND AFFINITIES OF LATEST CRETACEOUS EUROPEAN THEROPODS

Ceratosaurians are represented in the uppermost Cretaceous of Europe by at least four distinct forms, that is, the genera *Arcovenator*, *Betasuchus, Tarascosaurus* and an unnamed taxon from Hungary. The abelisaurids *Arcovenator* and *Tarascosaurus* are known in the Ibero-Armorican landmass, namely in Campanian localities from southern France (Tortosa *et al.* 2014), and tentatively in coetaneous Iberian sites, including Armuña, Chera and Laño. The temporal range of *Arcovenator* (or a closely related form) was thought to reach the upper Maastrichtian of southern Pyrenees (Fondevilla *et al.* 2019 and references), although there is no significant evidence that the isolated theropod teeth from Huesca and Lleida belong to this taxon. The affinities between these abelisaurids, which include small and larger forms, are still unresolved (Tortosa *et al.* 2014). An indeterminate abelisaurid has been reported from the Santonian of Iharkút in the Austroalpine region (Ősi & Buffetaut 2011). As regards *Betasuchus* from the Maastrichtian of Limburg (Rhenish–Bohemian Island), it may be an abelisaurid closely related to *Tarascosaurus* (Le Loeuff & Buffetaut 1991; Tortosa *et al.* 2014).

Among coelurosaurians, the phylogenetic positions of both *Paronychodon* and *Richardoestesia* are uncertain. Both may represent teeth of juvenile paravians (Longrich

2008; Sues & Averianov 2013). They have been reported in numerous localities and formations, indicating that they have a wide spatiotemporal range, including sites older than Late Cretaceous and other Laurasian landmasses outside of Europe. In the latest Cretaceous European archipelago, *Paronychodon* and *Paronychodon*-like teeth are known from the Turonian to the Maastrichtian, with records from the Austroalpine region, the Ibero-Armorican domain and the Haţeg island. With respect to *Richardoestesia* and *Richardoestesia*-like teeth, they are known from Campanian–Maastrichtian sites of the Ibero-Armorican landmass and the Haţeg island. Each one could represent a clade rather than a single heterodont taxon (Larson & Currie 2013; Sues & Averianov 2013; Averianov & Sues 2019), but more complete specimens are needed to test this hypothesis.

Maniraptoriformes is the most diversified theropod clade from the Santonian–Maastrichtian of the European archipelago. In a synthesis of the European Upper Cretaceous continental vertebrate record, Csiki-Sava *et al.* (2015) mentioned the presence of paravian taxa such as dromaeosaurids and birds, and the possible occurrence of alvarezsaurids, ornithomimosaurs and troodontids.

The ornithomimosaur record in Europe at the end of the Cretaceous consists of very scanty remains, such as a humerus fragment from the upper Maastrichtian of Bulgaria (most likely reworked from older deposits) and an ungual phalanx from the ?Coniacian–Santonian of Belgium (Mateus *et al.* 2010). The latter fossil was referred to as Coelurosauria indet. by Carrano *et al.* (2012). A few postcranial bones from Laño could belong to an ornithomimosaur; this material is still undescribed.

The putative presence of alvarezsaurids in the Maastrichtian of the Transylvanian landmass is based on isolated limb bones (Naish & Dyke 2004; Kessler *et al.* 2005), some of which were previously interpreted as having avian affinities (e.g. Harrison & Walker 1975). This and other material was reinterpreted as belonging to small non-avian tetanurans by authors such as Csiki & Grigorescu (1998). Thus, the precise affinities of the specimens remain elusive and no consensus has been reached to date on this matter (Csiki-Sava *et al.* 2015 and references therein).

