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José-Carmelo Corral, Ana Berreteaga, Francisco José Poyato-Ariza, Nathalie Bardet, Henri Cappetta, Marc Floquet, Humberto Astibia, Ainara Badiola, Xabier Pereda-Suberbiola

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ABSTRACT

The Quintanilla la Ojada section (Basque-Cantabrian Region, northern Spain) has yielded two assemblages of Late Cretaceous vertebrates, deposited during the Maastrichtian in coastal environments and related to a transgressive *lag* at the base of the Valdenoceda Formation. Numerous teeth of Elasmobranchii and Actinopterygii are the most prevailing fossil material, although scarce teeth of marine reptiles (Mosasauridae) and dinosaurs (Hadrosauridae) also occur. The presence of one hadrosaurian tooth, a terrestrial taxon, constitutes the first report of ornithischians in the Valdenoceda Formation. The fossil vertebrate association of Quintanilla la Ojada is similar to that discovered in Albaina (Treviño County, Burgos), also located in the Basque-Cantabrian Region, although relatively younger in age. Both fossil sites are characterised by a mixture of taxa from the northern and southern margins of the Mediterranean Tethys (north-European and north-African outcrops).

KEY WORDS
Noselachians,
actinopterygians,
mosasaurids,
hadrosaurians,
Maastrichtian,
Iberian Peninsula.

RÉSUMÉ

Stratigraphie, âge et paléontologie des vertébrés du gisement finicrétacé de Quintanilla la Ojada (Région Basco-cantabrique, Nord de l'Espagne) : une synthèse.

La coupe de Quintanilla la Ojada (Région Basco-Cantabrique, Nord de l'Espagne) a livré deux assemblages de vertébrés d'âge Crétacé supérieur, déposés durant le Maastrichtien dans des environnements côtiers et liés à un *lag* transgressif situé à la base de la Formation Valdenoceda. De nombreuses dents d'Elasmobranchii et d'Actinopterygii sont les plus fréquentes, bien que de rares dents de reptiles marins (Mosasauridae) et de dinosaures (Hadrosauridae) aient aussi été trouvées. La présence d'une dent d'hadrosaure, taxon terrestre, constitue la première mention d'ornithischiens dans la Formation Valdenoceda. L'association de vertébrés fossiles de Quintanilla la Ojada est similaire à celle découverte à Albaina (Comté de Treviño, Burgos), situé également dans la région Basco-Cantabrique, bien que d'âge légèrement plus jeune. Les deux sites fossilifères sont caractérisés par un mélange de taxons des marges nord et sud de la Téthys méditerranéenne (affleurements du Nord de l'Europe et du Nord de l'Afrique).

MOTS CLÉS
Néosélaciens,
actinoptérygiens,
mosasauridés,
hadrosauridés,
Maastrichtien,
Péninsule ibérique.

INTRODUCTION

Until relatively recently, our palaeontological knowledge of the Valdenoceda Formation was generally sparse, both in terms of micro- and macroinvertebrate studies. Microvertebrate fossils were described for the first time by Berreteaga (2008) from this Maastrichtian formation near the small village of Quintanilla la Ojada (Burgos, northern Spain). A few years later, this area was studied by Berreteaga *et al.* (2011) and Corral *et al.* (2015b), who described teeth and other small skeletal remains of actinopterygian and elasmobranch fishes recovered from a grey clayey dolostone unit at the base of this formation. Prior to this, marine vertebrate diversity from the western Pyrenees during the Maastrichtian was mostly documented from faunal assemblages reported by Bardet *et al.* (1999), Cappetta & Corral (1999) and Poyato-Ariza *et al.* (1999) from the Torme Formation at the fossil locality of Albaina in the Basque-Cantabrian Region (Treviño County municipality, Burgos). The vertebrate faunal content observed in Quintanilla la Ojada is similar to that in the Albaina deposits; however, the latter accumulated in more open-marine waters (see synthesis in Martín-Chivelet *et al.* 2019).

The productive beds within the Maastrichtian Valdenoceda Fm are exposed in two adjoining pits, which have been quar-

ried intermittently for silica sand, an exploratory trench and a road cut, all located near the village. More specifically, the pits lie in a narrow valley, southeast of the village, flanked by the Vienda Mountain Range to the east and the hilly area of the periclinal closure of the La Hoz-Lalastra anticline to the west. Nearby towns to the site are Villarcayo, Medina de Pomar and Trespaderne (see Fig. 1).

The aim of this paper is twofold. First, it is to introduce the vertebrate taxa discovered at the site of Quintanilla la Ojada, focusing on their palaeontological significance. Second, we present the remains of two other vertebrate groups that have not been described before, namely marine reptiles (mosasaurids) and dinosaurs (hadrosaurids).

GEOLOGICAL SETTING

The Quintanilla la Ojada site is located in the north-eastern flank of the Villarcayo Syncline (abbreviated as VY in Fig. 1), within the west-central part of the Basque-Cantabrian Region. This structure and surrounding folded areas are related to the Castilian Ramp domain, which broadly represents the distal part of a ramp-like platform developed in the Basque-Cantabrian Basin (northern continental palaeomargin of the

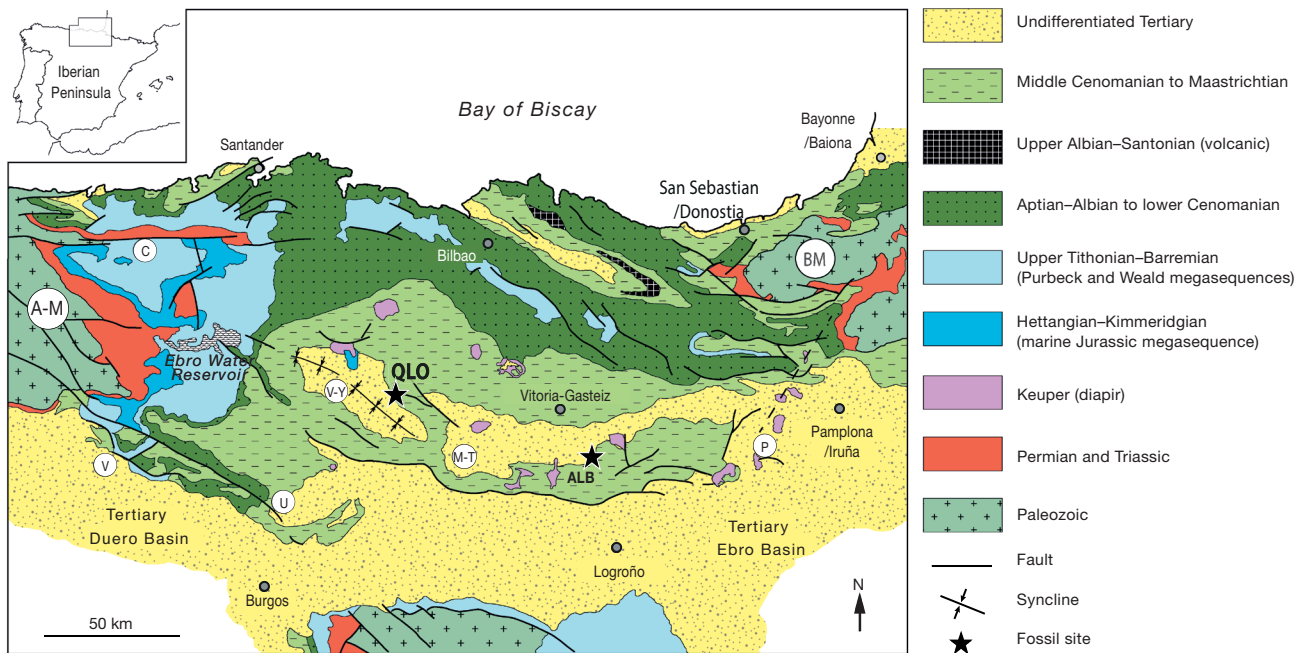


FIG. 1. — Generalized geological map of the Basque-Cantabrian Region (located in the insert map of the Iberian Peninsula). The star shows the location of the Quintanilla la Ojada site (QLO) from which vertebrate fossils were collected. Albaina site (ALB) has been included for reference. Abbreviations: **AM**, Asturian Massif; **BM**, Basque Massifs; **C**, Cabuerniga fault; **M-T**, Miranda-Treviño syncline; **P**, Pamplona fault; **U**, Ubierna fault; **V**, Villela fault; **VY**, Villarcayo syncline. Modified from Berreteaga *et al.* (2011).

Iberian plate) (Feuillée & Rat 1971; Floquet 1991). The exposed Upper Cretaceous to Paleogene sequence, which is about 900–1000 m thick in the northernmost area of this palaeogeographical domain, consists of siliciclastic and shallow marine carbonate rocks arranged in transgressive-regressive cycles (Floquet 1991, 1998; Berreteaga 2008).

The regression trend in the Basque-Cantabrian Basin during the Latest Cretaceous time resulted in the progradation of siliciclastic systems and the development of shallow marine environments which were inhabited by a varied fauna of chondrichthyan and osteichthyan fishes (López-Horgue & Poyato-Ariza 2005). Three formations have been formally designated by Floquet *et al.* (1982) to include Maastrichtian aged marine strata in the central-western part of the basin, namely (from older to younger): the Valdenoceda, Sobrepeña and Torme formations. Floquet *et al.* (1982: 433–434) named the Valdenoceda Formation for exposures of bioturbated limestone, in part dolomitized, deposited in a shallow subtidal to intertidal lagoonal environment during the early Maastrichtian. This succession organised into many superimposed upward-shallowing parasequences that contain rudists, gastropods and benthic foraminifera. The following carbonate microfacies types have been observed in the formation: packstone-rudstone, packstone-wackestone and wackestone-mudstone (see Berreteaga 2008).

GENERAL DESCRIPTION OF UNITS OBSERVED

The lower part of the Quintanilla la Ojada section (Fig. 2A) consists of bioclastic calcarenites that include green and red

algae, foraminifers, and ostracods, in addition to marine fossil macroinvertebrates such as sponges, bryozoans, brachiopods, molluscs (bivalves and gastropods), serpulids, echinoderms, and crustaceans (Floquet 1991). These calcarenite rocks correspond to the uppermost part of the Tubilla del Agua Formation (defined by Floquet *et al.* 1982), which is dated latest Santonian on the basis of its foraminifera and ammonite content (Floquet 1991, 1998; Gräfe 2005). Upwards, the series shows a gradual facies-transition to the frontal deltaic siliciclastic rocks of the Rioseco Member (Moradillo de Sedano Fm) – described by Floquet (1991) and named after the Rioseco section in the southern limb of the Villarcayo Syncline – and to the Sedano Formation (named by Floquet *et al.* 1982). Although the basal beds are not easily recognised at the outcrop, the “Rioseco-like facies” are composed of well-rounded quartz conglomerate and coarse-grained sandstone beds, arranged in metre-scale tabular sets with trough cross-stratification, which are interbedded with very thin laminated greenish siltstones (cm-thick beds). This siliciclastic unit (up to 60 m thick) shows noticeable thickness variations across the northern limb of the Villarcayo Syncline, in general decreasing in thickness to the northwest and southwards. The “Rioseco-like facies” in the Quintanilla la Ojada section represents the deposits of the Rioseco coastal system, which correlates with parts of the Moradillo de Sedano, Quintanaloma, and Sedano formations (Fig. 2B) (Floquet *et al.* 1982; Floquet 1991, 1998; Berreteaga 2008). These three formations are interpreted to represent a prograding deltaic system, including a distal delta front, a rudist

barrier framework and a deltaic plain setting, respectively (see Floquet 1991: fig. 215, p. 616; Berreteaga 2008).

