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Geologiako Gradua / Grado en Geología

Dinosauru teropodoen hortzen azterketa/ Study of isolated teeth of theropod dinosaurs

Errioxako Behe Kretazeoko espinosauruak Iberiar Penintsulako testuinguruan / Spinosaurids of the Early Cretaceous of La Rioja in an Iberian context

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1. ABSTRACT/ LABURPENA

Theropod remains are relatively common in the Early Cretaceous vertebrate sites from the Iberian Peninsula, being mostly known for their teeth. This is the case of the studied fossil sites located in Igea (La Rioja) where the Enciso Group crops out. Although the paleoenvironment of the Enciso Group is still under discussion, it represents an area where fluvial systems, fresh water-lakes and fluvial dominated coastal plains with marly lakes developed. Nine spinosaurid teeth have been found in four different fossil sites (Barranco de La Cañana, La Era del Peladillo, Peña Cárcena and Umbría de Costarrey). The teeth have been studied using qualitative and quantitative features and they have been compared with those from Teruel and other Iberian sites. In Igea two different baryonychine morphotypes have been described. The Morphotype 1 teeth show a similar morphology to the ones found in the Iberian Peninsula. Morphotype 2 tooth seems to differ from the known Iberian material, though no further conclusions can be currently done because of the scarcity of data.

Teropodoen arrastoak erlatiboki arruntak dira Iberiar Penintsulako Behe Kretazeoko ornodunen aztarnategietan, gehien bat hortz fosilen bidez ezagutzen direlarik. Igean (Errioxa) Enciso Taldekoak diren azaleramenduetan aurkitu eta lan honetan aztertu direnak kasu. Nahiz eta Enciso Taldeko materialek adierazten duten paleoinguruneari buruz eztabaida dagoen, bertan sistema flubialak, ur gezako lakuak eta ibaien menpeko kostaldeko ordokiak behatu dira. Guztira, bederatzi espinosaurio hortz fosil aurkitu dira lau fosil azaleramendu ezberdinetan (Barranco de La Cañana, La Era del Peladillo, Peña Cárcena eta Umbría de Costarrey). Hortz hauek azaltzen dituzten ezaugarri kualitatibo eta kuantitatiboak aztertu eta emaitzak Teruel eta beste Iberiar aztarnategi batzuetan aurkitutako hortzekin konparatu dira. Igean bi baryonychido morfotipo ezberdindu dira. Morphotype 1-eko hortz fosilak Iberiar Penintsulan aurkitu direnen antzekoak dira. Morphotype 2 bezala sailkatu den hortz fosila, aldiz, Iberiako materialetik aldendu egiten da, nahiz eta datu faltagatik, ondorio zehatzagorik ateratzea posible izan ez den.

2. INTRODUCTION

This final degree work is targeted to the palaeontological study of spinosaurid dinosaur fossil teeth found in the following Early Cretaceous fossil sites situated in Igea (La Rioja). The fossil sites, belonging to the Enciso Group, where the fossils have been found are: Barranco de La Cañada, Peña Cárcena, La Era del Peladillo 6 and Umbría de Costarrey. Besides these teeth, the abundance of other fossils is high, including pterosaurs, crocodylomorphs, fish, gastropods, bivalves, ostracods and plants.

The fieldwork has been done in order to get aware about the geological setting and to study the lithologies and fossil content in the sites, applying the stratigraphic, sedimentologic, tectonic, petrological and palaeontological knowledge. The work, however, is mainly focused on Vertebrate Palaeontology.

The study of isolated theropod teeth has a great interest due to different factors. Bones do hardly fossilize because they are pneumatized. However, teeth resistance is much higher because they are composed of enamel. Theropods used to replace the teeth so that a single individual could generate lots of them. Furthermore, theropod teeth are useful for systematic purposes since they show autopomorphic characters at the family level, even at the genus and species level. Therefore, the study of theropod teeth is very interesting in order to get aware of the paleodiversity of this group in time and space. More interestingly, the studied spinosaurid teeth are the first to be described in this area.

First of all, the objectives are detailed. Secondly, a classification of the Dinosauria phylogenetic clade is exposed, concentrating on the spinosaurids and its teeth. Furthermore, the geographical, geological and palaeontological settings are explained, describing the different deposits where the studied fossils have been found. Afterwards, the methodology used in the work is treated, describing the material, the field work, the laboratory work and the research work. Qualitative and quantitative teeth characters are explained subsequently. In the Systematic palaeontology, teeth are described and their main features are discussed. For a more accurate study, measures are compared with other data with the aim of a precise systematic attribution. Finally, conclusions are treated and a prospective is presented.

3. AIMS

The following final degree work has many goals, both direct and indirect.

An important aspect to consider is that the competences to search and to quote bibliographical sources are put into practice. The field research is focused on the fossil sites where the fossils have been found and their surroundings (stratigraphically at the base of the Enciso Group). Besides, the available information of spinosaurid dinosaurs, especially in the Iberian Peninsula, is analyzed. The information found in the bibliography is contrasted with field data via stratigraphic columns, cartography, fossil sites and outcrop measurements, binocular loupe, optical microscope and taphonomical studies. Fossil sites are described and the depositional processes are studied. The methods of fossil extraction and preparation are also put into practice.

Furthermore, the knowledge of the methodological study based on vertebrate fossil teeth, and especially on theropod teeth, is gained. The material has been described and a biometric study has been done. The teeth have been assigned from a systematic point of view. All the data obtained during this work have been compared with those of other spinosaurid teeth, and subsequently discussed.

Finally, with all the data obtained from the bibliography, field work, laboratory work and research studies, some conclusions are obtained, focusing on the studied theropod teeth. Future research studies are also presented.

This work has been a good experience to acquire a new and specialized terminology, as well as to familiarize myself with the methodological work in Vertebrate Palaeontology.

4. PALEONTOLOGICAL BACKGROUND

4.1. DINOSAURIA

Dinosauria is formally defined as "members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus* (the living house sparrow)" (Benton, 2012). Dinosaurs are distinguished from all other reptiles by some cranial and postcraneal (forelimb, pelvis and hindlimb) synapomorphies; these are shared derived characters that allow to distinguish dinosaurs from other organisms. Some other features are only seen in dinosaurs and a few of their closest relatives, not being strictly diagnostic (Benton, 2012; Brusatte, 2012).

Within the tetrapod group (animals with a backbone that have limbs with digits), dinosaurs are members of a speciose subgroup of reptiles called the Archosauria. Crurotari includes crocodylomorphs and their closest extinct relatives, whereas Avemetatarsalia includes birds, dinosaurs and pterosaurs (see Brusatte, 2012).

Dinosaurs are consider to be monophyletic, thus they all share a common ancestor (Figure 1). This clade is classically divided in two major groups: Saurischia (lizard-hipped) and Ornithischia (bird-hipped) (but see Baron *et al.*, 2017 for a different approach). Each of them can be divided into less inclusive subgroups.

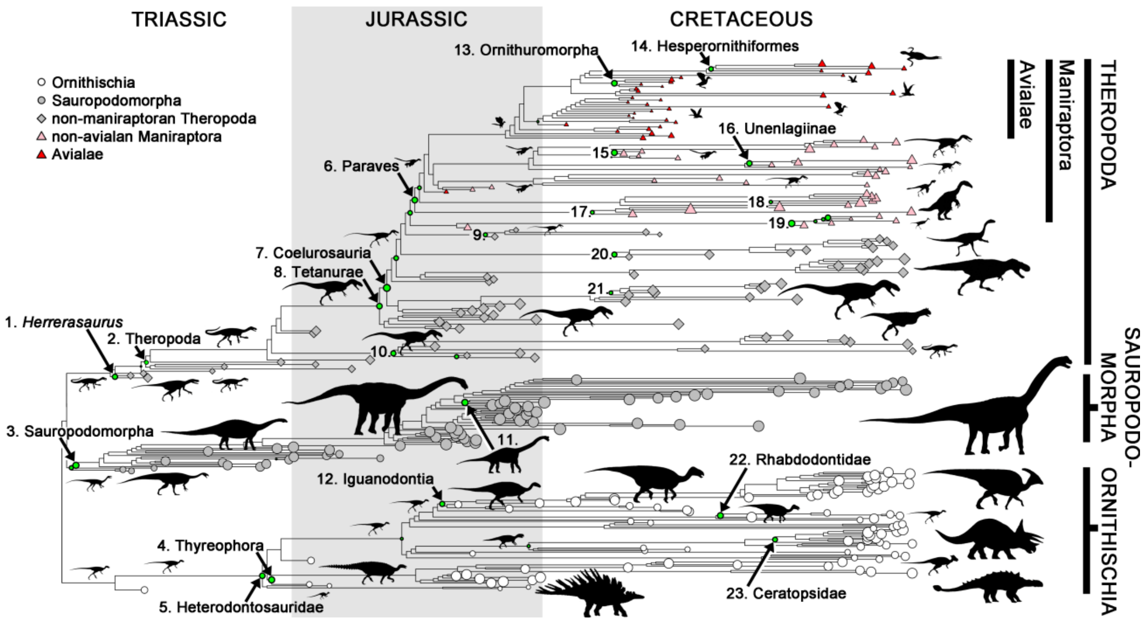


Figure 1. Dinosaur phylogeny showing nodes with exceptional rates of body size evolution. Exceptional nodes are numbered and indicated by green filled circles with diameter proportional to their down-weighting in robust regression analyses. The sizes of shapes at tree tips are proportional to log_{10}(mass), and silhouettes are indicative of approximate relative size within some clades. The result from one tree calibrated to stratigraphy by imposing a minimum branch duration of 1 Ma is shown (Benson *et al.,* 2014*).*

4.2. THEROPODA

Theropoda (meaning wild beast foot) forms a clade of bipedal tetrapods among which birds and all strictly carnivorous dinosaurs are found, with the exception of some plant eaters (Barrett, 2005), such as therizinosauroids, insectivores, omnivores or filter feeders. This clade appeared in the Late Triassic and rapidly acquired a worldwide distribution, being present on every continent by the Early Jurassic (Hendrickx *et al*., 2015a).