Paravians are represented in the uppermost Cretaceous sites of Europe by both non-avian theropods and birds (Avialae). The former consists mainly of dromaeosaurids and *Pneumatoraptor*. *Pneumatoraptor* is considered to be a basal paravian that has some similarities to dromaeosaurids (Ősi *et al.* 2010; Csiki-Sava *et al.* 2015). *Balaur*, *Pyroraptor* and *Variraptor* are commonly regarded as European endemic dromeosaurids (Turner *et al.* 2012; Csiki-Sava *et al.* 2015). Of all of them, only the dentition of *Pyroraptor* is known. The possible synonymy between *Pyroraptor* and *Variraptor*, both from the middle–upper

Campanian of southern France, is not yet fully resolved (Chanthasit & Buffetaut 2009). Furthermore, Allain & Taquet (2000) and Turner *et al.* (2012) indicated that *Variraptor mechinorum* lacks dromaeosaurid characters. Turner *et al.* (2012) found the phylogenetic position of *Pyroraptor* to be uncertain among Dromaeosauridae, although it never falls within the derived Laurasian dromaeosaurid clade. However, Hartman *et al.* (2019) suggested that *Pyroraptor* has affinities with South American Unenlagiinae. *Balaur* has been described as an aberrant dromaeosaurid with velociraptorine affinities (Csiki *et al.* 2010; Brusatte *et al.* 2013), although Cau *et al.* (2015) reinterpreted it as a flightless basal avialan. In the phylogeny performed by Pei *et al.* (2020) *Balaur* is again regarded as Velociraptorinae. In the current state of knowledge, it is not possible to say whether the latest Cretaceous dromaeosaurids of Europe form a single clade or whether they belong to several distinct lineages. What can be said is that unusual paravian theropods inhabited the Late Cretaceous European archipelago.

The presence of troodontids in these faunas was previously evoked on the basis of isolated teeth from Transylvania (Codrea *et al.* 2002, 2012; Smith *et al.* 2002) and Portugal (Antunes & Sigogneau-Russell 1992). Nonetheless, the evidence so far does not seem conclusive. Instead, the first unequivocal troodontid from the European archipelago is *Tamarro insperatus* (Sellés *et al.* 2021) from the Tremp Group of Lleida. This is a basal troodontid, apparently a jinfengopterygine (Sellés *et al.* 2021).

Fossil bird remains have been found in a number of European localities from the Santonian–Maastrichtian interval, and belong to at least two lineages: Enantiornithes and Ornithuromorpha. The enantiornithines consist of *Bauxitornis* from the Santonian of Hungary (Dyke & Ősi 2010; Ősi & Buffetaut 2011) and *Martinavis* from the upper Campanian to lower Maastrichtian of Languedoc (Walker *et al.* 2007). In addition to the Ibero-Armorican domain and the Austroalpine island, enantiornithine fossils are also known in the Rhenish–Bohemian island (Dyke *et al.* 2008) and the Transylvanian landmass (Wang *et al.* 2011*a*; Dyke *et al.* 2012).

Ornithuromorph fossils are quite rare in the uppermost Cretaceous of Europe. Rees & Lindgren (2005) identified skeletal elements of the aquatic herperornithiforms *Baptornis* and *Hesperornis* in marine Campanian strata of Scania, southern Sweden. In the Iberian Peninsula, a cervical vertebra of an ornithuromorph found in uppermost Cretaceous deposits of the Pyrenees has recently been described by Pérez-Pueyo *et al.* (2021). This ornithuromorph would be a cassowary-sized avialan and would probably be positioned outside Ornithurae (Pérez-Pueyo *et al.* 2021). Moreover, isolated bones found in the Maastrichtian type area (Dyke *et al.* 2002, 2008) and Transylvania (Wang *et al.* 2011*b*) have been referred to

Ornithurinae indet. Recently, Field *et al.* (2020) described the neornithine *Asteriornis maastrichtensis* from the Maastrichtian of Liège mainly on the basis of a three-dimensionally preserved skull. *Asteriornis* occupies a position close to the last common ancestor of Galloanserae (the clade that includes Galliformes and Anseriformes) and fills a phylogenetic gap in the early evolutionary history of crown birds (Field *et al.* 2020). Moreover, the co-occurrence of crown birds and avialan stem birds in the Maastrichtian of Belgium is worthy of consideration.