The “Rioseco-like” rocks are irregularly overlain by mudstones and coarse pebble conglomerates, with occasional marine vertebrate remains (named QLO1 bed) (see Figs 2A; 3A). These beds do not exceed 50 cm in thickness. The basal discontinuity is interpreted as a transgressive surface associated with ravinement processes, which can be correlated with the basal boundary of the transgressive-regressive depositional cycle (hereafter T-R cycle) DC12 – one of the many T-R cycles defined by Floquet (1998) within the Castilian Ramp (Fig. 2B). The transgressive phase of T-R cycle DC12 of Floquet (1998) is represented by the overlying sandy dolomites and organic-matter-rich mudstones with euhedral pyrite, organised in upward thinning, metre-scale sequences (see Fig. 3B). A particular bed (named QLO2 bed, Fig. 2A) of bioturbated dolomitized carbonates, occurring within the two first metres of the lower part of the Valdenoceda Fm and above the unconformable upper boundary of the Rioseco Member, is relatively fossiliferous, including scattered skeletal remains of fossils vertebrates, cheliped fingers of marine decapods and pyritized orbitoids (Berreteaga 2008; Berreteaga *et al.* 2008b). Upwards, a massive dolomite body (30–40 m thick) overlies these parasequences. Both basal parasequences and the overlying dolomite body are regarded by their sequence architecture as being laterally equivalent deposits of the Valdenoceda Fm, the age of which is thought to be late early Maastrichtian or early late Maastrichtian (Floquet *et al.* 1982; Floquet 1991), according to its rudistid fauna around its type locality (Berreteaga 2008; Berreteaga *et al.* 2010). After a gradual increase in the clay fraction of the dolomite, the series passes into variegated mudstones (about 30 m in thickness) assigned to the Sobrepeña Formation and considered to be upper Maastrichtian based on charophytes (Floquet 1991; Berreteaga *et al.* 2008a). Upwards, this unit is overlain by a series of characteristic whitish dolomitic marlstones with oolites and stromatolites, which are assigned to the Escaño Formation (named by Pluchery 1995), and aged Danian in the regional stratigraphical framework.

MATERIAL AND METHODS

Since the sand pits in the locality are operated intermittently, access to the most productive fossil-bearing layers is not always possible. Only a few teeth were collected *in situ*, being most of them obtained by hand picking on spoil piles coming from identified strata. The fossil locality includes a less productive horizon QLO1 (i.e., a conglomerate unit representing a transgressive lag deposit in between the underlying “Rioseco-like facies” and the Valdenoceda Fm) and several stacked parasequences of fossil-rich sandy carbonate (QLO2), which are common in the lower part of the Valdenoceda Fm, where most of the fossil vertebrates come from.

Large vertebrate specimens visible to the naked eye were directly surface-collected from the quarry face strata, but more often from spoil-piles. In that regard, the assemblage QLO1 is biased by the collecting methods (sampling of larger specimens). Most of the fossil remains, however, were recovered by

wet sieving over 300 kg of friable sandy carbonate rock from QLO2 beds (mesh sizes: 2 mm, 0.7 mm, 0.5 and 0.25 mm). Preliminary sorting and identification of the vertebrate microremains were carried out in the laboratory using a stereomicroscope. Further information is given in Berreteaga *et al.* (2011) and Corral (2018).

A limited number of fish remains from QLO2 and their sedimentary host rock have been analyzed using inductively coupled plasma mass spectrometry (ICP-MS) for their rare earth element (REE) content in order to ascertain the amount of taphonomic mixing (Berreteaga 2008). The taphonomic model for the site is based on general observations of skeletal elements of neoselachians (Corral *et al.* 2015b; Corral 2018) and actinopterygians (Berreteaga *et al.* 2011). Taxonomic assessment of the actinopterygian teeth is mostly made at higher-rank level. This is principally because the abrasion process on some of these fossils, and because they occur as isolated teeth. However, these fossil elements of actinopterygians have been categorized according to their different morphotypes, thus providing useful palaeoecological information (Poyato-Ariza *et al.* 1999; Berreteaga *et al.* 2011).

Most of the material was collected between 2000 and 2006 by E. Iriarte, one of the co-authors (A.Be.) and other parties associated with the Universidad del País Vasco (UPV-EHU) (see Berreteaga 2008). Additionally, further fieldwork over the last decade by the first author (J.-C.C.) has produced new material and supplementary data (see Corral 2018).

The fossil specimens discussed in this paper are housed and catalogued at the Arabako Natur Zientzien Museoa/Museo de Ciencias Naturales de Álava (MCNA) at Vitoria-Gasteiz, Spain. Fossil actinopterygians, formerly with the acronym EHUEP in Berreteaga *et al.* (2011) were transferred to the collections of the MCNA at the end of 2018, and given a museum number (see Appendix). Additionally, two replica specimens of a hadrosaurid tooth and a well preserved mosasaurid tooth crown, the original of which are held in a private collection (J.I. Sáez Laría, referred by the acronym JISL), have been accessioned to the palaeontological collection of the MCNA, so they can be further examined by visiting palaeontologists.

ABBREVIATIONS

Repository and institutional abbreviations

EHUEP	Euskal Herriko Unibertsitatea, Estratigrafía-Paleontología.
MCNA	Arabako Natur Zientzien Museoa/Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz;
UPV-EHU	Universidad del País Vasco/Euskal Herriko Unibertsitatea, Leioa (Bizkaia).

Private collection

Coll. JISL	J.I. Sáez Laría, Vitoria-Gasteiz.
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Abbreviations for geological descriptions

DC	depositional cycle;
ICP-MS	inductively coupled plasma mass spectrometry;
QLO1	Quintanilla la Ojada (Burgos), bonebed 1;
QLO2	Quintanilla la Ojada (Burgos), bonebed 2;
Rf	Rioseco facies;
REE	rare earth element;

T-R transgressive-regressive;
VNF Valdenoceda Formation.

TAPHONOMIC OBSERVATIONS

The vertebrate remains found at Quintanilla la Ojada are accumulated in the two distinct QLO1 and QLO2 fossil bonebeds, with inequality in the number of taxa present (see below). Both bonebeds have produced isolated skeletal elements, chiefly teeth under 2.5 cm.

Some of the elasmobranch teeth are preserved with their root partly or completely abraded as it commonly occurs in many other fossil sites, since osteodentine tissue is less hard than enameloid. Furthermore, some teeth of batomorph elasmobranchs occasionally exhibit occlusional wear (related to food crushing-grinding) which may be enhanced by natural abrasion before final burial. In general, selachian elements from bonebed QLO1 (containing five taxa) show a typical reddish brown mineralisation (Fig. 4A). The main taphonomic features observed in these specimens are abrasion wear (non-feeding related), which occurs along the crown edges and the root, post-burial damage due to compaction (e.g. cracking and cuspal fractures) and the presence of long vertical cracks (analogue structures to craze lines) affecting the enameloid enhanced by recent weathering. Elements from this assemblage range from grades 2-3 in Vullo's (2007) five-grade abrasion scheme, that is, most commonly complete teeth with light abrasion to incomplete teeth lacking part of the root elements. Their grade of abrasion and completeness are the result of the lithology and sedimentary facies of the deposit, indicating a high-hydrodynamism depositional setting. Thus, the QLO1 fossil bone assemblage corresponds to a lag concentration *sensu* Kidwell (1991), being characterised by having almost well preserved and eroded elements, the latter of which were purportedly supplied through exhumation and erosional resedimentation of laterally deposited sediments (Corral *et al.* 2015b). Elasmobranchs in the fossil bone assemblage QLO2 (containing 16 taxa) are mainly represented by isolated greyish black teeth (Fig. 4B), although a single dermal denticle of *Rajiformes* indet. has been also found. Taphonomic states, acquired after tooth shedding, include blunted cutting-edges, light polish, longitudinal breakage (with breaking off parts showing rounding of the fracture edges) and different grade of abrasion, unrelated to feeding, which is better observed in the less resistant dental tissues. Fossil diagenetic fractures are also visible in some elements of the assemblage. In addition, diagenetic pyrite in the porous osteodentine tissue and on the tooth surface was formed after burial in a reducing environment. Thus, the younger assemblage QLO2 is graded 1-3 in terms of Vullo's (2007) scheme, that is, a mixture of generally complete and incomplete, variably abraded teeth. QLO2 seems to represent an unsorted assemblage of relative high density elements because it includes both large and microscopic teeth, lacking other lighter skeletal elements such as vertebrae. Additionally, it seems to represent a "within-habitat time-averaged assemblage" (Kidwell 1998), as accumulations of this kind include mixed representatives from a single persistent community (Corral *et al.* 2015b).

Actinopterygian remains from the QLO2 fossil bone assemblage are represented by isolated elements, mostly teeth and a few fin spines. Other low density skeletal elements of actinopterygians, such as vertebrae, are lacking. This particular feature gives the idea of complete body disarticulation and, probably as well, intense selective transport of the skeletal parts as well (Berreteaga *et al.* 2011). This is supported by observation of post-mortem abrasion facets in the teeth of these fishes. Indeed, 95% of the teeth show a moderate to advanced abraded stage, according to Vullo's (2007) scheme, thus indicating heavy transport. Transport must have been produced during the biostratinomic phase, since the results of the geochemical analysis (e.g. distribution of rare earth elements) in the tooth samples allow to reject the hypothesis of taphonomic re-elaboration (Berreteaga 2008).

REVIEW OF VERTEBRATE FAUNAS OF THE VALDENOCEDA FORMATION

The Valdenoceda Fm at Quintanilla la Ojada has yielded a remarkable collection of isolated teeth and, to a lesser extent, skeletal remains of marine and continental Maastrichtian vertebrates (approximately 396 specimens identified, most to genus and species) (Table 1). At least 27 taxa have been recognised in the vertebrate fossil assemblage QLO2 according to estimates by Berreteaga *et al.* (2011), Corral *et al.* (2015b) and new data included in the present work. The aggregate composition is dominated by marine elasmobranchs (super-orders Galeomorphii and Batomorphii), accounting for about 45.4% (n=180) of the collected elements, and actinopterygian fishes (pycnodontiforms, amiiforms, elopiforms, aulopiforms and acanthomorphs), representing nearly 53% (n=209) of the total sample. Other vertebrate remains in the fossil assemblage QLO2 include mosasaurids and one dinosaur, but they are extremely rare (less than two per cent of the whole sample) (Fig. 5).

ELASMOBRANCHS

The Quintanilla la Ojada fauna of Elasmobranchii is represented by five orders, 11 families and 11 genera (Table 1). Their remains predominantly consist of teeth (Figs 6; 7A-N, Q-X), but dermal denticles are also known (Fig. 7O, P). This material has been formally described by Corral *et al.* (2015b).