Theropods, together with the sauropodomorphs, belong to the order Saurischia. All these dinosaurs have a common hip configuration (lizard hipped), where the pelvis bone is projected forward, whereas, in ornithischians it points backwards. Theropods are almost exclusively bipedal, exhibiting elongated necks and a long horizontally projecting tail.

Among the characteristic synapomorphies of theropods, they include an intermandibular articulation with a reduced overlap of the dentary and the postdentary elements, pneumatized (hollow) bones of the axial and appendicular skeleton, and very long tail prezygapophysis (articular elements of the neural arch in all vertebrae), generating a solid structure in which there is no relative movement of vertebra against vertebra (Holtz and Osmolska, 2004). Theropod dinosaurs form one of the most successful and morphologically diverse groups of tetrapods, surviving the Cretaceous-Paleogene extinction event and radiating as birds (Hendrickx *et al*., 2015a).

4.2.1. SPINOSAURIDAE

Modern phylogenetical analysis currently recover around 25 non-avian theropod subclades, most in ladder-like organization (Figure 2) (Hendrickx *et al*., 2015a)

Spinosauridae can be classified into the Megalosauria clade, gathering also the Megalosauridae. Spinosauridae is composed by a highly specialized theropods united by an elongated crocodile-like skull, spatulate snout with sigmoid alveolar margins, fluted conical teeth with minute or no denticles and an hypertrophied manual ungual (Hendrickx *et al.*, 2015a). *Ichtyovenator*, *Baryonyx*, *Suchomimus*, *Irritator* and *Spinosaurus* are spinosaurid genera.

Different studies propose that spinosaurids were at least partially piscivorous, while also feeding on dinosaurs and pterosaurs. They were large to very large theropods (8-17m long) and include the largest terrestrial predators discovered hitherto. They were also characterized by elongated neural spines that evolved into a bony sail in some members such as *Spinosaurus aegyptiacus* (Hendrickx *et al*., 2015a). Spinosaurids appeared in the Late Jurassic and seem to go extinct in the early Late Cretaceous (Hendrickx *et al*., 2015a).

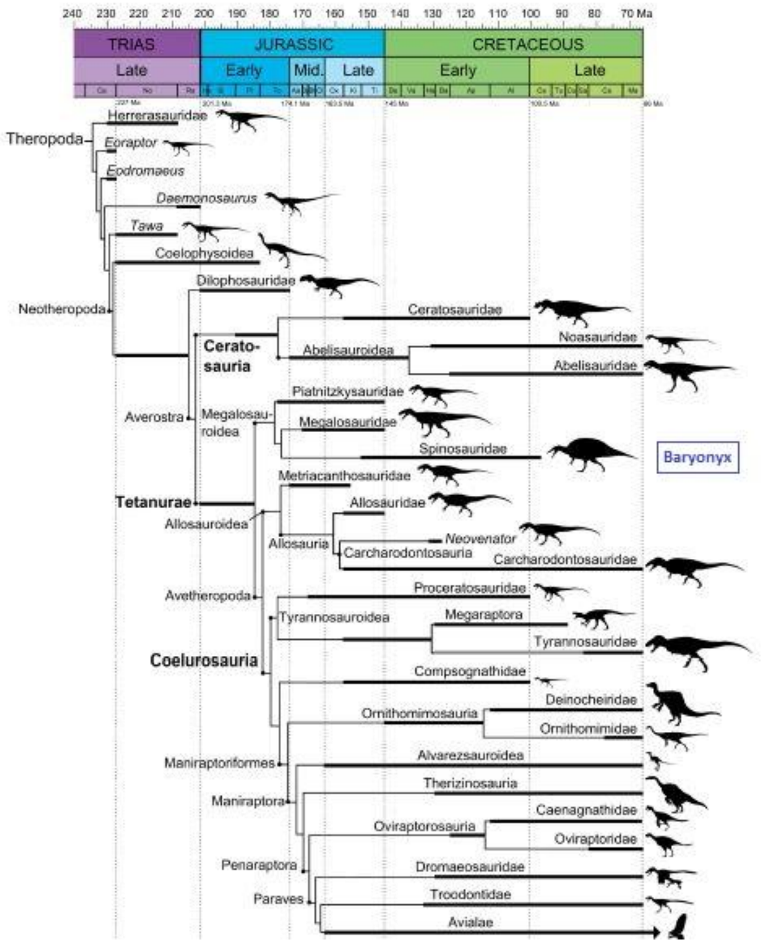


Figure 2. Phylogeny and stratigraphic distribution of theropod clades (modified from Hendrickx *et al*., 2015)

Most baryonychine fossil traces are known from Barremian and Aptian deposits of Europe. However, a baryonchine tooth has also been reported from the Early Cretaceous of Libya and a probable baryonychine tooth from the Santonian of China has been described drastically increasing the subclade's temporal range (Figure 3) (Bertin, 2010).

4.2.1.1. SPINOSAURID TEETH

Spinosaurid teeth, like those of other vertebrates, are composed of apatite and proteins. These tissues adopt two forms, enamel and dentin (Alonso, 2013). The enamel has bigger apatite crystals that make them harder and more resistant. Thanks to this, the teeth are the most abundant fossils of the theropod record.

Enamel texture is the pattern of sculpturing on the crown surface at submillimeter scale. In theropods, the enamel texture can be irregular, braided, veined, or anastomosed (Kohn, 1942). The enamel texture is usually omitted when describing teeth. However, it seems to have some phylogenetical potential in non-avian theropods (Buffetaut *et al*., 2008; Hendrickx and Mateus, 2014; Hendrickx *et al.*, 2015c). The most common enamel texture in this group of theropods is the anastomosed texture, which consists of multiple ridges dividing and reconnecting in an irregular way (Hendrickx *et al*., 2015b).

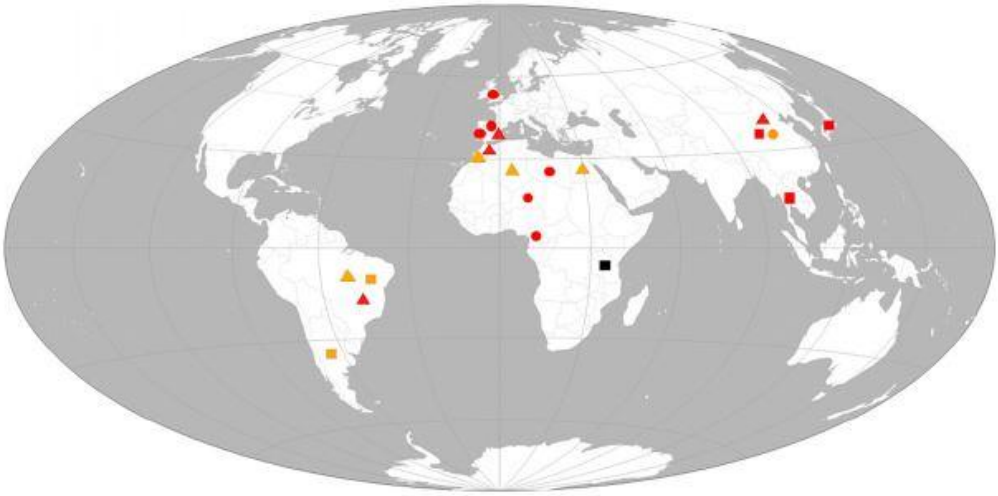


Figure 3. Geographic areas with reported spinosaurid bearing deposits. Triangles represent the presence of spinosaurines, circles represent the presence of baryonychines, and squares represent the presence of spinosaurids of indeterminate affiliation. Black: Late Jurassic; Red: Early Cretaceous (Pre-Cenomanian); Orange: Late Cretaceous (Cenomanian and younger) (Bertin, 2010).

According to spinosaurids, among the different types of tooth morphology they only have a conidont ("cone shaped tooth") morphology (Hendrickx *et al.,* 2015b). This type of tooth has a conical crown that has minute denticles or no denticles at all, and typically fluted surface. Conidont teeth also include acutely pointed apices, weakly distally recurved crowns, and minute denticles or unserrated carinae (Hendrickx *et al.,* 2015b). When the dentition is mostly composed of conidont teeth, it is called conidonty. Besides, theropods like spinosaurids, the conidonty exist in crocodylians and marine reptiles (Hendrickx *et al.,* 2015b).

Despite the fact that different crown ornamentations and attributes have been defined, flutes are the most common features of spinosaurid dentition. Flutes are narrow apicobasally oriented grooves separated by two subparallel and acute ridges. Flutes are also referred to as "striations", "ribs", "longitudinal grooves", "longitudinal ridges" or "ridges" (Hendrickx *et al.,* 2015b). The number of labial and lingual flutes is worthy of consideration, as well as the absence of this feature.

The studied teeth are isolated, shed teeth (those shed or non-articulated with the tooth-bearing bone) and teeth lost in vivo, either falling out due to the eruption of the replacement tooth or when processing the food, and therefore only preserving the crown and the basal-most part of the root (Hendrickx *et al.,* 2015b).

5. SETTING

5.1. GEOGRAPHICAL AND GEOLOGICAL SETTING

The fossil teeth studied in this work were found in the Cameros Basin. The Cameros Basin is located in the northern part of the Iberian Peninsula, encompassing territories which belong to the provinces of Soria, Burgos and La Rioja.

The Riojan sector of the Cameros Basin is situated in the most northwest part of the Iberian Mountain Range. It is restricted by the Ebro Basin to the north, by Demanda Chain to the west and by the other sectors of the basin to the south.

The research is focused on the locality of Igea, situated in the southeast of La Rioja. The fossil sites crop out in the south and southwest of Igea, more specifically between the main town and the Virgen del Villar hermitage (Table 1).