The taxon *Gargantuavis* is the subject of recent debate concerning its affinities with birds. It has been considered to be a flightless basal ornithurine mainly based on fossils from southern France and Laño (Buffetaut & Angst 2016, 2020 and references therein). This interpretation was recently questioned by Mayr *et al.* (2020*a*, *b*), who maintain that it is a non-ornithuromorph basal avian or even a specialized non-avian theropod closely related to *Balaur*. Gargantuaviids evolved on both the Ibero-Armorican landmass and the Transylvanian area. Like the enantiornithines, they did not survive the end-Cretaceous extinction event (Buffetaut 2002).

Finally, isolated limb bones from Transylvania referred previously to birds, such as *Bradycneme*, *Elopteryx* and *Heptasteornis*, have been reinterpreted as small non-avian theropods (Csiki-Sava *et al.* 2015 and references therein). The precise affinities of this material remain unclear.

## PALAEOBIOGEOGRAPHY OF EUROPEAN LATEST CRETACEOUS THEROPODS

Current evidence indicates the presence of multiple ceratosaurian lineages in the European archipelago until the end of the Cretaceous (Carrano & Sampson 2008; Tortosa *et al.* 2014). Based on the French fossil record, Tortosa *et al.* (2014) suggested that small abelisaurids probably came from an Albian stock of basal abelisaurids (represented by *Genusaurus* from Provence), which diverged into different lineages. In that way, *Tarascosaurus* and the taxon from Trets-La Boucharde could be basal abelisaurids from relict Albian lineages that survived in an archipelago environment, as well as the Iharkút taxon from the Santonian of Hungary (Ősi & Buffetaut 2011). Meanwhile, medium–large-sized forms such as *Arcovenator* and the Pourcieux taxon seem to have affinities with Indo-Madagascar majungasaurine abelisaurids (Tortosa *et al.* 2014; also Delcourt 2018). This might suggest, as a working hypothesis, that a trans-Tethysian dispersal event occurred between Europe and the Indo-Madagascar landmass via Africa during the latest Cretaceous, probably in the Campanian–Maastrichtian time ('Atlantogean model' of Ezcurra & Agnolin 2012). Recent work supports such a

dispersal throughout the last part of the Late Cretaceous (Parmar & Prasad 2020; Khosla 2021 and references therein). *Betasuchus* represents one of the latest surviving ceratosaurs in Europe (Carrano & Sampson 2008).

The affinities of *Paronychodon* and *Richardoestesia* are currently poorly understood. Both taxa are tentatively regarded as Coelurosauria *incertae sedis* (Larson & Currie 2013; Williamson & Brusatte 2014). The geographical distribution of *Paronychodon* and *Richardoestesia* in Asia, Europe and North America suggests the presence of Laurasian biogeographic connections during the Cretaceous (Csiki-Sava *et al.* 2015).

If ornithomimosaurs achieved a widespread distribution in the Early Cretaceous (Allain *et al.* 2014), they seem to be more restricted in the Late Cretaceous, with records in western North America and Asia; fossils from Laño (and Bulgaria?) could attest to their presence in Europe. Even if confirmed, it is still unclear whether they come from an endemic stock of European ornithomimosaurs or from a dispersal event from Asiamerican sources. As far as is known, the presence of ornithomimosaurs in the Late Cretaceous of Europe should be viewed with caution.

According to Csiki-Sava *et al.* (2015), several waves of dispersal between Asia and Europe can be hypothesized during the Late Cretaceous based on the current dinosaur fossil record. One event (or series of events) around the Campanian–Maastrichtian boundary could deliver taxa such as velociraptorine dromaeosaurids (and perhaps alvarezsaurids) into the Transylvanian landmass. However, the uncertain position of *Balaur* within deinonychosaurs sheds little light on its biogeographical affinities. An interchange between Asia and Europe could also explain the occurrence of possible tracks of oviraptorosaurs and therizinosauroids in emergent areas of the eastern European craton (Gierliński 2015). With respect to alvarezsaurids, a dispersal from Asia to South America via Europe before the Late Cretaceous cannot be excluded, but this hypothesis would imply the discovery of fossils in Africa (Naish & Dyke 2004; Ding *et al.* 2020). If, as suggested by Hartman *et al.* (2019), *Pyroraptor* has unenlagiine affinities, then this would match with the presence of traditionally Gondwanan clades such as large abelisaurids in the latest Cretaceous of Europe.