The relatively diverse lamniform component of the selachian fauna (see Table 2) includes anacoracid, otodontid, odontaspidid and serratolamnoid sharks. The anacoracid genus *Squalicorax* Whitley, 1939, of infrequent occurrence, is represented by the species *Squalicorax pristodontus* (Agassiz, 1843), *S. kaupi* (Agassiz, 1843) and *Squalicorax* sp. Teeth of *S. pristodontus* are distinctive in that the crown is broad triangular with convex mesial and straight, or slightly concave, distal margins, cutting edges are crenate (round-toothed), and serrations are strong, increasingly asymmetrical towards the base of the crown (Fig. 6A-B). Other tooth material with a triangular crenate crown is referred to *S. kaupi* (Fig. 6C-D). The teeth of *S. kaupi* are

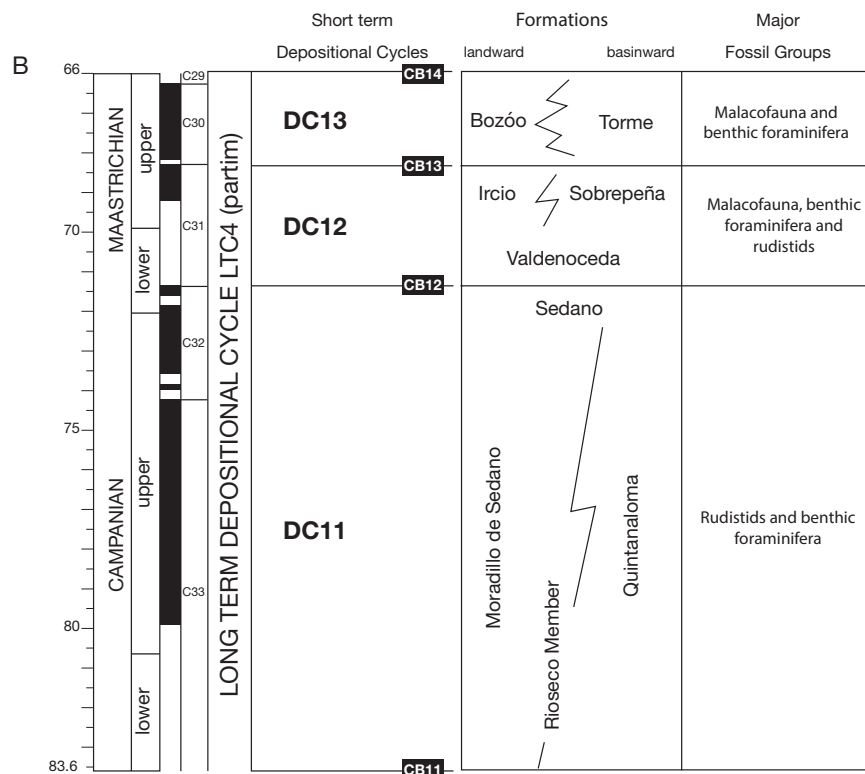
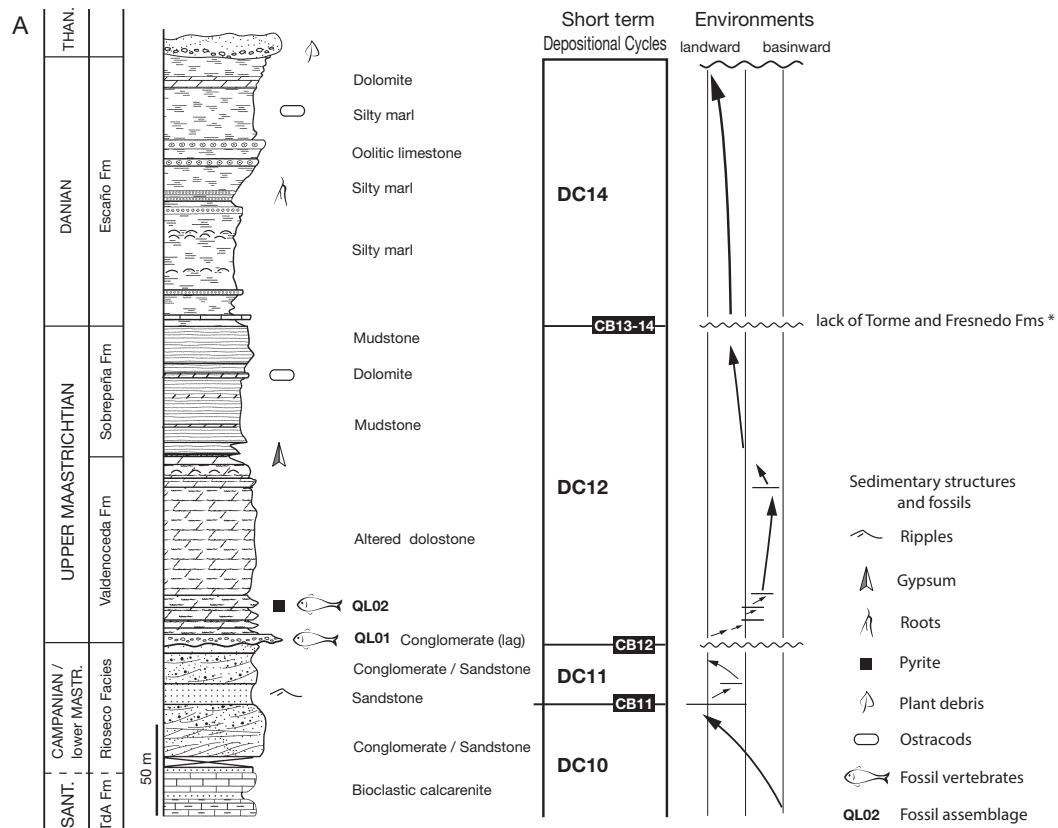


FIG. 2. — **A**, Generalized stratigraphic column for the Campanian-Maastrichtian at Quintanilla la Ojada (Burgos, Spain); the “Rioseco-like” facies includes the Moradillo de Sedano Formation and units equivalent to the Quintanaloma and Sedano formations (modified after Corral *et al.* 2015b); **B**, Uppermost Cretaceous transgressive-regressive (T-R) cycles, stratigraphic formations and the major fossil groups in the northern domain of the Castilian Ramp (modified after Floquet 1998). Key: (*) after Pluchery (1995), Berreteaga (2008); **DC**, depositional cycle; **CB**, cycle boundary; **SANT.**, Santonian; **TdA Fm**, Tubilla del Agua Formation.



FIG. 3. — Facies associations of the Valdenoceda Formation as exposed at the Quintanilla la Ojada sand pits (from Corral 2018): **A**, Pit exposure showing the cross-bedded sandstone of the “Rioseco facies” (**Rf**) that is overlain by a basal lag deposit (QLO1) and several stacked parasequences of sandy carbonates included within the Valdenoceda Fm; **B**, Metre-scale carbonate parasequences within the basal part of the Valdenoceda Fm (VNF), including the one containing the fossil-rich deposit QLO2. Key: **SB**, sequence boundary. Scale bar (arrowed): 2 m.



FIG. 4. — Tooth specimens of the anacoracid shark *Squalicorax pristodontus* (Agassiz, 1843) showing characteristic mineralisation and different taphonomic states. **A**, from assemblage QLO1, MCNA 15158; **B**, from assemblage QLO2, MCNA 15150. Photographs taken from Corral (2018).

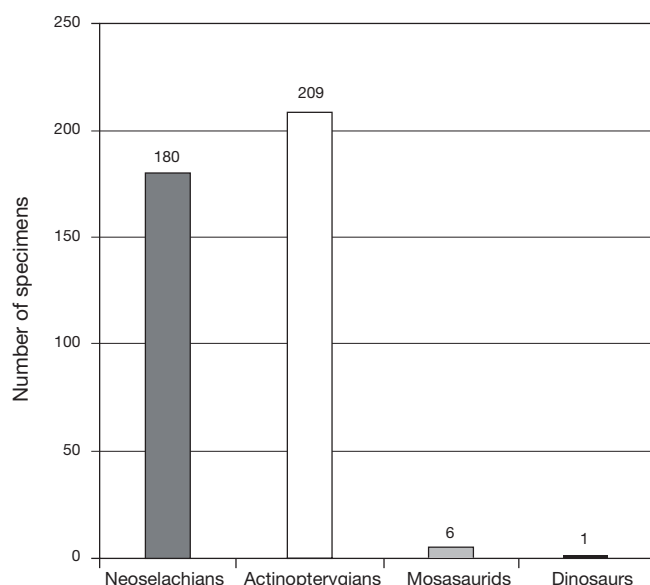


FIG. 5. — Bar graph showing number of elements of the higher vertebrate groups identified at Quintanilla la Ojada (**left**). Pie chart showing relative representation of these groups (**right**). Graphs are based on number of individual elements found at the site.

relatively smaller than those of *S. pristodontus* and clearly different in having a distinct distal heel at the base of the crown (in contrast to the concave distal crown margin of *S. pristodontus*). In addition, crown serrations are smaller and more symmetrical than those observed in *S. pristodontus* (Cappetta & Case 1975). Only a few teeth, which are similar in overall shape to those of *S. kaupi*, are tentatively referred to *Squalicorax* sp. on the basis of having double crenate cutting edges (Fig. 6E-F). A small-sized tooth,

which is referred to *Cretolamna* sp. aff. *C. appendiculata* (Agassiz, 1843) (Fig. 6G-H), is the only otodontid taxon found in the assemblage. This specimen shows a broaden cusp flanked by a pair of low, broad lateral cusplets, corresponding to an anterior tooth position. Two odontaspisid taxa are recognised, namely *Carcharias heathi* Case & Cappetta, 1997 (Fig. 6K-L), the teeth of which occur uncommonly, and *Carcharias* sp. (Fig. 6M-N), identified from one small parasymphyseal and one intermediate teeth. Since the latter are highly modified teeth, they may well correspond to the only odontaspisid species found in the Quintanilla la Ojada assemblages. The teeth of *Carcharias heathi* as described by Case & Cappetta (1997) are medium-sized with a triangular, isosceles shaped crown that is sigmoidal in profile. Cutting edges do not reach the base of cusp in anterior tooth rows. These specimens typically show two lateral cusplets (shorter in lateral teeth) that flank the main cusp. The labial boundary of the enameloid crown slightly overhangs the root and in some specimens it has a V-shape. A shallow groove is located in the weak lingual protuberance of the root. The serratolamnoid *Serratolamna serrata* (Agassiz, 1843) is a relatively common taxon in bonebed QLO2 (Fig. 6I-J). These teeth are easily distinguishable by their smooth crown with continuous cutting edges. Two pairs of small diverging cusplets (with an additional third distal cusplet on some lateral teeth) flank a slender triangular cusp, which can be either symmetrical (in anterior and anterolateral tooth positions) or slanted towards the commissure (in lateral and posterior positions). The teeth show a rectangular root, flattened labiolingually, with two asymmetric lobes (see Case & Cappetta 1997).

All carcharhiniform teeth belong to the family Triakidae and are referred to *Palaeogaleus faujasi* (Geyn, 1937) (Fig. 6O-P).