Fossil site	**Latitude**	**Longitude**
La Era del Peladillo 6	42º 04’ 57’’	-2º 02’ 38’’
Peña Cárcena	42º 03’ 45’’	-2º 00’ 47’’
Barranco la Cañana	42º 03’ 36’’	-2º 01’ 41’’
Umbría de Costarrey (UCR1)	42º 03’ 10’’	-2º 02’ 16’’
Umbría de Costarrey (UCR2)	42º 03’ 20’’	-2º 02’ 18’’

Table 1. Coordinates of the fossil sites studied in this work.

The intraplate rifting stages occurred during the Mesozoic were responsible for the emplacement of a set of extensional basins within the Iberian Domain (Álvaro *et al*., 1979; Salas and Casas, 1993; Casas-Sainz and Gil-Imaz, 1998). The Cameros basin was initiated during the main rifting period starting in the Late Jurassic and ending in the Early Cretaceous. Tisher (1966) established the initial stratigraphic framework subdividing the synrift deposits into five groups named Tera, Oncala, Urbión, Enciso and Oliván (Figure 4), which are chronologically ordered from oldest to youngest.

This work is focused on the Enciso Group, where the studied fossil teeth have been found. The Enciso Group is more than 2000 metres thick, with its lower part mainly formed by fluvial deposits (Clemente *et al*., 2010). The middle and upper parts present a wide range of lithologies from littoral and lacustrine deposits to evaporites and limestones, alternating with marls containing desiccation cracks, fine grained siltstones and siltstones with ripples and hummocky cross-stratification. The deposits are arranged into carbonate and siliciclastic units and divided in open lacustrine, siliciclastic marginal lacustrine, shoreface association, carbonate lake margin, desiccated open lacustrine limestone and palustrine carbonate facies. The palaeoenvironment of the Enciso Group has been set as a siliciclastic to carbonate mixed lacustrine system with occasional marine incursions (Doublet *et al*., 2003). Doublet (2004) suggested that the Enciso Group was Early Barremian-Middle Albian in age.

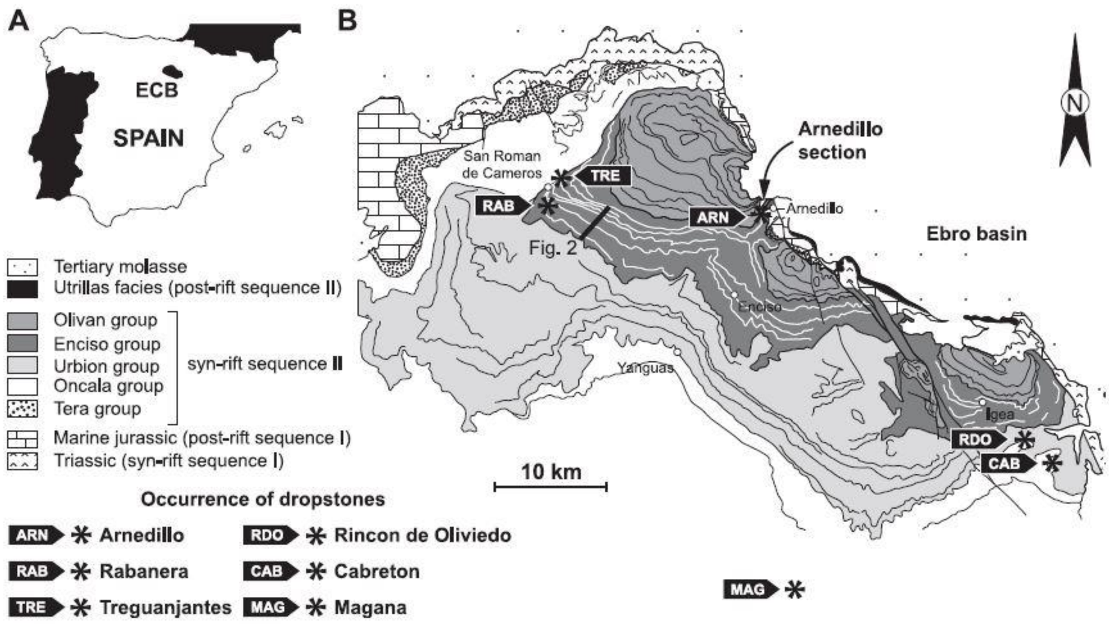


Figure 4. Geological sketch of the eastern Cameros Basin. (A) Geographic location of the Cameros Basin (ECB). (B) Geological map of the eastern Cameros Basin (Doublet and Garcia, 2003).

The Enciso group has not suffered a wide range of tectonic deformation. The strata form a practically homoclinal structure. The orientation varies from N80°-90°E, even though some strata show a N110°E strike. They dip to the N, NE or NW about 15-25 degrees. The observed deformation is mostly concentrated in vertical strike-slip faults, with a N-S or a NE-SW movement and without a big displacement. Small normal faults can also be distinguished. Some of them are filled with calcite or quartz veins, showing a linetation of around a 50/030.

In the area where most of the fossils have been found, the following lithologies have been recognized (Figure 5): marls, sandstones, limestones and argillaceous limestones.

The marls show pink or grey tones toward the bottom of the series, whereas towards the top they are whitish. They are massive, but poorly consolidated with no sedimentary structures. The ostracods are very abundant, especially in the lower part of the series, where they form lumachelles. There have also been discovered fossil remains of fish, crocodiles, theropod dinosaurs and silicified trunks. The marls can contain gypsum lamellae and mollusc lumachelles formed by *Eomiodon* (bivalve), *Cerithium* and *Glauconia* (gastropods) (Agirrezabala *et al*., 1985). These lumachelles show a silicified matrix and recrystallization of the micrite to sparite. The load deformation is quite important in these rocks.

The limestones are micritic, being classified as wackestones. They show a high percentage of organic matter and very often *Cypridea* ostracods (J. Rodriguez-Lázaro, 2017, pers. comm.), and some filamentous algae can be identified. The limestones are rather black or gray, which weathered acquire a yellowish or brownish colour. Disarticulated fossil remains of fish, such as teeth, scales and spines, as well as gastropods and other invertebrates are found throughout the series. At the top of the limestones, algae meshes and desiccation cracks have been observed. It contains lithoclasts, monocrystalline quartz grains and mica muscovites. Some of the ostracods fossils show clapotage structures (A. Aranburu, 2017, pers. comm.). However, the complete ones are filled with sparite, monosparite and quatz. The matrix is partially recrystallized to sparite, as well as the ostracods. Besides, an uncompleted silicification can be observed which is developed mainly in the ostracod lumachelles. Furthermore, the veins are filled with calcite and quartz. Sometimes some ostracod injection to the matrix can be observed. The wackestone beds also show irregularities in the upper surface, where transported sediments of different grain size, bioclasts and other fossils have been deposited.

The sandstones vary from a fine grained to coarse grained quartzarenites to quartzwackes, with mostly monocrystalline quartzs. Some of the quartz grains present pressure sutures. They usually show a high amount of muscovite and an unknown phyllosilicate (probably smectite; A. Aranburu, 2017, pers.comm.), sometimes intercalated. They can be massive or can present different sedimentary structures, such as current or wave ripples, parallel laminations and small dunes. The matrix is sometimes calcified or silicified. Agirrezabala *et al*. (1985) also identified slumps and load structures. Likewise, the beds contain soft pebbles, carbonate nodules, plant remains and transported trunks like the fossilized trunk of Igea, as well as organic structures. Bioturbations are usual. In the base of some of these rocks, some dinosaur ichnites can be found as casts (positive relief).

The argillaceous limestones show a grey-bluish coloration, with a very marked lamination. They mostly appear in the base of the mudstones, where they reach the highest thickness. They can also be interstratified with the marls and sandstones.

5.2. PALAEONTOLOGICAL SETTING

Besides the teeth here studied, other fossils have been identified during the fieldwork. The body fossils belong to invertebrates, vertebrates and plants. Furthermore, different levels with dinosaur tracks have been established.

Invertebrates

Fossils of ostracods, gastropods and lamellibranchs are known throughout this part of the series. Ostracods are the dominant fossils, being present in almost every rock. The major concentrations are found in the base of the formation, where they form accumulations of lacustrine origin (Agirrezabala *et al*., 1985). Gastropods are both of freshwater and salted water-marine form (Agirrezabala *et al.,* 1985). During the fieldwork, only the presence of *Glauconia* has been documented. However, Agirrezabala *et al.* (1985) could define more gastropods in the Igea outcrops (i.e. *Cerithium*). Bivalves also include lacustrine or fluvial (freshwater) and marine or transitional (brackish) forms (Agirrezabala et *al.*, 1985). During the field work, *Emiodon* lumachelles have been found, some of them exceeding 20 centimetres in thickness.