Although the occurrence of troodontids on the basis of isolated teeth in the latest Cretaceous European archipelago is still weakly supported, the probable jinfengopterygine *Tamarro insperatus* supports the migration of this clade from Asia to Europe (Sellés *et al.* 2021). Dispersal events that might have happened in Laurasia during or even before the Late Cretaceous may account for their presence in Europe (Ding *et al.* 2020).

Among birds, enantiornithines had a widespread geographical distribution during the Late Cretaceous that

includes Asia, Europe, Madagascar, and North and South America (Chatterjee 2015 and references therein). Such a distribution is not surprising if we consider that these birds had good flight ability and therefore a great dispersal potential (Walker *et al.* 2007; Csiki-Sava *et al.* 2015). The hesperornithiform distribution is relegated to the northern hemisphere, mainly North America, with fewer records in Eurasia (Rees & Lindgren 2005; Bell & Chiappe 2015). The presence of this group of specialized diving birds in Europe could be the result of a dispersal event. Meanwhile, flightless gargantuaviids were presumably the result of endemic evolution in insular environments of the European archipelago at the end of the Cretaceous (Buffetaut & Angst 2020).

Finally, the discovery of the neornithine *Asteriornis* in Belgium challenges the hypothesis of a Gondwana cradle for crown bird evolution (Field *et al.* 2020). New Mesozoic fossils are necessary to identify the geographical origin of Neornithes and to clarify precisely the role played by Europe in their early diversification.

Csiki-Sava *et al.* (2015) noted that the uniqueness of the Late Cretaceous European vertebrate bioprovince lies in the prevalence of certain endemic lineages and the absence of otherwise geographically widespread clades (including well-known groups such as tyrannosaurids). Theropods certainly played a major role in European latest Cretaceous faunas. The intricate evolutionary history of European theropods was shaped both by endemic evolution of a European stock that evolved in isolation (basal abelisaurids, gargantuaviids) and by a complex array of immigration events originating from Asiamerican sources (derived dromaeosaurids, *Paronychodon* and *Richardoestesia* clades, and troodontids) and Gondwanan continents (derived abelisaurids).

Dispersal events proposed for European theropods may be related to dispersal events for other clades of dinosaurs and continental vertebrates. For instance, lambeosaurine hadrosaurids probably dispersed from Asia to the Ibero-Armorican landmass during the Campanian–Maastrichtian (Prieto-Márquez *et al.* 2013; Longrich *et al.* 2021). The occurrence of neoceratopsian dinosaurs and zhelestid mammals in the European archipelago would also be the result of dispersal events from Asia during the Late Cretaceous (Csiki-Sava *et al.* 2015 and references). Moreover, a dispersal route between eastern North America and western Europe in the latest Cretaceous is plausible for batrachosauroid urodeles and, tentatively, metatherian mammals (Williamson *et al.* 2014; Csiki-Sava *et al.* 2015). In contrast, there is evidence for intermittent biotic interchange between Gondwana and the European archipelago throughout the Late Cretaceous, with southern migrants including characiform teleosteans, mawsoniid coelacanths, bothremydine turtles, sebecosuchian crocodyliforms and perhaps madtsoiid snakes (Csiki-Sava *et al.* 2015; Rabi &

Sebök 2015; Sellés *et al.* 2020 and references). Among dinosaurs, the close relationship of a titanosaurian sauropod from the Campanian of Egypt to penecontemporaneous forms known only from Europe and Asia suggests a dispersal event between Europe and Africa during the latest Cretaceous (Sallam *et al.* 2018). Also, the discovery in the upper Maastrichtian of Morocco of a lambeosaurine hadrosaurid nested to European forms shows that lambeosaurines dispersed to northern Africa via Europe at the end of the Cretaceous (Longrich *et al.* 2021).