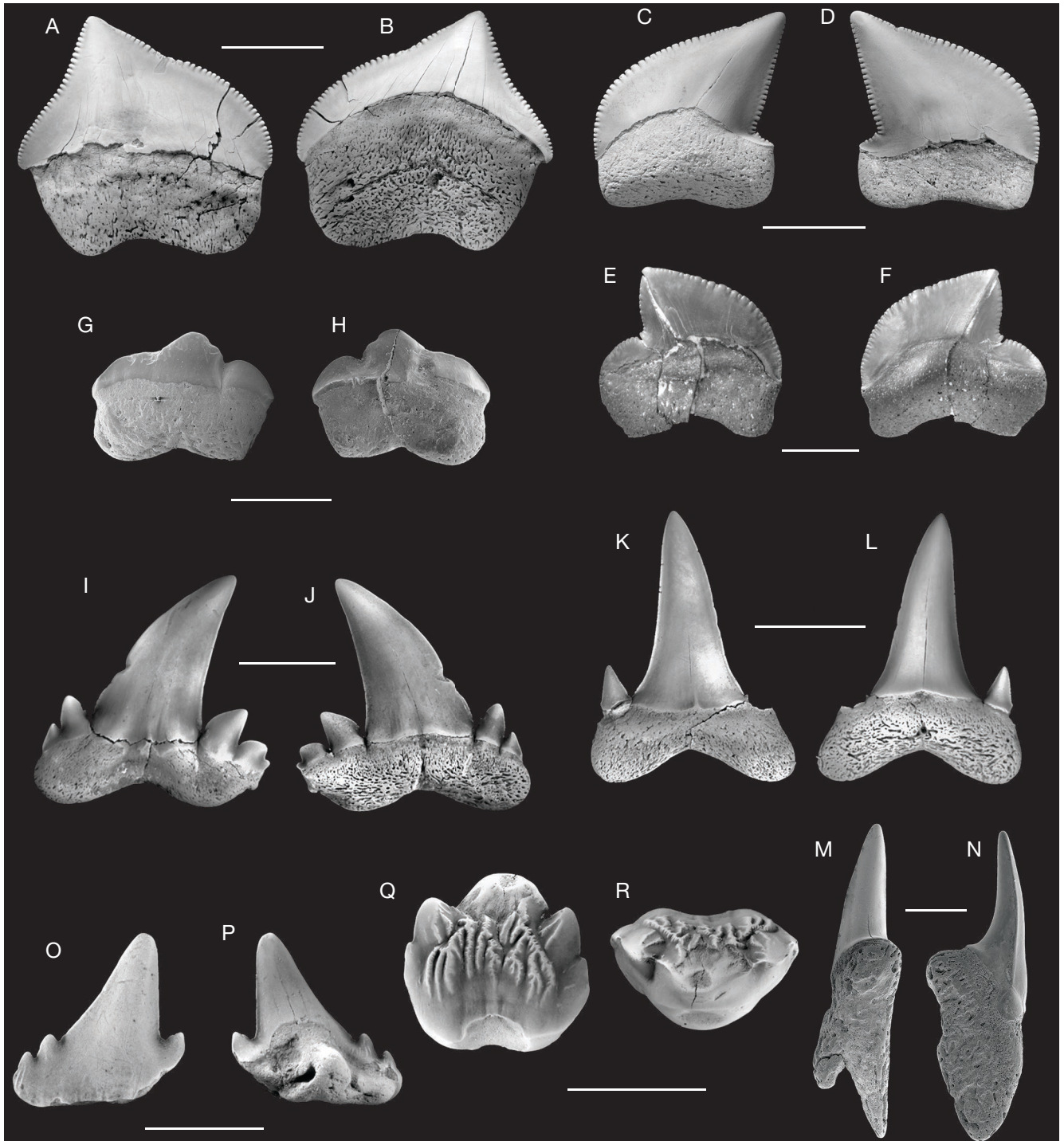


FIG. 6. — Selection of neoselachian sharks from the Maastrichtian Valdenoceda Formation at Quintanilla la Ojada, Burgos (modified from Corral *et al.* 2015b). **A, B**, *Squalicorax pristodontus* (Agassiz, 1843); Lateral tooth in labial (A) and lingual (B) views, MCNA 14811; **C, D**, *Squalicorax kaupi* (Agassiz, 1843), lateral tooth in lingual (C) and labial (D) views, MCNA 14690; **E-F**, *Squalicorax* sp., anterolateral tooth in labial (E) and lingual (F) views, MCNA 14693; **G, H**, *Cretolamna* sp. aff. *Cretolamna appendiculata* (Agassiz, 1843), anterior tooth in labial (G) and lingual (H) views, MCNA 14802; **I, J**, *Serratolamna serrata* (Agassiz, 1843), upper lateral tooth in labial (I) and lingual (J) views, MCNA 14697; **K, L**, *Carcharias heathi* Case & Cappetta, 1997, upper lateral tooth in labial (K) and lingual (L) views, MCNA 14711; **M, N**, *Carcharias* sp., parasymphyseal tooth in oblique lingual (M) and lateral (N) views, MCNA 14715; **O, P**, *Palaeogaleus faujasi* (Geyn, 1937), lateral tooth in labial (O) and lingual (P) views, MCNA 14724; **Q, R**, *Plicatoscyllium lehneri* (Leriche, 1938), anterolateral tooth in labial (Q) and apical (R) views, MCNA 14722; **C, D** from the discontinuous lag deposit QLO1, the rest from bone assemblage QLO2. Scale bars: **A, B**, 1 cm; **C, D**, 5 mm; **E, F**, 4 mm; **G, H**, 2 mm; **I-L**, 5 mm; **M, N**, 1 mm; **O, P**, 2 mm; **Q, R**, 2 mm.

The teeth of this species, which are larger than those of any other species in the genus, are characterised by having a high cusp, subconical and biconvex in cross section. Besides this,

they are characterised by a main cusp flanked by a pair of two short cusplets. The crown shows short basilolabial folds located in the marginal zone of the mesial heel (Fig. 6O), and the

root, although heavily abraded, includes a lingual protuberance and the remnants of a broad and deep nutritional groove. Orectolobiform teeth are extremely rare in Quintanilla la Ojada. All identifiable orectolobiforms are referred to the ginglymostomatid *Plicatoscyllium lehneri* (Leriche, 1938) on the basis of the identification made by one of us (H. C.; see Corral *et al.* 2015b). The teeth of *P. lehneri* are symmetrical and medium-sized. The crown includes two pairs of lateral cusplets flanking the broad conical cusp. Marked irregular wrinkles are present on the labial side of the crown, covering an area roughly triangular in shape. The root, damaged by severe taphonomic abrasion, includes a strong lingual protuberance pierced by a central foramen (Fig. 6Q-R).

Two batoid orders (Rajiformes and Myliobatiformes) have been identified in bonebed QLO2. The rajiform fauna is represented by four species referred to the genera *Rhinobatos* Link, 1790, *Vascobatis* Cappetta & Corral, 1999 and *Ganopristis* Arambourg, 1935.

Some diagnostic features included in the diagnosis of *Rhinobatos echavei* (*Rhinobatidae*) are (Cappetta & Corral 1999): a rather thick crown, being broader mesiodistally, with a well-marked transverse keel, which is concave labially, and constrictions behind both marginal angles (in occlusal view); a relatively broad, protruding medial uvula and two short marginal uvulae; and a labial extension of the crown to form a medially broad visor. Additionally, in this taxon the root is slightly narrower than the crown, its lingual notch being broad and round. The root branches are separated by a well marked groove in which a large foramen opens. A large circular foramen is located on each marginolingual face of the root (Fig. 7A-D).

The teeth of *Rhinobatos ibericus* Cappetta & Corral, 1999 are narrower and more labiolingually elongated, with a regularly convex labial margin. They present a less developed marginal uvula with a lanceolate end flanked by two short rounded labially-pointing marginal uvulae, a strong median process under the visor and a shorter root. These features make the teeth of *R. ibericus* very distinct from those of the other species of the genus discovered in the fossil assemblage QLO2 (Fig. 7E-H).

Several specimens are regarded as belonging to the uncommon ray species *Vascobatis albaitensis* Cappetta & Corral, 1999 (*Rhinobatoidei* incert. fam.), on the basis of teeth of rhombic (or truncated rhombic) shape in occlusal view, with a smooth cuspidate crown that exhibit a straight transverse keel running across, in occlusal view, a projecting visor formed by an overhanging of the labial face the crown, a short rounded median uvula, and a short root (narrower than the crown), which is heart-shaped in basal view, with a concave labial area where a large circular foramen opens (Fig. 7I-K).

Ganopristis leptodon Arambourg, 1935 (*Sclerorhynchidae*) is represented by rostral and oral teeth (Fig. 7L-N). The rostral teeth of this species are characterised by a smooth pointed and slightly sigmoidal cap, dorsoventrally flattened, separated from the peduncle by a basal bulge (Fig. 7L). The oral teeth of the species are small, wider than long, with a cuspidate crown (either smooth or ornamented with short, radiating wrinkles

on the surface of the enameloid) that presents a convex labial margin in occlusal view and forms a subtle apron (Fig. 7N). The root is divided into two lobes, which are flat and roughly subtriangular in basal view; the root lobes are separated by a deep groove with a foramen (Fig. 7N).

Additionally, a single isolated dermal denticle assigned to Rajiformes indet. is present in the fossil assemblage QLO2 (Fig. 7O-P). This element shows a basal plate that is almost circular in outline, and a smaller enameloid cap, the apex of which is posteriorly oriented, with the anterior margin undulate in outline.

Myliobatiform rays in assemblage QLO2 are referred to *Dasyatoidea* incert. fam. (*Coupatezia fallax* (Arambourg, 1952)) and *Rhombodontidae* (*Rhombodus binkhorsti* Dames, 1881 and *Rhombodus* sp.). The extremely rare *Coupatezia fallax* (Fig. 7Q-S) is known by having small teeth that are mesiodistally elongated. Their crown is low, bearing a straight transverse cutting crest, and vermiculate ornamentation is observed on the reniform labial face, which includes a labial visor regularly concave (Fig. 7S). The lingually displaced root is low and as wide as the crown, bearing a pair of lobes, the bases of which are triangular and practically flat. The teeth belonging to the myliobatiform elasmobranch *Rhombodus binkhorsti* are by far the most abundant in the collection (representing over 33% of the identified teeth) (Fig. 7T-V). This taxon, exhibiting a global distribution during the Maastrichtian, is characterised by having medium-sized diamond shaped teeth, as seen in occlusal view, that are set in a grinding pavement arrangement (Arambourg 1952; Cappetta 1987). When unworn, the slightly convex crown is high, showing four subvertical marginal faces which are covered with dense vertical wrinkles. A transversal bulge is developed across the base of the lingual marginal faces (Fig. 7U). The labial visor is salient. The root is smaller than the crown and has two lobes, triangular in dorsal view, which are separated from each other by a deep median groove. Finally, other uncommon rhombodontid teeth have a low and almost flat crown with a subhexagonal face with alveolate ornamentation as seen in occlusal view (Fig. 7W-X). These teeth, which are significantly small compared to those of *Rhombodus binkhorsti*, are tentatively referred to *Rhombodus* sp.

OSTEICHTHYANS

Osteichthyan remains consist of teeth of pycnodontiforms, amiiforms, elopiforms and aulopiforms, plus fragmentary acanthomorph spines (Table 1). The material, which includes more than 200 specimens, was described in detail by Berreteaga *et al.* (2011). There are ten different tooth morphotypes in Quintanilla la Ojada in addition to the fin spines, indicating a minimum estimation of eight actinopterygian species (F. J. P.-A., pers. obs.).