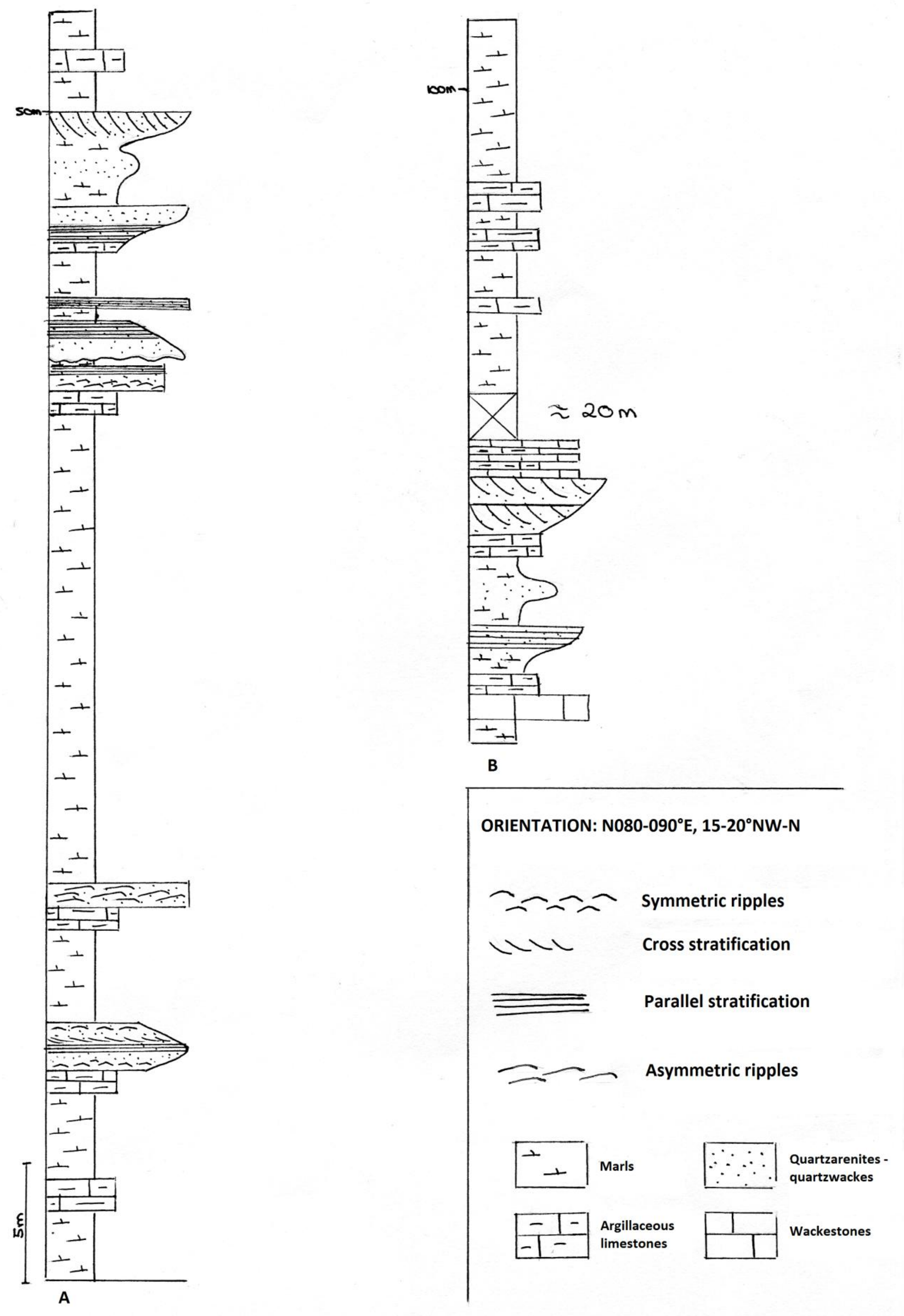


Figure 5. See figure caption in the next page.

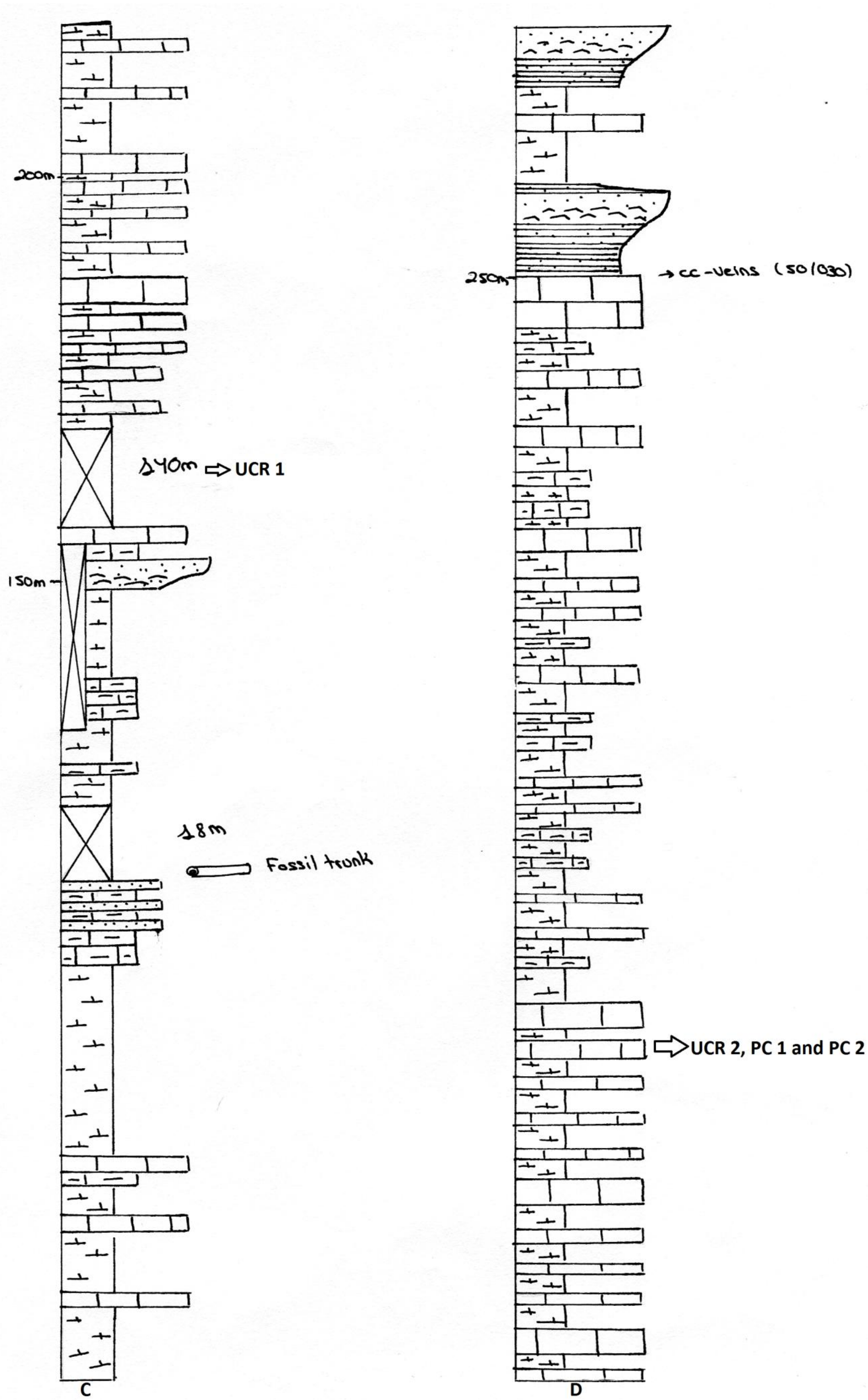


Figure 5. General stratigraphic column of the base-middle part of the Enciso Group (from A to D). UC 1 and UC 2: Umbría de Costarrey fossil site. PC 1 and PC 2: Peña Cárcena fossil site.

Vertebrates

The vertebrates are represented by the fossils of fish, crocodilians, theropod dinosaurs, pterosaurs, turtles as well as undetermined bones and coprolites. Fish fossils are the dominant vertebrate remains, such as scales, teeth, vertebrae and selachian spines. Some specimens consist of partial articulated skeletons of actinopterygians. Fragmentary material of *Lepidotes*, like rhomboidal scales and crushing teeth, are usually found at the fossil sites. Isolated teeth of crocodilians are also quite abundant. The teeth are conical in shape and show ridges on the enamelled crown. *Bernissartia sp.*, *Goniopholis sp.* and *Pholidosaurus sp.* are the three taxa found in the sites (Viera and Torres, 2013). The putative coprolites could also belong to crocodilians because of their helical winding (Agirrezabala *et al*., 1985).

Pterosaurs and baryonichid dinosaurs are represented by isolated teeth. These were collected at Peña Cárcena and Barranco la Cañada sites. Finally, some levels show a wide range of ichnites (Figure 6). Ornithopod, sauropod and theropod tracks have been identified in the upper part of the strata (Díaz Martinez, 2013; Pérez Lorente, 2015). Most of these ichnites pertain to theropods.

Figure 6. Dinosaur ichnites found as casts (positive relief) in the sandstones in the Umbría de Costarrey (UC 1).

Plants

Few plant remains were discovered in the studied area. They belong to conifer and fern trunks, which were probably deposited after certain transportation.

Tempskya riojana fragments are the most abundant ferns and usually appear at the base of the Enciso Group (Viera and Torres, 2013). Conifer trunks are scarce and fragmentary, although some of them reach big dimensions. Although they are totally silicified, their inner structure can be appreciated.

The algal remains are very abundant in the area, and are associated with carbonate rocks, corresponding to tidal flats (Agirrezabala *et al.,* 1985). They also appear as oncolites or algal meshes.

5.3. PALAEOENVIRONMENTS

Ostracods appearing in the sample suggest a fresh or slightly brackish nature of the limestones (J. Rodríguez-Lázaro, 2017, pers. comm.). Furthermore, clapotage structures show a shallow coastal and wave dominated palaeoenvironment for the limestone creation, may be a coastal lake or lake with evaporation stages where limestones and marls deposited. The sandstones were also formed in the foreshore.

Agirrezalaba *et al*. (1985) interpreted the Enciso Group as a deltaic plain with almost no slope, where two different environments developed. In the base of the series, there is a clear dominancy of detritic and marly facies that correspond to a lacustrine environment. Its thickness reaches the 200 m and there are some levels with fossils of *Viviparus* and Unionid gastropods. Other deposits were formed in a tidal plain, under brackish conditions. *Emiodon* and other invertebrate lumachelles can be found in these rocks. This type of environment can be interpreted as a muddy inter- and supratidal tidal plain where periods of carbonate sedimentation occurred with a sporadic, but repetitive, character. Between those periods of marine influence, the flooding plain deposits are predominant, with the sedimentation of sandstones and palaeochannels.

Clemente (2010) encompasses three formations in the Enciso Group of the western Cameros Basin, Río Ciruelos which is made of fluvial deposits, Hortigüela which consists of fresh water lacustrine carbonates and Golmayo representing a fluvial dominated coastal plain with marly lakes. The Río Ciruelos Formation composed by deposits of a fluvial system with an N, NW and NE proximal-distal trend. Towards the NW and W it changes towards the Hortigüela Formation carbonate lake, partly dominated by biogenic (cyanobacteria) and partly by physical processes. The Golmayo Formation is the deposit of a fluvial dominated coastal plain, with a SW-NE proximal-distal trend, with diluted carbonate coastal lakes, also partly controlled by the biogenic growth of cyanobacteria and partly by physical processes, waves, water currents and underflows. The Enciso Group represents a semi-enclosed basin open towards the north. This was a mixed depositional system with siliciclastics and carbonates, partly dominated by physical processes, by waves (Doublet *et al.,* 2003) and partly dominated by biogenic processes (cyanobacteria).