## EFFECT OF THE INTRA-MAASTRICHTIAN FAUNAL TURNOVER ON IBERO-ARMORICAN THEROPODS

Several studies have noted that a dinosaur faunal turnover occurred during the last 10 myr of the Cretaceous in the Ibero-Armorican domain (Fondevilla *et al.* 2019 and references therein). Indeed, Le Loeuff *et al.* (1994) were the first to propose that this event took place between the early and late Maastrichtian. Vila *et al.* (2016) dated the faunal change to around the C31r–C31n reversal, in the early late Maastrichtian, and therefore it was thought to be a relatively fast event on the geological time scale. Nevertheless, the recent re-evaluation made by Fondevilla *et al.* (2019) suggested a wider time span for the faunal turnover, starting in the early Maastrichtian and ending in the early late Maastrichtian, and, hence, lasting around 2.5–2.8 myr.

According to Vila *et al.* (2016), the pre-turnover assemblage would be composed of nodosaurid ankylosaurs, rhabdodontid ornithopods, titanosaurian sauropods, and abelisaurid and dromaeosaurid theropods, until the arrival of hadrosauroids and post-turnover titanosaurians. Instead, Fondevilla *et al.* (2019) deduced that during the Campanian and earliest Maastrichtian the nodosaurids, rhabdodontids, pre-turnover titanosaurians and small–medium-sized theropods dominated the Ibero-Armorican ecosystems, while hadrosauroids were scarce. During the early Maastrichtian, post-turnover titanosaurians would have appeared in the island and cohabited until the early late Maastrichtian (Fondevilla *et al.* 2019). Furthermore, nodosaurids seem to go extinct at 68 Ma and rhabdodontids at 69 Ma, after the arrival of lambeosaurine hadrosaurids at 70 Ma (Vila *et al.* 2016; Fondevilla *et al.* 2019).

Previous studies do not show that large and small non-avian theropods from the Ibero-Armorican landmass were negatively affected by this faunal turnover during the Maastrichtian (Torices *et al.* 2015; Vila *et al.* 2016; Fondevilla *et al.* 2019).

The large-sized theropods recognized in the Ibero-Armorican island most often belong to Abelisauridae (see

The Upper Cretaceous theropod fossil record in Europe). Most of the abelisaurid remains are fragmentary or are represented by isolated teeth, but *Arcovenator escotae* and *Tarascosaurus salluvicus* have been described in southern France based on more complete material. *Tarascosaurus* is known only from lower Campanian deposits whereas *Arcovenator* has been recovered in several upper Campanian Ibero-Armorican sites. Nevertheless, if the remains from Les Tuillières site belong to *Arcovenator*, the temporal range of this genus could be extended up to the early Maastrichtian, contrary to what was previously proposed (Marmi *et al.* 2016; Pérez-García *et al.* 2016; Puertolas-Pascual *et al.* 2018; Fondevilla *et al.* 2019). Therefore, it seems that pre-turnover abelisaurids do not go through the faunal change. It is not yet possible to deduce to what extent abelisaurids were affected during and after the turnover in the Ibero-Armorican domain because the middle–large-sized theropod remains recovered in these sites have not been studied in detail. However, it is highly likely that some of these teeth belong to abelisaurid ceratosaurians different from *Arcovenator*, which could indicate the persistence of this family throughout the Maastrichtian.

On the basis of isolated teeth, cf. *Richardoestesia* and similar morphotypes have been identified in the French and Spanish uppermost Cretaceous deposits (Ortega *et al.* 2015; Torices *et al.* 2015; Marmi *et al.* 2016; this study). These teeth have been found in upper Campanian to upper Maastrichtian deposits of the Ibero-Armorican domain, indicating little to no effect of the faunal turnover on theropods. It is worth noting that these teeth are extremely scarce in the French deposits compared with the Spanish localities.