Four of the morphotypes correspond to Pycnodontiformes (basal Neopterygii: Poyato-Ariza 2015). Eight molariform teeth, oval to subcircular in occlusal view (Fig. 8A-B), are referred to Pycnodontiformes indet. These teeth are typical of the vomer and prearticular of this order (Poyato-Ariza & Wenz 2002; Poyato-Ariza 2005). Nine incisiform teeth (Fig. 8C-E) and three branchial teeth (Fig. 8F-G) are assigned

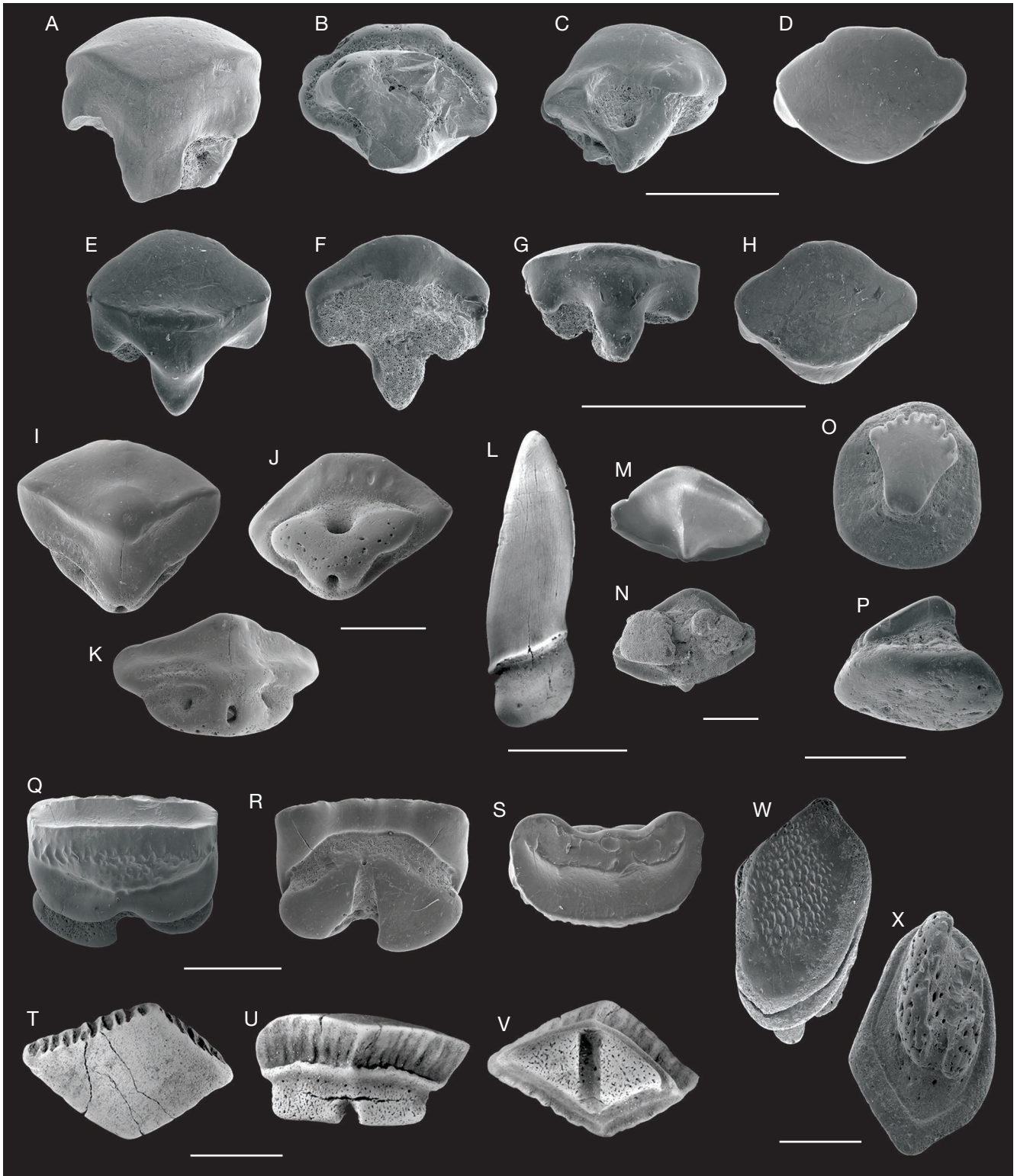


FIG. 7. — Selection of batomorphs from the Maastrichtian Valdenoceda Formation at Quintanilla la Ojada, Burgos (modified from Corral *et al.* 2015b). **A–D**, *Rhinobatos echavei* Cappetta & Corral, 1999, lateral tooth in occlusal (A), basal (B), lateral (C) and labial (D) views, MCNA 14728. **E–H**, *Rhinobatos ibericus* Cappetta & Corral, 1999, lateroanterior tooth in oblique occlusal (E), basal (F), lingual (G) and labial (H) views, MCNA 14729. **I–K**, *Vascobatis albaitensis* Cappetta & Corral, 1999, lateral tooth in occlusal (I), basal (J) and lingual (K) views, MCNA 14736. **L–N**, *Ganopristis leptodon* Arambourg, 1935: **L**, rostral tooth in dorsal/ventral views, MCNA 14749; **M**, **N**, oral tooth in occlusal (M) and basal (N) views, MCNA 14745. **O**, **P**, Rajiformes indet., dermal denticle in occlusal (O) and lateral (P) views, MCNA 14803. **Q–S**, *Coupatezia fallax* (Arambourg, 1935), lateral tooth in occlusal (Q), basal (R) and labial (S) views, MCNA 14753. **T–V**, *Rhombodus binkhorsti* Dames, 1881, lateral tooth in occlusal (T), lingual (U) and basal (V) views, MCNA 14758. **W**, **X**, *Rhombodus* sp. lateral tooth in occlusal (W) and basal (X) views, MCNA 14801. All from bone assemblage QLO2. Scale bars: **A–K**, 1 mm; **L**, 4 mm; **M–S**, 1 mm; **T–V**, 5 mm; **W**, **X**, 1 mm.

to Pycnodontoidea indet. The presence of fully incisiform premaxillary and dentary teeth is regarded as a diagnostic character of Pycnodontoidea (Poyato-Ariza & Wenz 2002). The branchial tooth morphotype (large, hook-like) has for a long time been assessed to “*Stephanodus*”, which is clearly a parataxon. This morphotype is found in the branchial chamber of a number of Pycnodontoidea (Kriwet 1999; Poyato-Ariza & Wenz 2002, 2005). Although elongated branchial teeth have been reported outside the Pycnodontoidea, the type of broad pharyngeal tooth found in Quintanilla la Ojada has never been described in non-pycnodontoid pycnodontiforms. In addition, three incomplete molariform teeth are provisionally attributed to cf. *Anomoeodus*. These teeth are about three times longer than wide in occlusal view and relatively large in size (up to 9.8 mm long in the biggest, incomplete tooth). The absence of ridges, crenulations or any other kind of ornamentation (Kriwet 1999; Poyato-Ariza & Wenz 2002) in these teeth is probably due to biostratinomic abrasion.

Amiiforms are represented by eleven small, conic-styliiform teeth (Fig. 8H-I). These teeth, with pointed, well defined enameloid, glossy crowns, straight to slightly curved in lateral view, are typical of the Amiidae, which are small to medium-sized fishes with ichthyophagous diet and predatory habits (Grande & Bemis 1998). The Quintanilla sample is referred to cf. Amiidae indet. (Berreteaga *et al.* 2011).

Teleosteans are a numerically vast component of the ichthyofauna of Quintanilla la Ojada in the number of teeth. Phyllodontids (phyllodontines, paralbulines) and enchodontids are present in the assemblage. Three phyllodontine teeth are known (Fig. 8J). These teeth are somewhat similar to the molariform teeth of pycnodonts, but much more flattened (thickness less than one third of diameter in occlusal view). In addition, the dentine and enamel are less developed than those of pycnodont molariform teeth, and they lack the small central cavity observed in all pycnodont molariform teeth in basal view. Unlike pycnodont teeth, phyllodont teeth grow as very closely arranged replacement sets (Estes 1969). This morphotype of flattened teeth is consistent with that of *Phyllodus*, but generic assessments are mostly based on characters of complete tooth plates (Poyato-Ariza *et al.* 1999). Thus, isolated teeth of Quintanilla la Ojada are better referred to Phyllodontinae indet.

Nearly 120 specimens, approximately one third of the whole sample, are robust and globular-shaped teeth of Paralbulinae (Fig. 8K-L). Paralbulinae teeth grow as replacement sets, although the teeth are much less compact than in phyllodontine sets; individual teeth are quite high, fairly spherical. Such tooth morphology is coherent with that of *Paralbulina* but no complete tooth set is known in Quintanilla la Ojada. Consequently, all these isolated teeth are assigned to Paralbulinae indet.

Enchodontids are represented by 41 teeth, some of them of large size (up to 190 mm long) (Fig. 8M-Q). Three different types of caniniform-like teeth can be distinguished on the basis of differences in relative length and in the contour of the crown (i.e., straight or sigmoid in labial/lingual view; straight or curved backwards in mesial/distal view).

These morphotypes probably represent at least two distinct enchodontid species (Berreteaga *et al.* 2011). Nevertheless, the material is quite fragmentary and key characters are not observable to allow consistent assessment to *Enchodus* or to another genus (Poyato-Ariza *et al.* 1999). Therefore the teeth are referred to Enchodontidae indet.

Besides teeth, seven basal fragments of fin spines are known (Fig. 8R, S). True fin spines (azygous, unsegmented, bilaterally fused) characterize Acanthomorpha (Johnson & Patterson 1993; Poyato-Ariza *et al.* 1999). As fin spine morphology within the different teleostean groups is not thoroughly comprehended, the Quintanilla la Ojada specimens are considered as Acanthomorpha indet.

MARINE REPTILES

Mosasauroid squamates are represented in Quintanilla la Ojada by three tooth crowns in different grades of preservation and three tooth fragments showing enamel. One tooth is almost complete except for its apex (Fig. 9A-E). Its crown is high and slender. It bears two carinae and presents U-shaped morphology because of the two asymmetrical convex surfaces, the labial one having five well defined facets whereas the lingual one is larger with about seven poorly marked facets. All these characteristics indicate that this crown is an anterior tooth of the genus *Mosasaurus* Conybeare, 1822 (Russell 1967; Bell 1997). The number of labial and lingual facets differs from the European species *M. hoffmanni* Mantell, 1829 and *M. lemonnieri* Dollo, 1889 and falls within the range of *M. beaugei* Arambourg, 1952 and *M. missouriensis* (Harlan, 1834) (see Bardet *et al.* 2004). However, *M. beaugei* is up to now only known from the Maastrichtian of the Southern Tethys Margin (North of Africa and Middle East) (see Bardet 2012) and *M. missouriensis* from the late Campanian of North America (South Dakota, Montana, Alberta) (see Konishi *et al.* 2014). Due to the scarcity of this material, this tooth from Quintanilla la Ojada is referred to *Mosasaurus* sp. Another tooth, the apex and basement of which are missing due to recent breakage, is also assigned to *Mosasaurus* sp. on the basis of the presence of strongly faceted surfaces on the crown (Bardet *et al.* 2004) (Fig. 9F-H). This tooth probably comes from the median portion of the jaw as the crown bears two carinae, located anteriorly and posteriorly, and seemingly appears to represent the same taxon as the previously described tooth, but its poor preservation precludes precise taxonomic determination. A third specimen exhibits a low, slightly transversely compressed crown and the occlusal surface is abraded. It shows similarities with the teeth of *Prognathodon* Dollo, 1889, which are characterised by a smooth, silky enamel, and the lack of anterior carina, so it is provisionally referred to this genus (Berreteaga 2008) (Fig. 9I-L). This tooth resembles the specimen MCNA 5487 from Albaina, attributed to *Leiodon anceps* by Bardet *et al.* (1997, 1999). As this species is now considered a *nomen dubium* by Schulp *et al.* (2008), MCNA 5487 is here also referred as *Prognathodon* sp. Finally, three more teeth from Quintanilla la Ojada are too fragmentary for an accurate identification; they are here assigned to Mosasauridae indet.