5.4. FOSSIL SITES

The spinosaurid teeth have been found in four areas next to Igea (La Rioja) (Figure 7). The fossil sites show a low concentration in remains. Over the work, the following sites have been studied: La Era del Peladillo 6, Barranco de La Cañada, Peña Cárcena and Umbría de Costarrey.

Figure 7. Orthophoto of the Igea area of Igea where the fossil sites are located. A) La Era del Peladillo 6. B) Barranco de La Cañada. C) Peña Cárcena. D) Umbría de Costarrey. Map accessed through the public domain: https://www.google.es/maps.

a) La Era del Peladillo 6 (PL 6)

La Era del Peladillo 6 is one of the fossil sites studied in the Enciso Group, although it has not been possible to correlate it with the main stratigraphic column. The stratum that has yielded a spinosaurid tooth (ICIPR 26) is located in the upper part of the series, in the same layer where crop out several dinosaur tracks (Díaz Martínez, 2013), having a N080°E, 20°NW orientation. La Era del Peladillo is one of the most noteworthy dinosaur ichnofossil sites of La Rioja, with seven different levels that have provided a large amount of dinosaur tracks (Díaz Martínez, 2013; Pérez Lorente, 2015). As there was not an adequate outcropping, non column was built. However, it pertains to the middle section of the Enciso Group (sensu Pérez-Lorente, 2015: p. 10, table 1.2), Aptian. Lithology: carbonatic.

The layer that has yielded the fossil tooth ICIPLR 26 crops out at the top of a mudstone. Algal films and desiccation cracks are the most representative structures found. This level also contains a wide range of ichnites, with a dominance of theropod footprints. Moreover, parts of an articulated fish skeleton and isolated scales have also been found in this area.

Since there is no transporting evidence, the fossil is considered to be autochthonous (from a taphonomic point of view).

b) Barranco de La Cañada (LCÑ)

The Barranco de La Cañada fossil site (Figure 8) corresponds to the middle part of the series Lower section of the Enciso Group (sensu Pérez Lorente, 2015. p. 10). Upper Barremian to Aptian. Lithology: Siliciclastic. The orientation of the strata, where the ICIPLR 30 and ICIPLR 32 fossil teeth have been discovered, is N110°E, 15°NE.

As in the other sites, teeth were found at the top of a mudstone. This stratum shows irregularities in the upper part. Accumulations of a higher grain size can be distinguished in the depressions. Part of them belongs to fossil remains or bioclasts. Besides the spinosaurid teeth, a possible ornithopod tooth, fish scales, *Lepidotes* and pterosaur teeth, *Glauconia* gastropod shells and sauropod and theropod ichnites have been found in the same level. Desiccation cracks and algal films are the main structures of the stratum.

The presence of gastropod shells and *Lepidotes* scales and teeth could indicate the fresh or brackish nature of the mudstone.

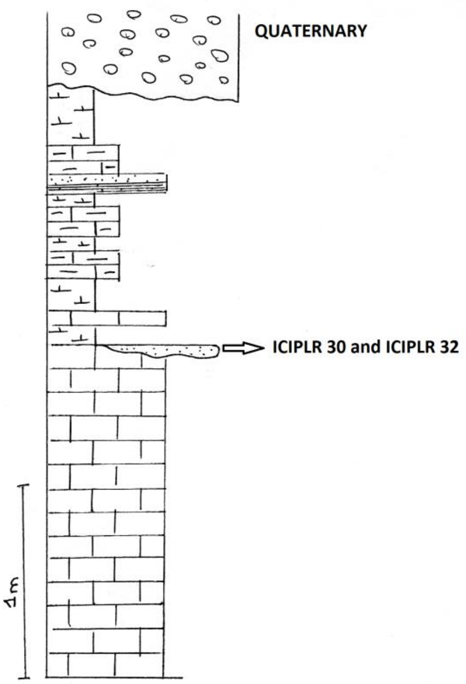


Figure 8. Stratigrafic column built in the Barranco de La Cañada fossil site, where ICIPLR 30 and ICIPLR 32 teeth have been recovered. The fossil teeth have been found in the depressions of the limestone with other coarse grain size sediments.

c) Peña Cárcena (PC 1-2)

The Peña Carcena fossil site (Figure 9) crops out in the lower part of the Enciso Group. In this area the fossil teeth ICIPLR 28 and ICIPLR 33 have been recovered. The main orientation of the strata is N080°E, 15°NW.

In spite of an adjusted dextral strike-slip fault in the area where the fossil teeth have been found, a good stratigraphic correlation can be done. The teeth were discovered in the upper part of a mudstone layer. As in Barranco de La Cañada, the stratum also shows irregularities at the top, being the teeth and other fossils found inside a sort of depressions. Together with the spinosaurid teeth, *Lepidotes* scales and teeth, other fish remains and undetermined vertebrate bones have been identified.

Below the mudstones, some coprolites and fern trunks of *Tempskya riojana* were discovered.

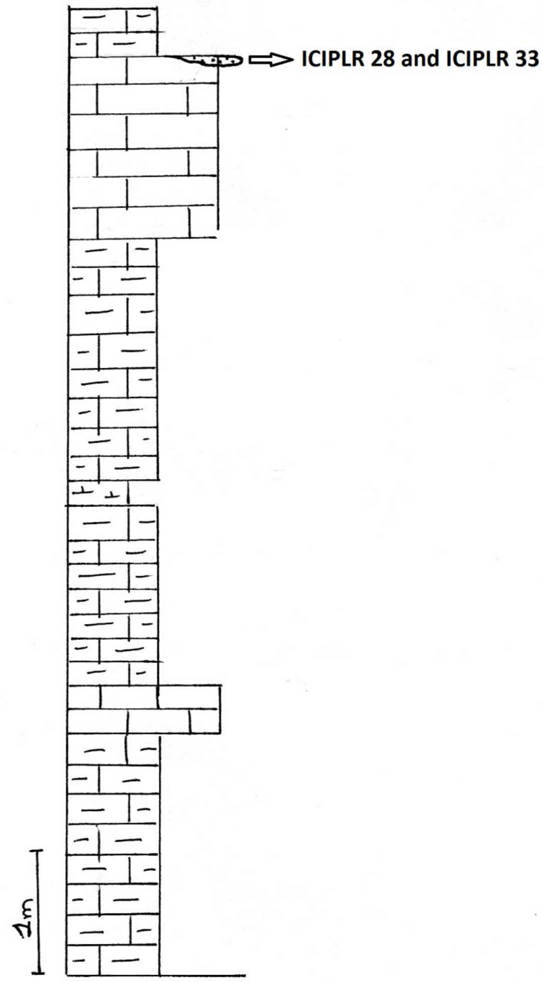


Figure 9. Stratigrafic column built in the Peña Cárcena fossil site, where ICIPLR 28 and ICIPLR 33 teeth have been discovered. The fossil teeth have been recovered in the depressions of the limestone with other coarse grain size sediments.

d) <u>Umbría de Costarrey (UCR 1-2)</u>

In Umbría de Costarrey, two fossil sites (Umbría de Costarrey 1 and Umbría de Costarrey 2) can be differentiated (Figure 10). The layer's orientation is N080°E, 20°NW. In each sites a stratigraphic column was built.

(a) Umbría de Costarrey 1 (UCR 1)

In this area, two close fossil sites have been studied. The tooth ICIPLR 31 comes from a thin argillaceous limestone and the second fossil, ICIPLR 27, has been found in a marly layer. Because of the undergrowth, it was not possible to make a detailed study of the area.

(b) Umbría de Costarrey 2 (UCR 2)

The UCR 2 site corresponds to the first limestone set. The fossils ICIPLR 29 and ICIPLR 34 were found in the area. Nevertheless, the specific layer (or layers) is unknown.