Teeth belonging to *Paronychodon* have not yet been recognized in the latest Cretaceous French localities. In Portugal and Spain, cf. *Paronychodon* sp. or similar forms have been described in several sites from the late Campanian to late Maastrichtian (Antunes & Sigogneau-Russell 1991; Ortega *et al.* 2015; Torices *et al.* 2015; Marmi *et al.* 2016; this study). Hence, it seems that these theropods were not affected by the intra-Maastrichtian faunal turnover, being present in the pre- and post-turnover communities.

Paravians are the most diverse group of non-avian theropods in the Ibero-Armorican landmass, as evidenced by the indeterminate paravians, indeterminate dromaeosaurids, dromaeosaurines and velociraptorines identified.

Indeterminate paravians with unserrated teeth might have had a wider palaeogeographical extension than previously noted. They are present in a number of sites in the Ibero-Armorican domain (see Systematic Palaeontology, above), even though the Paraves indet. morphotype from Laño can be documented with certainty only at this site. If these specimens do belong to the Paraves indet.

morphotype from Laño, these theropod taxa would also show a wide temporal range, being present in pre- and post-turnover dinosaur assemblages, and suggesting that they were not affected by the faunal change. Nevertheless, further studies are needed to confirm this.

Dromaeosaurids were by far the most common theropods in the latest Cretaceous Ibero-Armorican landmass, being found in several Iberian and French sites. They are represented by isolated teeth and also by postcranial remains. Indeed, *Pyroraptor olympius* and *Variraptor mechinorum* have been described in French deposits. The first genus was previously identified in a few Iberian sites (Torices *et al.* 2015), but there is not sufficient evidence to attribute the Iberian teeth to this genus or to a closely related taxon. Although dromaeosaurids seem to be widely and well represented in the Ibero-Armorican landmass, the affinities between these theropods are unknown. In addition, few or no comparisons have been made between the teeth assigned to these taxa, therefore currently it is not possible to determine whether different taxa are represented in this material. Furthermore, some teeth may belong to abelisaurids or to *Richardoestesia*. Therefore, a detailed study of the teeth is of utmost importance to elucidate the possible taxa present in each assemblage, their affinities and the possible effects of the faunal turnover in the Ibero-Armorican domain.

In the light of these issues, the current data indicate that the family Dromaeosauridae was present throughout the latest Cretaceous (middle?–late Campanian to late Maastrichtian) in the Ibero-Armorican landmass, and therefore that dromaeosaurids would be part of the theropod assemblages before, during (co-existence period) and after the faunal turnover. However, given that the attributions made at the subfamily level are rare, hindering the establishment of the temporal range of dromaeosaurines and velociraptorines, it is not possible to assess the effect of the faunal change at this level. It seems that velociraptorines are present in the pre-turnover community as well as in the post-turnover community (Baiano *et al.* 2014; Ortega *et al.* 2015). Furthermore, the present study suggests that *Pyroraptor* can be documented with certainty only in the middle Campanian deposits of France (contrary to Fondevilla *et al.* 2019), while the temporal range of *Varirapto*r is wider and extends from the middle–late Campanian to the early Maastrichtian. Therefore they apparently did not survive the intra-Maastrichtian faunal turnover.

Other non-avian theropods and avialans are known in the Ibero-Armorican landmass, but they are too poorly represented in the fossil record to provide precise information on the impact of the faunal turnover on them.

There have been previous attempts to enumerate the theropod taxa in the pre- and post-turnover communities, as well as to shed light on the changes in

palaeobiodiversity during the intra-Maastrichtian faunal turnover (Sellés *et al.* 2014; Torices *et al.* 2015; Vila *et al.* 2016). Nevertheless, the studies to date do not enable confident quantification of the number of theropod taxa. Indeed, a thorough revision and comparison of the French, Portuguese and Spanish tooth samples is needed.