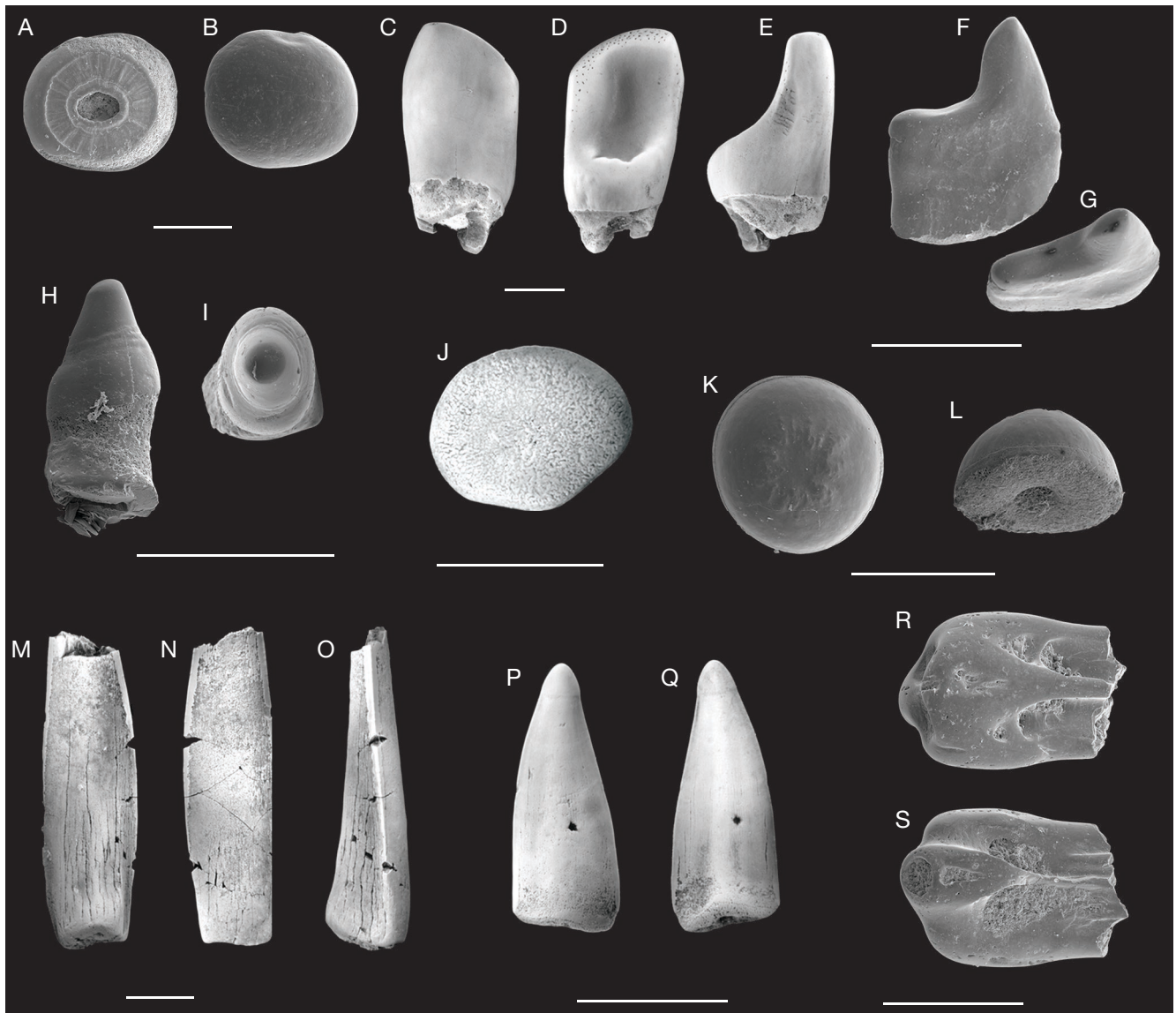


FIG. 8. — Selection of actinopterygians from the Maastrichtian Valdenoceda Formation at Quintanilla la Ojeda, Burgos (modified from Berreteaga *et al.* 2011). **A, B**, Pycnodontiformes indet., molariform tooth in basal (A) and occlusal (B) views, MCNA 15939; **C–G**, Pycnodontoidea indet.: **C–E**, incisoriform tooth in labial (C), lingual (D) and mesiodistal (E) views, MCNA 15942; **F, G**, branchial tooth in lateral (F) and apical (G) views, MCNA 15944; **H, I**, cf. Amiidae indet., conic-styliiform tooth in mesiodistal (H) and occlusal (I) views, MCNA 15946. **J**, Phyllodontinae indet., flattened tooth in occlusal view, MCNA 15947. **K, L**, Parabulinae indet., globular tooth in occlusal (K) and basal inclined (L) views, MCNA 15948. **M–Q**, Enchodontidae indet.: **M–O**, caniniform tooth (morphotype A in Berreteaga *et al.* 2011) in labial (M), lingual (N) and mesiodistal (O) views, MCNA 15950; **P, Q**, caniniform tooth (morphotype C in Berreteaga *et al.* 2011) in lingual (P) and labial (Q) views, MCNA 15952. **R, S**, Acanthomorpha indet., fragmentary fin spine in posterior (R) and anterior (S) views, MCNA 15953. All from bone assemblage QLO2. **A, B**, 1 mm; **C–G**, 2 mm; **H, I**, 1 mm; **J**, 4 mm; **K, L**, 1 mm; **M–Q**, 4 mm; **R, S**, 1 mm.

DINOSAURS

A single isolated dinosaur tooth has been discovered in the assemblage QLO2 (cast MCNA 15151, original in the private collection of J.I. Sáez Laría as JISL 3137) (Fig. 10). The specimen preserves only the dental crown, which is broken at the base. The preserved height of the crown is 16.5 mm and the maximum width is 6.5 mm. The enamelled surface of the crown is lanceolate to rhomboidal in shape, and bears a straight primary ridge. Accessory ridges are absent. The mesial and distal margins of the crown seem to have highly reduced denticles. In mesial or distal view, the median primary ridge, as well as the whole crown, is curved (convex) forward. The

crown is apically truncated by a wear facet, which is sub-hexagonal in occlusal view, forming an angle of about 70° with the enamelled surface.

The presence of a wear facet indicates that it was a functional tooth. The narrow, lanceolate to rhomboidal crown, with a prominent median ridge on the enamelled side and showing a sub-hexagonal wear facet in occlusal view is typical of hadrosaurid teeth (Horner *et al.* 2004). Due of the narrowness of the crown and to the height/width ratio over 2.5, this tooth could come from the maxilla.

Hadrosauroids are represented in the Maastrichtian of the Ibero-Armorican Domain by a number of lambeosaurines

and non-hadrosaurid forms (Pereda-Suberbiola *et al.* 2009a; Prieto-Márquez *et al.* 2013; Csiki-Sava *et al.* 2015). The QLO2 tooth is roughly similar in shape to the maxillary teeth of the dental batteries of *Canardia* (Haute-Garonne, Tricouté 3 site; Prieto-Márquez *et al.* 2013) and *Pararhabdodon* (Lleida, Sant Romà d'Abella site; see Prieto-Márquez & Wagner 2009). Those maxillary teeth show a single straight ridge centred at the midline of the enamelled surface, no subsidiary ridges and very reduced or absent denticles (papillae) (see Prieto-Márquez *et al.* 2013). Instead, large papillae are present apically on the crown of an isolated maxillary tooth from the Cassagnau 1 site (Haute-Garonne; Prieto-Márquez *et al.* 2013). Direct comparisons with other taxa, such as *Arenysaurus* and *Blasisaurus* from Arén (Huesca; see Pereda-Suberbiola *et al.* 2009b; Cruzado-Caballero *et al.* 2010) are not possible because there are not well-preserved maxillary teeth. The recently described lambeosaurine *Adynomosaurus arcanus* from Lleida (Costa de les Solanes site; Prieto-Márquez *et al.* 2019) does not preserve the dental battery. Given the fragmentary nature of the material from Quintanilla la Ojada, the QLO2 tooth is referred to Hadrosauridae indet.

The hadrosaurid tooth from QLO2 (Fig. 10) constitutes the only dinosaurian fossil known to date from the Valdenoceda Formation of Burgos, and it represents the third record of this group of dinosaurs in the latest Cretaceous of the Basque-Cantabrian Basin. Previously, a partial femur of a hadrosauroid (LU-JL-LAÑ001) was described from the late Maastrichtian marine deposits of the Laño Quarry at Albaina (Pereda-Suberbiola *et al.* 2015b), which had been ascribed to the Torme Formation (see Corral *et al.* 2015a; this work). Also, an isolated tooth (MCNA 10510) was found in a fluvial deposit from Laño 1 site (Pereda-Suberbiola *et al.* 2003). MCNA 10510 is smaller and more fragmentary than the QLO2 tooth. It could belong to either a hadrosaurid or a basal hadrosauroid. Laño 1 site is late Campanian in age based on magnetostratigraphical evidence (Corral *et al.* 2015a), and, so far, it is the only Iberian site where a hadrosauroid fossil has been found in association with rhabdodontid and titanosaurian remains, indicating the presence of duck-billed dinosaurs before the Maastrichtian (Pereda-Suberbiola *et al.* 2015a, b). Finally, an isolated ornithopod caudal centrum was reported by Berreteaga (2008) in the next younger upper Maastrichtian Sobrepeña Formation at Urria site (northern Burgos), which was tentatively referred to Hadrosauridae indet. based on the presence of separated articular facets for the haemal arches.

DISCUSSIONS ON AGE AND COMPOSITION OF THE VERTEBRATE PALAEOCOMMUNITY

AGE OF THE FOSSILIFEROUS DEPOSITS

The Valdenoceda Fm, as exposed at Quintanilla la Ojada, is bounded below by the “Riosco-like facies” (Fig. 2), which represents the deposits of both the Riosco coastal system (in part equivalent to the Moradillo de Sedano, Quintanaloma and Sedano formations) deposited during the Campanian to early Maastrichtian, as stated in Floquet (1991, 1998, 2004)

and Berreteaga (2008). The deepening of the northern domain of the Castilian Ramp during the Maastrichtian favoured the presence of requieniid and radiolitid rudists (e.g. *Apricardia toucasiana* (d'Orbigny, 1850), *Distefanella* gr. *lumbricalis* (d'Orbigny, 1842), *Biradiolites angulosus* (d'Orbigny, 1842), *Biradiolites* sp. gr. *angulosus* (d'Orbigny, 1842), *Lapeirousia* sp. aff. *trigeri* (Coquand, 1860), *Lapeirousia* sp. and *Radiolites* sp.) in shallow coastal settings with carbonate sedimentation (Floquet 1991). This same author claimed an early – but not earliest – Maastrichtian to probably early late Maastrichtian age for the Valdenoceda Fm based on the identified molluscs, unfortunately not particularly diagnostic in Floquet's (1991) words.

The vertebrate assemblages QLO1 and QLO2 derive from the lower part of the Valdenoceda Fm, the lithology of which is carbonate (i.e., dolomitised marlstone and sandy dolomite). In this context, the youngest assemblage QLO2 has yielded a distinctive selachian fauna, where the presence of the species *Carcharias heathi*, *Coupatezia fallax*, *Plicatoscyllium lehneri*, *Rhombodus blinkhorsti* and *Serratolamna serrata* indicates a late Maastrichtian age (see Cappetta *et al.* 2014). Additional information can be extracted from the evolution of the crown shape observed in teeth of the anacoracid *Squalicorax pristodontus*, which shows a linear tendency to be mesiodistally symmetrical (equilateral triangle like shape) towards the end of the Maastrichtian (Cappetta *et al.* 2014). Since the tooth crown of the *S. pristodontus* specimens recovered at Quintanilla la Ojada does not have this characteristic shape (Fig. 4), a late but not latest Maastrichtian age is suggested for the assemblage QLO2 (Corral *et al.* 2015b).