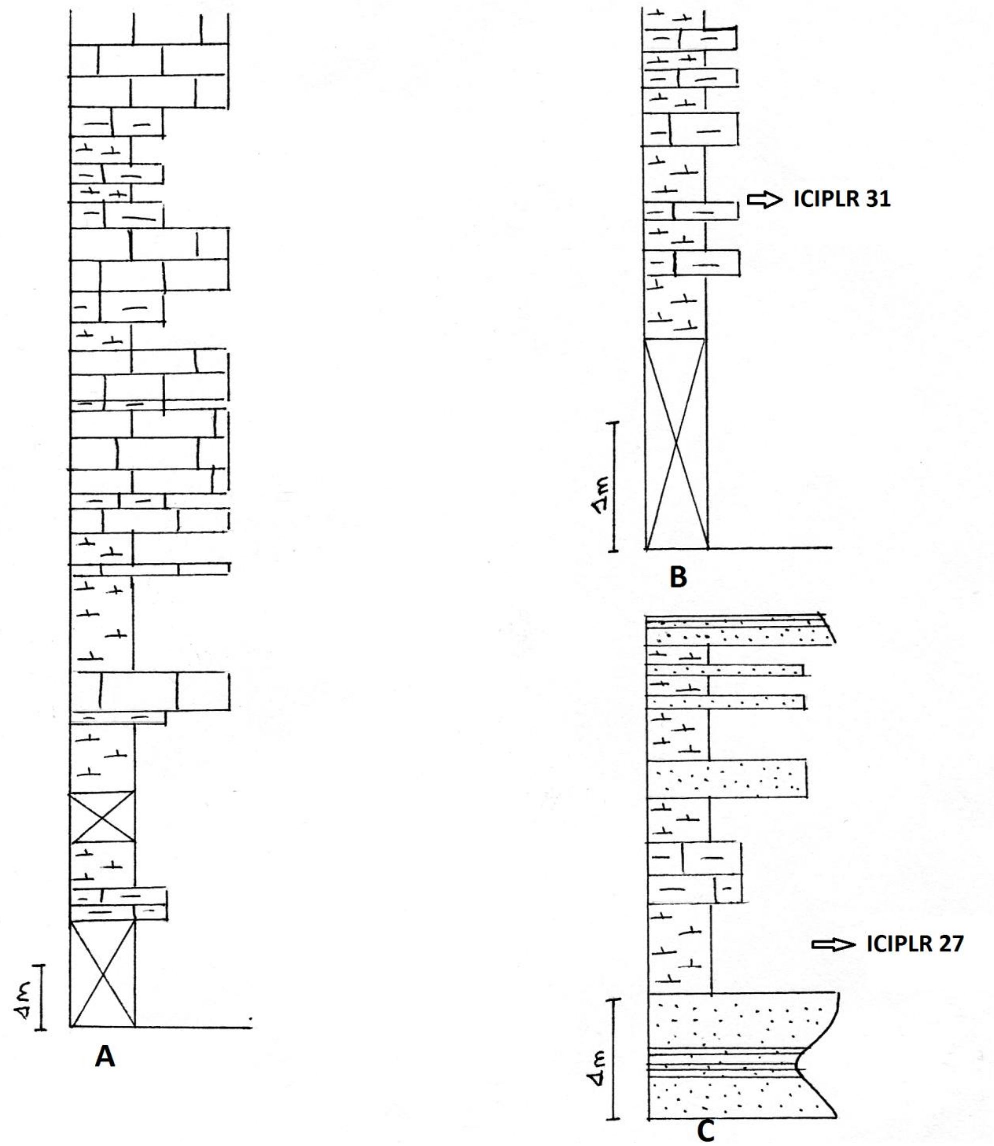


Figure 10. Stratigrafic columns built in the Umbría de Costarrey fossil sites, where ICIPLR 27, ICIPLR 29, ICIPLR 31 and ICIPLR 34 teeth have appeared. A) Umbría de Costarrey 2. B) and C) Umbría de Costarrey 1. ICIPLR 27 tooth has been found in a marly layer and ICIPLR 31 in an argillaceous limestone stratum.

6. METHODOLOGY

6.1. FOSSIL MATERIAL

6.1.1. LIST OF MATERIAL

The material studied in this Final Degree Work consists of nine theropod (Dinosauria) teeth found in different stratigraphic sections or layers from the Enciso Group of Igea, La Rioja. Furthermore, other fossil remains obtained during the field work have been treated as well as the most representative lithologies.

The list of studied material is: ICIPLR 26, ICIPLR 27, ICIPLR 28, ICIPLR 29, ICIPLR 30, ICIPLR 31, ICIPLR 32, ICIPLR 33 and ICIPLR 34.

6.1.2. LABELLING

The labelling has been made in the order the teeth were extracted in the field. ICIPLR is the abbreviation of Igea Centro de Interpretación Paleontológica de La Rioja.

6.1.3. FIELD WORK

Different geological disciplines that were touched in this work include vertebrate and invertebrate palaeontology, sedimentology, stratigraphy, sedimentary petrology and tectonics.

The study of the area has started with a general column. This column is situated in the basal part of the Enciso Group, where most of the samples have been found. All the lithologies, fossils, sedimentary structures and geometrical relationships are showed there. The faults have also been taken into account for a better correlation of the strata. Smaller columns have been built in most of the fossil sites with the possible best degree of accuracy in all the disciplines. Representative samples (fossils and rocks) have also been picked for a further investigation. Besides, the possible conditions of deposition have been studied.

Some teeth have been found during the field work. Other specimens available for the study were discovered previously. Once the tooth has been located, the extraction work starts. Firstly, a Paraloid (hardener) patina, diluted in acetone is applied, making the tooth more resistant. After letting it dry, a square around it is sculpted with a chisel. Secondly, the tooth is removed blowing with the chisel in the longitudinal side. Finally, the fossil piece is kept in a plastic bag, in order to be cleaned and prepared in the laboratory.

6.1.4. LABORATORY WORK

Once the fossil is removed, it is carried to the laboratory. Afterwards, the remaining sediment is removed via mechanical (by hand) and chemical processes. If the tooth is broken it is pasted with glue. Cracks are also filled with cellulose nitrate (Imedio) in order to protect it from the acids. When no crack is developed in the fossil, it is put directly in the acetic acid, because of the protection the enamel gives to it. As the sediment usually is composed of carbonates, this is dissolved in an acid solution with a concentration approaching the 8%. During the following days, the tooth is controlled until its complete cleaning. After this, the acid is removed and the fossil is deposited in a box.

6.1.5. RESEARCH WORK

During the research work, the data and samples collected in the field have been treated. The general and specific columns have been firstly analysed separately. Afterwards, the small stratigraphic columns have been situated in the main one using orthophotos. The whole set of columns have finally been studied.

The rock samples have been studied by direct visual observation and optical loupe magnification. Furthermore, thin sections of the most interesting and representative rocks have been made and assayed under the optical microscope, studying the fossil content, the depositional environment and the diagenesis (taphonomy). The pictures have been taken in a binocular loupe as well as in a camera. Afterwards, the images have been modified and a sheet has been prepared in Photoshop using the software of the research team of my supervisors.

Teeth have been examined precisely. On the one hand, qualitative characters have been studied. On the other hand, the quantitative or morphometric characters have been measured. With the obtained data, different morphotypes have been set. Besides, some graphics have been created in other to compare the information with a database. Finally, the fossil teeth have been tentatively assigned to a taxon (Systematic palaeontology).

6.2. NOMENCLATURE, CHARACTERS AND CRITERIA

Before the study of the fossil material found in Igea, the most important terminology for theropod teeth is explained based on the one proposed by Hendrickx *et al*. (2015b). These authors have summarised and standardized a list of anatomical, morphological, and morphometric terms and abbreviations for each tooth anatomical subunit and each measurement previously taken on theropod teeth. Although the nomenclature used is wide, in this work only the useful terms for the studied fossils are defined (Figure 11).

The anatomical terminology follows the nomenclature proposed by Smith and Dodson (2003) and Smith *et al.* (2005) for general tooth anatomy:

- The **crown** is the portion of the tooth covered with enamel, composed of hydroxyapatite, typically situated above the gum and protruding into the mouth (Schwenk, 2000; McGraw-Hill, 2003), being the inner core composed by dentine (Hillson, 2005). The crown usually includes labial and lingual surfaces, which can be identified in theropods, including some spinosaurids.
- The **root** is the portion of the tooth beneath the gum and embedded in an alveolus or an open alveolar groove.

- The **apex** is the tip of the crown (crown apex) or the root (root apex) of a tooth (Schwenk, 2000; McGraw-Hill, 2003; Smith and Dodson, 2003). The crown apex can be serrated, smooth, or worn showing spalled surfaces or wear facets.
- The **cervix** is the transition between the crown and the root and corresponding to the basal extension of the enamel layer (Hendrixck *et al.,* 2015b).
- The **carina** is a sharp, narrow, and well-delimited ridge or keel-shaped structure running apicobasally on the crown and, in some cases, on the root base, and typically corresponding to the cutting edge of the tooth (Hendrickx *et al.,* 2015b). The carinae can be divided in mesial or distal carina. Not every theropod teeth have carinae, as it occurs in some spinosaurids. Denticles can appear in the carena.
- A **denticle** is an elaborate type of serration corresponding to a projection of dentine covered with enamel along the carina

There is also a wide range of anatomical features that can help to determine and identify the isolated theropod teeth to the family level, sometimes even to the genus and species level. However, the tooth orientation and position on the jaw are much more difficult to resolve. The positional nomenclature broadly follows the one proposed by Smith and Dodson (2003):

- The direction towards the jaw symphysis is called **mesial**. It is also referred to the surface that faces the jaw symphysis.
- The direction towards or surface that faces the posterior end of the jaw symphysis referred as **distal**.
- The surface or direction pointing from the skull outwards, thus towards the lips or cheeks, is denominated **labial**.
- The surface and direction towards the skull midline, thus facing to the tongue, is called **lingual**.

Dentition can also be classified in mesial or lateral dentition. However, the differentiation between them is not relevant for spinosaurid teeth due to the fact that there is almost no variation among them (Hendrickx *et al.,* 2015b).

6.2.1. QUALITATIVE CHARACTERS

These are the features relating to or concerned with quality or qualities, and not quantities or amounts. The main characters used in this work are based on Alonso (2013) and Alonso and Canudo (2016).

- Tooth shape.
- Position of the carina.
- Presence or ausence of denticles, morphology and position.
- Crown ornamentation.

- Cross-section type: there is a diversity of possible shapes of the crown cross-section and it can be used not only to assign the tooth to the mesial or lateral dentition, but also to certain theropod clades (Hendrickx *et al.,* 2015b). However, it is very difficult to determine the crown position of the teeth within this family. The most important or common cross-section types that appear in the Spinosauridae dentition are the subcircular or the elliptical.
- Enamel texture.
- Teeth taphonomy and general condition.

6.2.2. QUANTITATIVE CHARACTERS

These are the features capable of being measured by quantity. Morphometric measurements are as important as the teeth anatomy or features so that different fossils can be compared. These measurements follow Smith *et al.* (2005) and Hendrickx *et al.* (2015b).

- **Crown Base Length (CBL)**: mesiodistal distance measured at the level of the cervix.
- **Crown Base Width (CBW)**: distance measured in the crown base at mid-length, perpendicular to the crown base length, and at the level of the cervix.
- **Crown Height (CH)**: apicobasal extent to the distal margin of the crown from the most distal part of the cervix to the apex.
- **Apical Length (AL)**: apicobasal extent of the mesial margin of the crown. It is taken from the most mesial part of the cervix to the apex (Smith *et al.,* 2005).
- **Crown Base Ratio (CBR)**: ratio expressing the labiolingual narrowness of the base crown and corresponding to the quotient of CBW by CBL (CBR = CBW / CBL).
- **Crown Height Ratio (CHR)**: ratio expressing the crown elongation and corresponding to the quotient of CH by CBL (CHR =CH / CBL).
- **Denticle mesial and distal density (MDD and DDD)**: the number of denticles per milimeter on the mesial and distal margins.