Overall, it seems that at the family level the non-avian theropods were not affected by the intra-Maastrichtian faunal turnover, with seemingly abelisaurids, dromaeosaurids and the genera *Paronychodon* and *Richardoestesia* present in both the pre- and post-turnover communities. Hence, the observed general trend tentatively supports the ideas of Torices *et al.* (2015), Vila *et al.* (2016) and Fondevilla *et al.* (2019). It is worth noting that, contrary to what was previously thought, it seems that *Arcovenator*, *Pyroraptor*, *Variraptor* and closely related forms did not go through the turnover and that they disappear from the record before it occurred. Nevertheless, most of the theropod remains are fragmentary and disarticulated, which hinders the taxonomic identification, the determination of the precise affinities of the fossils and, thus, the quantification of the theropod taxa in the Ibero-Armorican landmass.

## CONCLUSION

The systematic re-analysis of 120 isolated theropod teeth from the continental Upper Cretaceous vertebrate-bearing beds of the Laño quarry in the northern Iberian Peninsula, together with 107 additional teeth studied for the first time, has led to the identification of seven morphotypes and five theropod taxa at the site. These taxa include a medium–large-sized abelisaurid (*Arcovenator* sp.) and four small theropods (Dromaeosauridae indet., Paraves indet., cf. *Paronychodon* sp. and cf. *Richardoestesia* sp.). Two indeterminate paravian and two cf. *Richardoestesia* sp. morphotypes have also been distinguished in the Laño sample, however, the possibility that these tooth morphotypes are due to heterodonty cannot be excluded.

All the teeth recovered from the Laño quarry indicate that the site is much richer than previously thought and that it is indeed the richest Upper Cretaceous site in the Iberian Peninsula and Europe for theropod teeth. Furthermore, it has been possible to demonstrate the great palaeobiodiversity of theropods in the Laño site, given the presence of one, and possibly two, medium–large-sized non-avian theropods, four small-bodied non-avian theropods and a large terrestrial bird (*Gargantuavis*). The small theropods are the most numerous and diverse at the site.

The European Upper Cretaceous (Turonian–Maastrichtian) theropod outcrops are mainly located in the Ibero-Armorican domain and central Europe. The most numerous and diverse sites are located in the Iberian Peninsula, southern France, and Romania, but the Iharkút locality (Hungary) does also have a considerable theropod assemblage. According to the most common non-avian theropod remains, the usual medium–large-sized theropods are regarded as abelisaurid ceratosaurians, and indeterminate theropods are represented by teeth that may also belong to abelisaurids. The more diverse small non-avian theropods are represented by different dromaeosaurids, isolated teeth grouped as *Paronychodon* and *Richardoestesia*, troodontids and, probably, other paravians similar to those seen in Laño. Avialans (birds) are also found in the sediments of the Late Cretaceous European archipelago, that is, hesperornithiforms, enantiornithines, gargantuaviids (whose phylogenetic position is currently under debate) and basal ornithurines. Therefore, the common latest Cretaceous theropod assemblage, also found in Laño, is characterized by the presence of one or two medium–large-sized theropods and plenty of small forms, which are the most abundant and diverse category of dinosaurs.

The theropod assemblage present at the Laño site and other European localities represents a mixture of European endemic taxa, Asiamerican elements and Gondwanan theropods, which could have reached Europe throughout the Cretaceous in different dispersal events. If correct, this interpretation supports a biogeographic connection during the Cretaceous between Asia, Europe and North America, as well as Europe and the Gondwanan landmasses.

Although an intra-Maastrichtian faunal turnover has been suggested to explain changes in biodiversity among the herbivorous dinosaurs of southern Europe, many of the theropod groups represented in the Ibero-Armorican landmass before the turnover are still present during and after the event, therefore it seems that this faunal turnover did not directly affect the theropods. Nevertheless, it is not yet possible to establish the results of this faunal turnover at the subfamily or genus level due to the fragmentary nature of the specimens.

Finally, this systematic review of the abundant isolated teeth in the European fossil record could shed light on the possible affinities and palaeobiodiversity of European abelisaurids, dromaeosaurids, indeterminate paravians and indeterminate large theropods.

## DATA AVAILABILITY STATEMENT

Data for this study, including the measurements of the Laño tooth sample, database and the European Upper Cretaceous (Turonian–Maastrichtian) theropod record, are available at: https://doi.org/10.5061/dryad.4xgxd258x

*Editor.* David Button

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