Age determination has also benefited from regional sequence stratigraphical correlation. Thus, the Valdenoceda Fm is related to the onset of the T-R cycle DC12 in the lower Maastrichtian, according to Floquet (1998). It is noteworthy to mention that the T-R cycle DC13 is poorly represented across the northern limb of the Villarcayo Syncline due to local palaeogeographical conditions (Floquet 1991; Pluchery 1995; Berreteaga 2008). The Quintanilla la Ojada succession is overlain by mud-dominated sediments (from supratidal sabkha to lagoonal environments) of the upper Maastrichtian Sobrepeña Formation (Floquet *et al.* 1982; Floquet 1991, 1998; Berreteaga 2008). At Laño quarry (Treviño County, located about 60 km eastward of Quintanilla la Ojada in the southern central part of the Basque-Cantabrian Basin), an early late Maastrichtian age for the upper part of the Sobrepeña Formation is indicated on the basis of magnetostratigraphic dating (Corral *et al.* 2015a). In addition, the age of the Torme Formation as exposed in Albaina is estimated to be late Maastrichtian on the basis of stratigraphical relations (Baceta *et al.* 1999; Berreteaga 2008), selachian biostratigraphy (Cappetta & Corral 1999), and palaeontological data supplied by baculitid ammonites (Corral 2018) and large benthic foraminifera *Orbitoides* (Ciry 1939; Floquet 1991) (Fig. 2B).

With the current knowledge of both micro- and macrofossil occurrences and their stratigraphical position within the Valdenoceda Fm, the vertebrate assemblages from Quintanilla

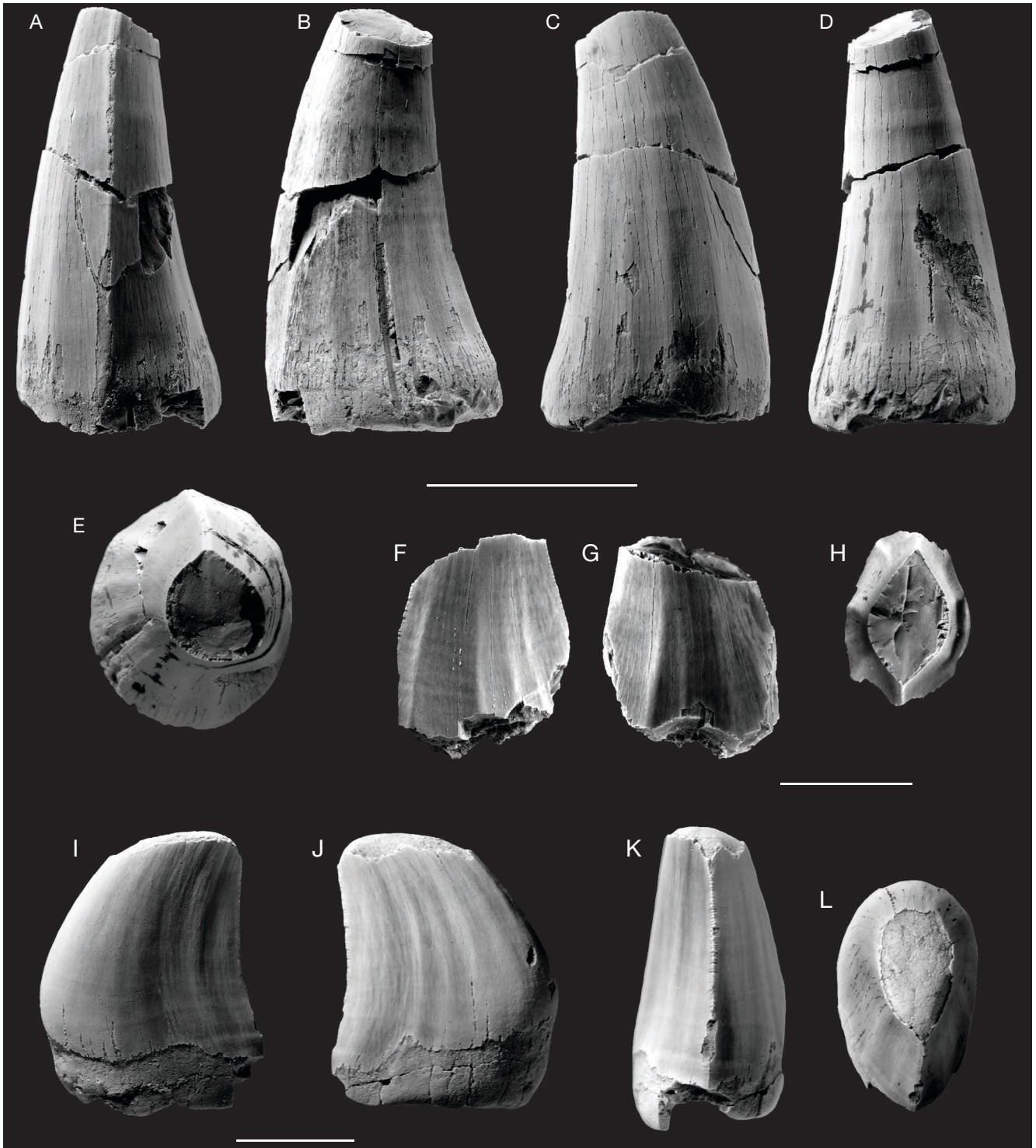


FIG. 9. — Mosasaurids from the Maastrichtian Valdenoceda Formation at Quintanilla la Ojada. **A-H**, *Mosasaurus* sp.: **A-E**, anterior tooth in anterior (A), lingual (B), labial (C), posterior (D) and occlusal (E) views, JISL-2124 (MCNA 16233 cast); **F-H**, latero-posterior tooth in lateral (F, G) and occlusal (H) views, MCNA 14903. **I-L**, *Prognathodon* sp.: posterior or pterygoid tooth in lingual (I), labial (J), posterior (K) and occlusal (L) views, MCNA 14840. All from bone assemblage QLO2.

la Ojada are relatively older than those of the Albaina beds (Torme Fm, the relationships of the formations are graphically shown in Fig. 2B). In this regard, it should be noted that the final depositional cycle DC13 is absent in the Quintanilla la Ojada section (see Fig. 2A).

Accordingly, the QLO2 fossils should be assigned to the base of the late Maastrichtian, on the basis of the regional sequence stratigraphical correlation and the biostratigraphic information provided by the typically Maastrichtian selachian taxa (Berreteaga 2008; Corral *et al.* 2015b), although the

exact age of such assemblages remains to be fully ascertained by future research.

PALAEOCOMMUNITY STRUCTURE

The isolated teeth and other skeletal fragments recovered from the Valdenoceda Formation at Quintanilla la Ojada represent a diverse marine vertebrate community comprising selachians, actinopterygians and reptiles (Fig. 5). Selachians have been found to form the most diverse community of marine predators with 16 taxa (Fig. 11). The recovered tooth elements for each taxon are provided in Table 2. Based on these data, three teeth (1.7%) belong to Orectolobiformes, 69 (38.3%) belong to Lamniformes, three (1.7%) belong to Carcharhiniformes, 24 (13.3%) belong to Rajiformes, and 81 (45%) belong to Myliobatiformes. These tooth assemblages represent a wide diversity of small nektonic rays and active coastal pelagic sharks, inhabitants of temperate to subtropical shallow environments developed in the Castilian Ramp (southwestern part of the Basque-Cantabrian Basin) during the Maastrichtian. Taken as a whole, the fossil material contains a diversified association of rays (including representatives of the taxa Rhinobatidae, Rhinobatoidei, Sclerorhynchidae, Dasyatoidea and Rhombodontidae), bottom-dwelling sharks (including representatives of the families Ginglymostomatidae and Triakidae) and nektonic sharks (including representatives of the families Anacoracidae, Odontaspidae, Odonotidae and Serratomnidae). Lamniformes is the most diversified shark order present in the Valdenoceda Fm with seven species (Fig. 11). Extant representatives of this order include active hunters and opportunistic scavengers, as well, feeding on actinopterygians and inhabiting inshore waters from the intertidal zone to the outer shelf. Triakidae (Carcharhiniformes) and Ginglymostomatidae (Orectolobiformes) sharks, which are underrepresented in Quintanilla la Ojada, complete the fossil record of sharks. Many extant triakids are opportunistic carnivores, inhabiting muddy bottoms in water depths ranging from intertidal to outermost shelf. Similarly, extant ginglymostomatids are inshore bottom dwelling sharks, broadly speaking, although some species may occur up to several tens of metres deep, according to Compagno (1984). The various species of batoids (Batomorphii) present in the Valdenoceda Fm are included in the orders Rajiformes (sclerorhynchids, rhinobatids and their closest relatives) and Myliobatiformes (rhombodontids and dasyatoids), representing almost half of the elasmobranch elements present in assemblage QLO2. Members of these two orders are benthic carnivores feeding on small prey that live within or close to the sea bottom.

With regards to the actinopterygians, the Quintanilla la Ojada (Table 3, Fig. 12) association can be compared with that of Albaina (Treviño County). Both associations share the highest rank taxa (with the exception of Amiiformes, only known in Quintanilla la Ojada) and are similar in relative abundance of fossils as well (Berreteaga *et al.* 2011). For instance, enchondontid and especially paraboluline teeth are very abundant in both localities, whereas phylloodontine teeth are rather scarce. Nevertheless, some differences in lower rank taxa are known. The generic assignments that can be made for pycnodonts are

different: cf. *Anomoeodus* sp. from Quintanilla la Ojada *versus* cf. *Paramicrodon* sp. from Albaina. The acanthomorph fin spines of Quintanilla la Ojada are quite different from those of Albaina (Poyato-Ariza *et al.* 1999), and this also suggests the occurrence of distinct taxa.

The Basque-Cantabrian ichthyofauna and those from other coeval localities of the Iberian Peninsula are dominated by durophagous ecomorphotypes (Poyato-Ariza *et al.* 1999), showing a mixture of basal neopterygians (i.e., pycnodonts) and derived teleosts. Such mixture exemplifies the changes in composition experienced by actinopterygians during the Late Cretaceous: teleostean taxa achieved a huge evolutionary radiation during the Late Cretaceous whereas pycnodonts saw their geographic distribution progressively reduced at this time (López-Horgue & Poyato-Ariza 2005; Poyato-Ariza 2005). Moreover, these are the youngest of a few known examples of Cretaceous localities in which pycnodonts and durophagous teleosts did coexist in a situation of actual competition for the same resources, at the end of the ichthyofaunal replacement that had actively started back in the Aptian-Cenomanian (Poyato-Ariza & Martín-Abad 2016).

The marine reptile associations of Quintanilla la Ojada and Albaina are rather poor both in terms of diversity and in number of elements collected, with only a few mosasaurid taxa (*Mosasaurus* Conybeare, 1822, *Prognathodon* Dollo, 1889 and *Platecarpus* Cope, 1869; the latter genus only known in Albaina) and an indeterminate elasmosaurid plesiosaur (only present in Albaina) (Bardet *et al.* 1999). Even so, the aggregate assemblage is the most diverse known to date from the Late Cretaceous of the Iberian Peninsula (Bardet *et al.* 2008). Similarly to the mixed character of the selachian faunas, mosasaurids from the Basque-Cantabrian Region include elements from both the northern (Belgium-Netherlands) and southern (Morocco) margins of the Mediterranean Tethys (Bardet 2012).

In the marine Albaina beds, a partial femur of a hadrosauroid ornithopod has been previously described (Pereda-Suberbiola *et al.* 2015b). The hadrosauroid tooth (Fig. 10) discovered in marine deposits of the Valdenoceda Fm represents another example of continent-derived vertebrates. Consequently, the occurrence of hadrosauroid fossils in shallow marine environments is interpreted as the result of passive transport from the mainland.