It ought to be considered that not every measure can be taken due to the preservation of the studied material.

7. SYSTEMATIC PALAEONTOLOGY

7.1. TEETH DESCRIPTION

The teeth are conical (cone-shaped), with a distally curved crown and a pointed apex. The tooth crown is subcircular or elliptical in cross-section, being only slightly compressed labiolingually. The surface of the crown is typically fluted. The carinae may be finely serrated, with chisel-shape denticles, or unserrated. They all show a usual anastomosed texture.

Two morphotypes can be distinguished in the Igea samples (Figure 12). The followed criteria are those used by Alonso and Canudo (2016) (see also Alonso, 2013).

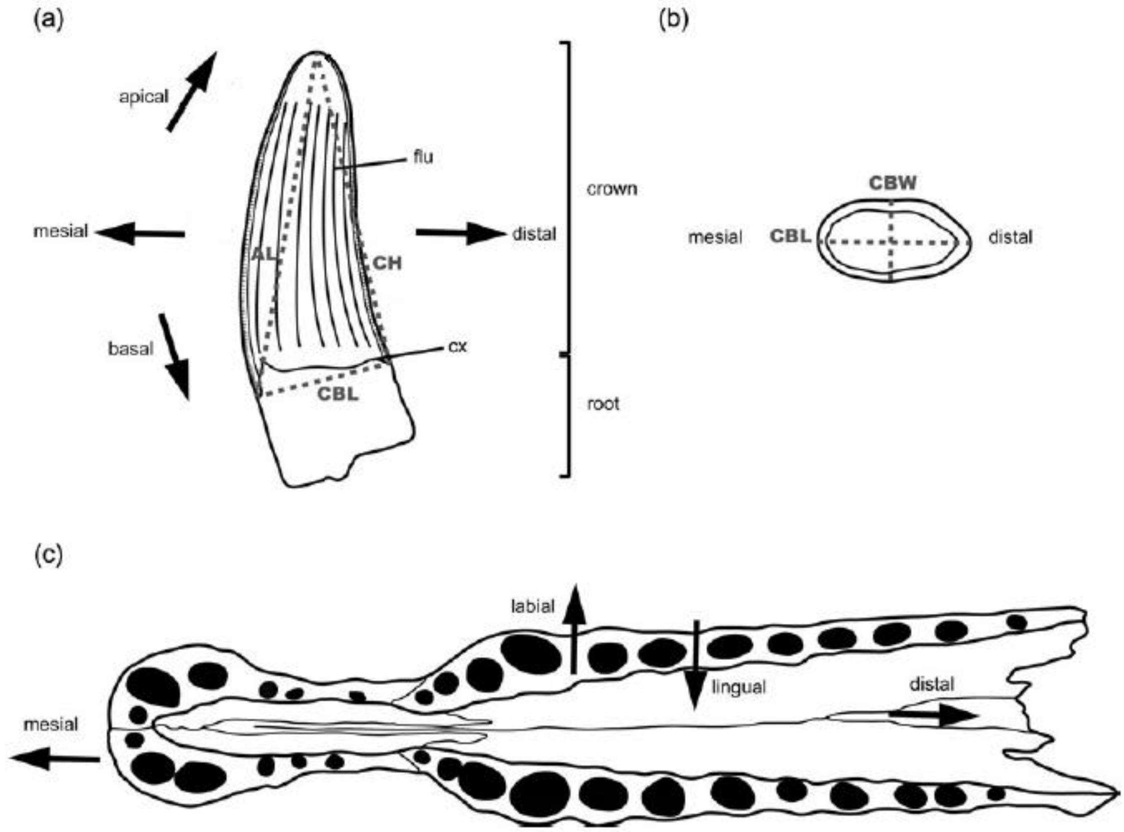


Figure 11. Positional and tooth nomenclature. (a) Spinosaurid tooth in lateral view. AL, Apical Length; CBL, Crown Base Length; CH, Crown Height; cx, cervix; flu, fluted enamel. (b) Cross-section of the tooth at the level of the cervix. CBW, Crown Basal Width; CBL, Crown Base Length. (c) Dorsal view of an upper jaw of *Spinosaurus*. Modified from Dal Sasso *et al.* (2005).

a. Morphotype 1

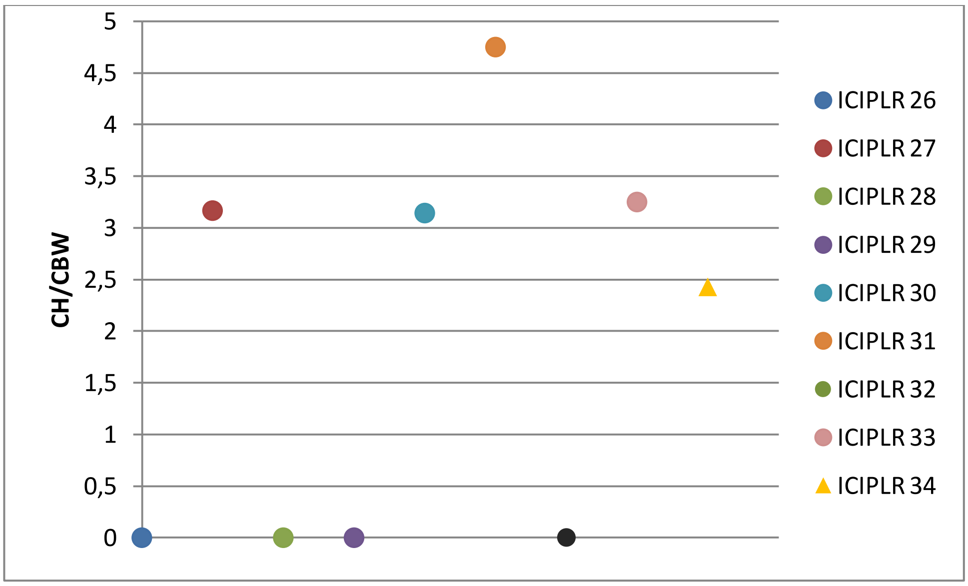
Teeth of Morphotype 1 show a variable state of preservation; hence not every anatomical feature could have been studied. The mesial side of the teeth is convex whereas the distal margin is concave. The labial side is convex and the lingual margin is straight. The cross section is elliptical. Crown height ranges from 14 to 30 mm. All the teeth contain mesial and distal carinae, though it is not preserved in all of them. Most of the teeth show serrations in both carinae, but some teeth do not have it in the mesial carina. Some of them do not have serration in any of the carinae; this may be due to taphonomical processes. Carinae are located on the mesiodistal axis of the crown, or very close to it, starting close to the cervix. Denticles are chisel-shaped. Denticle density per millimetre varies between 5 and 6. There is no difference between the mesial and the distal size of the denticles. The denticles are perpendicular to the margin of the teeth. Both faces of the teeth bear enamel ornamentation consisting of a maximum of 10 and a minimum of 5 flutes oriented apicobasally. The average number of the flutes is 8-9 in the labial surface and 7 in the lingual surface. The flutes start almost in the cervix and do not reach the apex.

Five fossil teeth from Igea (ICIPLR 26, ICIPLR 27, ICIPLR 30, ICIPLR 31 and ICIPLR 33) can be classified in this morphotype. Other teeth found in Igea are preliminarily included in this morphotype, but they show some differences. The fossil teeth ICIPLR 29 and ICIPLR 32 have a more subcircular cross section and a straight distal margin. With regard to the fossil teeth ICIPLR 28, it lacks enamel on a wide area of its surface, hence the ornamentation is lost. Furthermore, the apex it totally eroded. Nevertheless, its general morphology looks similar to that of other teeth of Morphotype 1.

b. Morphotype 2

The tooth ICIPLR 34 has been classified as Morphotype 2. This tooth does not show a very good state of preservation. The mesial side is convex, whereas the distal margin is concave. The labial side is convex and the lingual margin is concave. The cross section is subcircular. Crown height is 18 mm. The tooth only has a mesial carina, though it is partially conserved. It is located on the mesiodistal axis of the crown, starting close to the cervix. There is no apparent serration on it. Both faces of the teeth bear enamel ornamentation which consists of a maximum of 16 and a minimum of 14 flutes or ridges oriented apicobasally. The flutes or ridges start almost in the cervix and do not reach the apex.

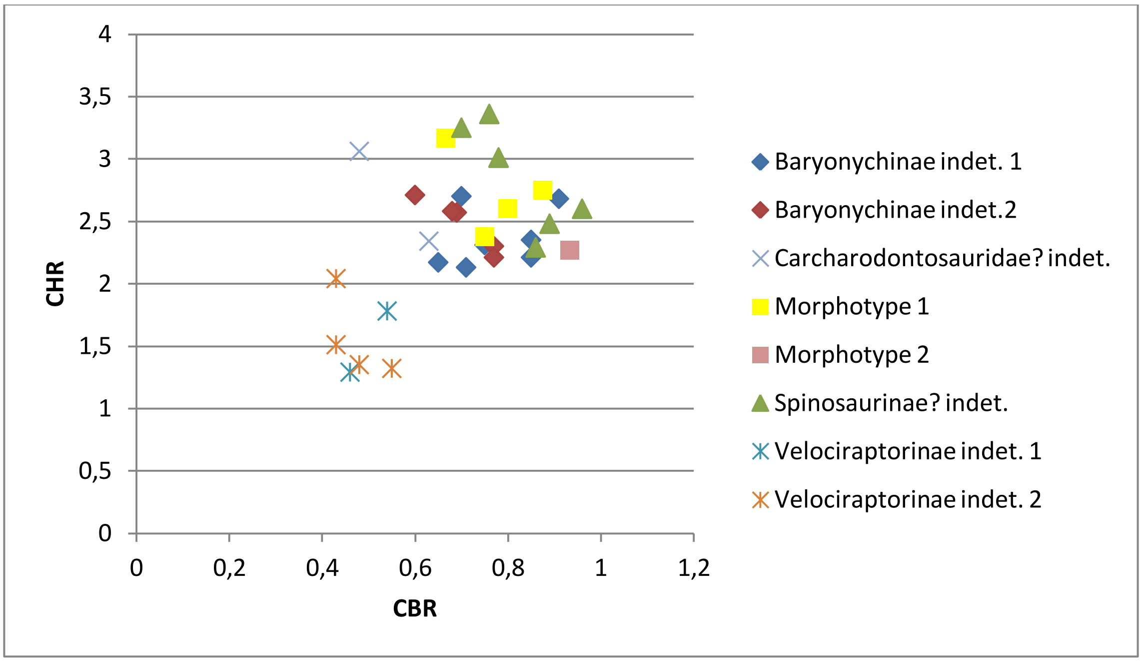
Furthermore, being aware of the scarcity of samples and its low representation, a biometric study has been attempted. The graphic 1 reveals the relation of the Crown Height (CH) and the Crown base width (CBW) (CH/CBW). The teeth ICIPLR 26, ICIPLR 28, ICIPLR 29 and ICIPLR 32 show a value of zero, because it is not possible to take these measures. The teeth ICIPLR 27, ICIPLR 30 and ICIPLR 33 (morphotype 1) show a similar ratio. The teeth ICIPLR 31 and ICIPLR 34 vary from the other values. The tooth ICIPLR 31 differs from the rest of the morphotype 1 samples because of its diagenetical compaction.



Graph 1. Relation of the Crown Height (CH) and the Crown base width (CBW) (CH/CBW) of the teeth found in Igea.

Figure 12. Baryonychinae dinosaur teeth from the fossil sites of Igea (La Rioja). 1: ICIPLR 27; 2: ICIPLR 28; 3: ICIPLR 26; 4: ICIPLR 30; 5: ICIPLR 29; 6: ICIPLR 31; 7: ICIPLR 32; 8: ICIPLR 33; 9: ICIPLR 34. a: labial; b: lingual; c: mesial and d: distal views. Scale bar: 1 cm.

The graphic 2 represents the relations between the Crown Height Ratio (CHR) and Crown Base Ratio (CH) of the studied teeth compared with the teeth studied by Alonso (2013). The fossil teeth of Igea show similarities with the Baryonychinae indet., morphotype 1 and Baryonychinae indet., morphotype 2 and Spinosaurinae? indet., but not with both morphotypes of Velociraptorinae indet. and Carcharodontosauridae? indet.



Graph 2. Relations between the Crown Height Ratio (CHR) and Crown Base Ratio (CH) of the studied teeth compared with the teeth studied by Alonso (2013).

7.2. DISCUSSION

Spinosaurid teeth, compared to other theropods, have a subcircular-elliptical cross section and an anastomosed texture. The crown is straight or slightly curved and conical shaped that have minute denticles or no denticles at all, and typically fluted surface (Hendrickx *et al.,* 2015b). Baryonychine teeth differ from the Spinosaurine teeth due to a more elliptical cross section and a more pronounced distal curvature (Alonso and Canudo, 2016).

The teeth found in Igea are referred to baryonychine spinosaurids as Baryonychinae gen. et. sp. indet. These morphotypes (Morphotype 1 and Morphotype 2) have fluted enamel on the labial surface, unlike *Baryonyx walkeri* from the Early Cretaceous of England (Charing and Miller, 1997). *Ostafrikasaurus crassiserratus* teeth from the Late Jurassic of Tanzania have larger denticles and, in consequence, a lower denticle density per mm (Buffetaut, 2012). Asiatic forms such as *Siamosaurus suteethorni* from the Early Cretaceous of Thailand have more ridges on the teeth surface (Buffetaut and Suteethorn, 1999). Other spinosaurids such as *Suchomimus tenerensis* from the Early Cretaceous of Niger (Sereno *et al.,* 1998) have a microgranular ornamentation on the edges of the tooth.

The baryonychine teeth found in Igea differ from the contemporaneous ones of the Blesa Formation found at the La Cantalera-1 (Alonso, 2013; Alonso and Canudo, 2016) site and of the Morella Formation of Castellón (Canudo *et al.,* 2008) because of the higher amount of flutes and the lower denticle density per mm. In some teeth, the presence or absence of denticles and its density on the mesial and distal carinae is difficult to determine due to the state of preservation. However, the observed features in baryonychine teeth from Teruel and Castellón are quite similar to those of the Morphotype 1. The flutes in Morphotype 2 are more abundant and thinner. It presents only a distal carena with no apparent serration.

Spinosaurid teeth from the Barremian-Aptian of the Wealden facies of Salas de los Infantes in Burgos (Torcida Fernández-Baldor *et al.*, 2003) have similar flutes and denticle density per mm, but a more circular cross section, compared with Morphotype 1 teeth of Igea.

8. CONCLUSIONS

Generally throughout the whole series, there is a widespread silicification in the rocks and fossils. Besides, some of the identified veins where filled with quartz. The origin of this process is unknown, also if it happened in the same process or in different ones.

According to the fossil remains, there is a clear low diversity in the area. Nevertheless, the remains are usually very abundant in the geological record, typical of fluctuating conditions. Generally, the data obtained during the field work suggests a fresh or slightly brackish nature of the limestones. Clapotage structures show a shallow coastal and wave dominated palaeoenvironment for the limestone origin, may be a coastal lake or lake with evaporation stages where limestones and marls deposited. The sandstones were also formed in the foreshore, comprehending the spreading of the fossil remains throughout the series.

The study of Barranco de La Cañada and Peña Cárcena suggests a clear transport of the fossils. This material is concentrated in the depressions of the limestones, so probably once the limestone was partially lithified or because of the big cohesion of the muddy sediments, a current transported the sediment and vertebrate remains from the land to the site, depositing them in the depressions of the layer, where there was a wave dominancy. In La Era del Peladillo 6 and Umbría de Costarrey 1 there is no transport evidence. However, no further interpretations can be done.

The fossils associated to each fossil site are: pterosaur remains, fish scales, *Lepidotes* teeth, dinosaur tracks and gastropods in Barranco de La Cañada, ichnites and fish remains in La Era del Peladillo 6, fish scales and teeth, bone splinters, a theropod tooth and indeterminate bones in Peña Cárcena and dinosaur ichnites in Umbría de Costarrey.

Nine isolated theropod teeth have been studied in the four fossil sites of the Lower Cretaceous (Barremian-Aptian) of Igea. These teeth belong to spinosaurids. The study has showed two morphotypes that are assigned to a Baryonychinae, but not to Baryonyx. The Morphotype 1 is similar to other baryonychid teeth described in the Iberian Peninsula (Teruel, etc.). The Morphotype 2 is only represented by a single tooth, but it could belong to a different taxon. This can only be verified with the finding of new material. The prospective work hypothesis is that two species of baryonychid could be represented in Igea.

The bivariant analysis of CBR-CHR has helped to locate the studied teeth in a correct taxonomic position comparing the measures with other databases. This analysis shows the general morphology of the teeth and has proved to be a useful tool when it comes to discriminating between the teeth of different theropod groups. However, it does not discriminate at the morphotype level because these are based on specific qualitative or quantitative characters that are not expressed in the bivariant analysis.

The results obtained with biometric and statistical analysis are consistent with each other and do not contradict the systematics performed. On the contrary, they support in a quantitative way the classification established at a more than general level. The lack of teeth samples for the Morphotype 2 does not allow to discriminate between both morphotypes, whereas a relationship between the Morphotype 1 teeth has been established.

It should also be noted that postcranial (and cranial?), including vertebrae, a hind limb and a presumable humerus of spinosaurid have been found in the same area and whose studies are yet to be done. At least in some sites (Barranco de La Cañada, La Era del Peladillo 6 and Umbría de Costarrey) the material of spinosaurids (body fossils) appears associated with theropod and other dinosaur ichnites, something that is not common in the dinosaur record.

To conclude, the area studied during the field work has provided a lot of information of different geological fields. Unlike other deposits found in the Iberian Peninsula, dinosaur tracks and fossil bodies are common in Igea, so the potential in Vertebrate Palaeontology is tremendous.

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11. ANNEX 1: QUALITATIVE AND QUANTITATIVE FEATURES OF THE STUDIED TEETH.

	ICIPLR 26	ICIPLR 27	ICIPLR 28	ICIPLR 29	ICIPLR 30	ICIPLR 31	ICIPLR 32	ICIPLR 33	ICIPLR 34
SHAPE									
Mesial	convex	convex	*	convex	convex	convex	convex	convex	convex
Distal	concave	concave	*	strike	concave	concave	strike-concave	concave	concave
Labial	convex	convex	*	convex	convex	convex	missing	convex	convex
Lingual	missing	strike	*	strike	strike	strike	strike	strike	concave
Cross section	elliptical	elliptical	elliptical	elliptical-subcircular	elliptical	elliptical	elliptical	elliptical	subcircular
Crown Base Length (CBL)	14mm	8mm	8mm	*	8mm	9mm	9mm	5mm	7,5mm
Crown Base Width (CBW)	*	6mm	5mm	6mm	7mm	6mm	*	4mm	7mm
Crown Height (CH)	30mm	19mm	*	19mm	22mm	19mm	14mm	13mm	18mm
Apical Length (AL)	31mm	21mm	*	20mm	20mm	20mm	17mm	10mm	17mm
Crown Base Ratio (CBR)	*	0,75	0,63	*	0,88	0,67	*	0,8	0,93
Crown Height Ratio (CHR)	2,14	2,38	*	*	2,75	3,17	2	2,6	2,27
Denticle Density (DD)	*	5-6 denticle/mm	*	*	*	*	5 denticle/mm	*	*
CARINA									
Distal	yes	yes	no	no	yes	yes	yes	yes	no
Mesial	yes	yes	no	*	yes	*	yes	*	yes
Serration	no apparent	distal and mesial	no	no	distal and mesial	no apparent	distal	*	no apparent
Denticles	no	yes	no	*	yes	no	yes	no	no

(*): no information