PALAEOBIOGEOGRAPHICAL CONSIDERATIONS

During the Late Cretaceous the northern margin of the Iberian Peninsula lay further south than today, between the warm-temperate marine province of western Europe (Belgian and Dutch basins in northern Europe: Mons and Hesbaye-Maastricht) and the Moroccan subtropical province in western Africa (Fig. 13). Such palaeogeographical location also conditioned the composition of the Quintanilla la Ojada elasmobranch fauna during the Maastrichtian, when a distinctive fish fauna dominated by active pelagic selachians and nektonic rays thrived in the Basque-Cantabrian shallow shelf waters.

The distribution and abundance of the selachian taxa in the Quintanilla la Ojada site have been established with regard to

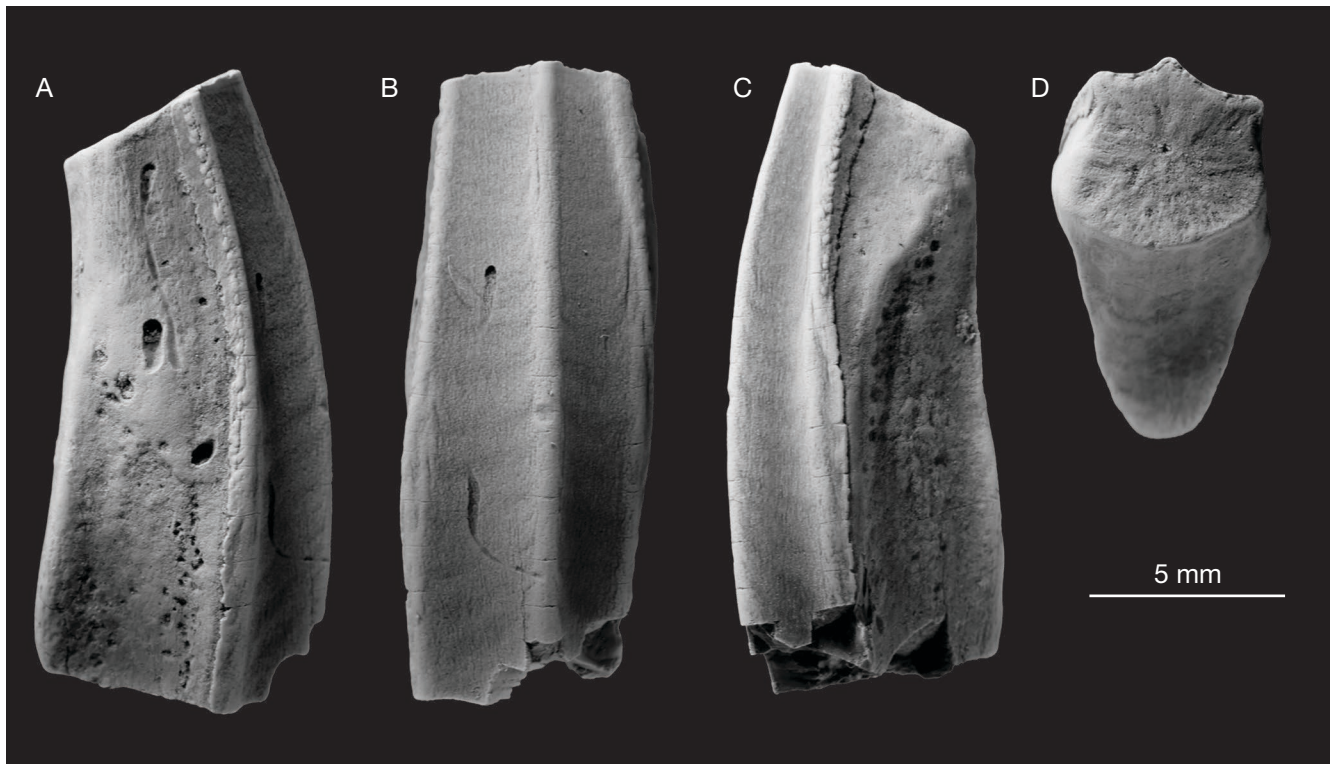


FIG. 10. — Hadrosauridae indet. from bone assemblage QLO2 in the Quintanilla la Ojada locality, Valdenoceda Formation (Maastrichtian). **A–C**, Tooth in mesial or distal; **B**, lingual; **D**, and occlusal views, JISL-3137 (MCNA 15151 cast).

the western European and Moroccan assemblages (see Corral *et al.* 2015b). Thus, the absence of clear barriers along the eastern Atlantic Region allowed many selachian taxa, especially those with good swimming capabilities (e.g. *Squaliconax kaupi*, *S. pristodontus*, *Serratolamna serrata*, *Cretolamna appendiculata*, *Coupatezia fallax*, *Ganoprists leptodon* and *Rhombodus binkhorsti*) to connect the warm-temperate and subtropical/tropical marine provinces. However, the considered subtropical shark species *Carcharias heathi* and *Plicatoscyllium lehneri*, cooccurring in northern African seas and northern Iberia, did not extend to reach further north into the warm-temperate North European province (Netherlands and Belgian basins) and the carcharhiniform shark *Palaeogaleus faujasi*, which is also represented in temperate regions of Europe, is lacking in Africa. Additionally, some taxa became exclusively restricted to the Basque-Cantabrian Region, as a number of the total elasmobranch species (about 18%) are endemic to this biogeographical area.

Another important aspect is that the Valdenoceda Formation at Quintanilla la Ojada contains a selachian fauna quite similar to the aggregate assemblage observed at Albaina (Treviño County) from rocks of the younger Maastrichtian Torme Formation (see Cappetta & Corral 1999). However, the following elasmobranchs have not been found at Quintanilla la Ojada yet: *Carcharias* aff. *gracilis*, *Odontaspis bronni*, *Chiloscyllium* sp., *Ataktobatis variabilis*, *Dalpiazia stromeri* and *Rhombodus andriesi*. This feature may be related to their range of temporal distribution, a taphonomic/collecting bias, or a combination of both; this needs to be eventually veri-

fied. Finally, the observation of certain level of endemism in the known batoids (e.g. *Rhinobatos echavei*, *R. ibericus* and *Vascobatis albaitensis*, purportedly bottom dwelling elements with limited dispersal capabilities) indicate a certain grade of separation of this area in the Basque-Cantabrian Region from other biogeographical regions (also supported by the Albaina data; see Corral *et al.* 2015b).

All this indicates that the mixed nature of the selachian faunas from the Basque-Cantabrian Region during the Maastrichtian could be attributed to palaeolatitudinal preferences (Bardet *et al.* 1999; Cappetta & Corral 1999; Bardet 2012; Corral *et al.* 2015b). The Quintanilla la Ojada fauna presents a mixture of species from two geographically separated areas: the northern, warm-temperate marine North European Province and the southern, subtropical North African Province. But contrary to the Albaina record, the QLO1 and QLO2 assemblages do not contain any exclusive Gondwanan component (Corral *et al.* 2015b). Active pelagic sharks of the order Lamniformes, together with *Plicatoscyllium lehneri* and the pelagic myliobatiform ray *Rhombodus binkhorsti*, are also reported from North and Central America (for a review see Corral *et al.* 2015b and references therein). Ocean surface currents (i.e., the North Atlantic gyre) were likely to facilitate the elements interchange between marine biogeographical provinces located on both western and eastern North Atlantic regions. At that time, selachian interchange across the Atlantic was possible as revealed by several shared cosmopolitan species (see Darteville & Casier 1943; Welton & Farish 1993; Noubhani & Cappetta 1997; Cappetta 2012).

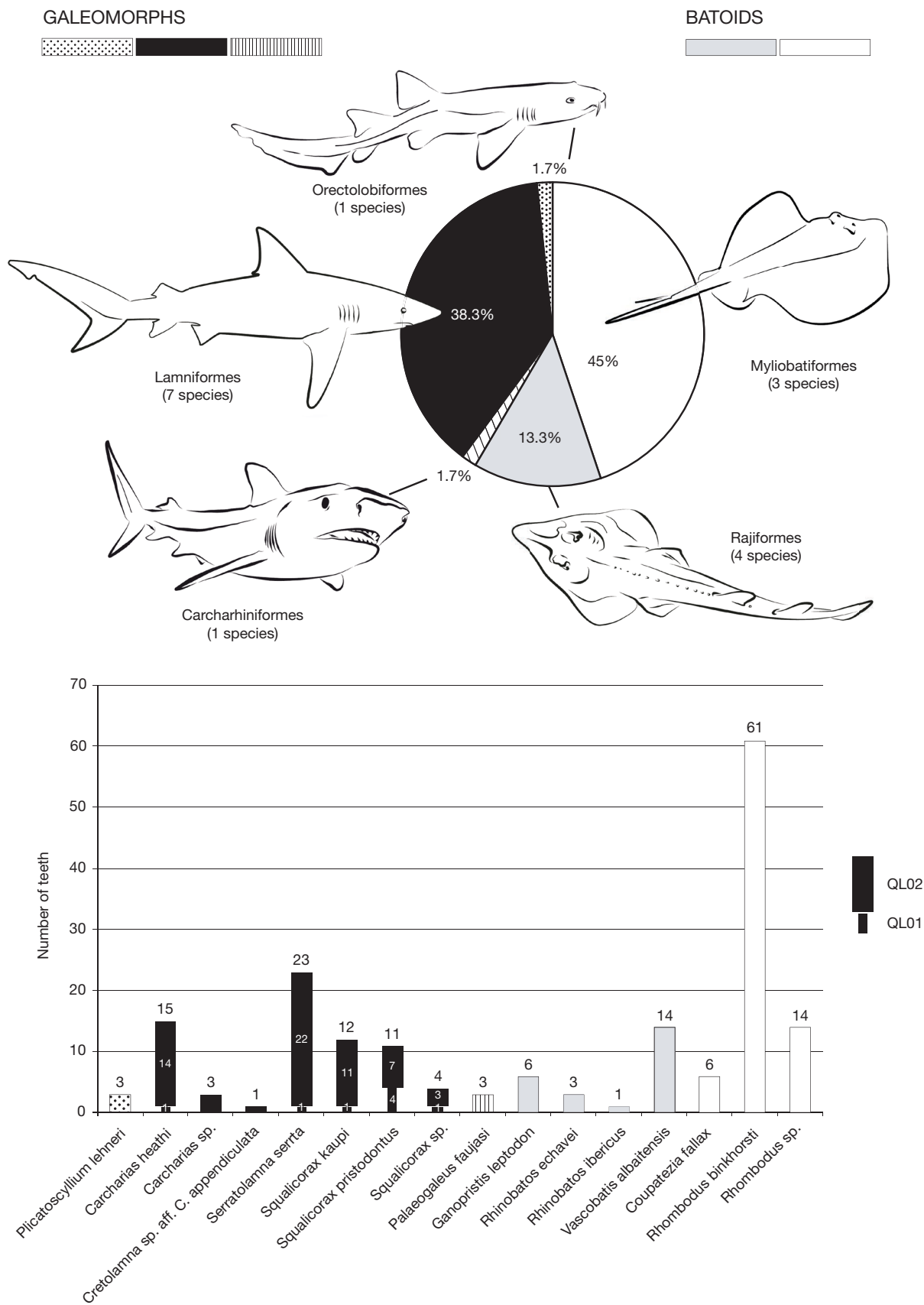


FIG. 11. — Percent relative abundance of teeth from major elasmobranch taxonomic groups in the Quintanilla la Ojada site (above), modified from Corral (2018); drawings depict a member of the group (not to scale). Number of elements identified to taxon (below) recovered from the site as shown in Table 2; colour of the bar relates to the elasmobranch order and bar width is used to differentiate between assemblages QLO1 (thin bar) and QLO2 (thick bar).

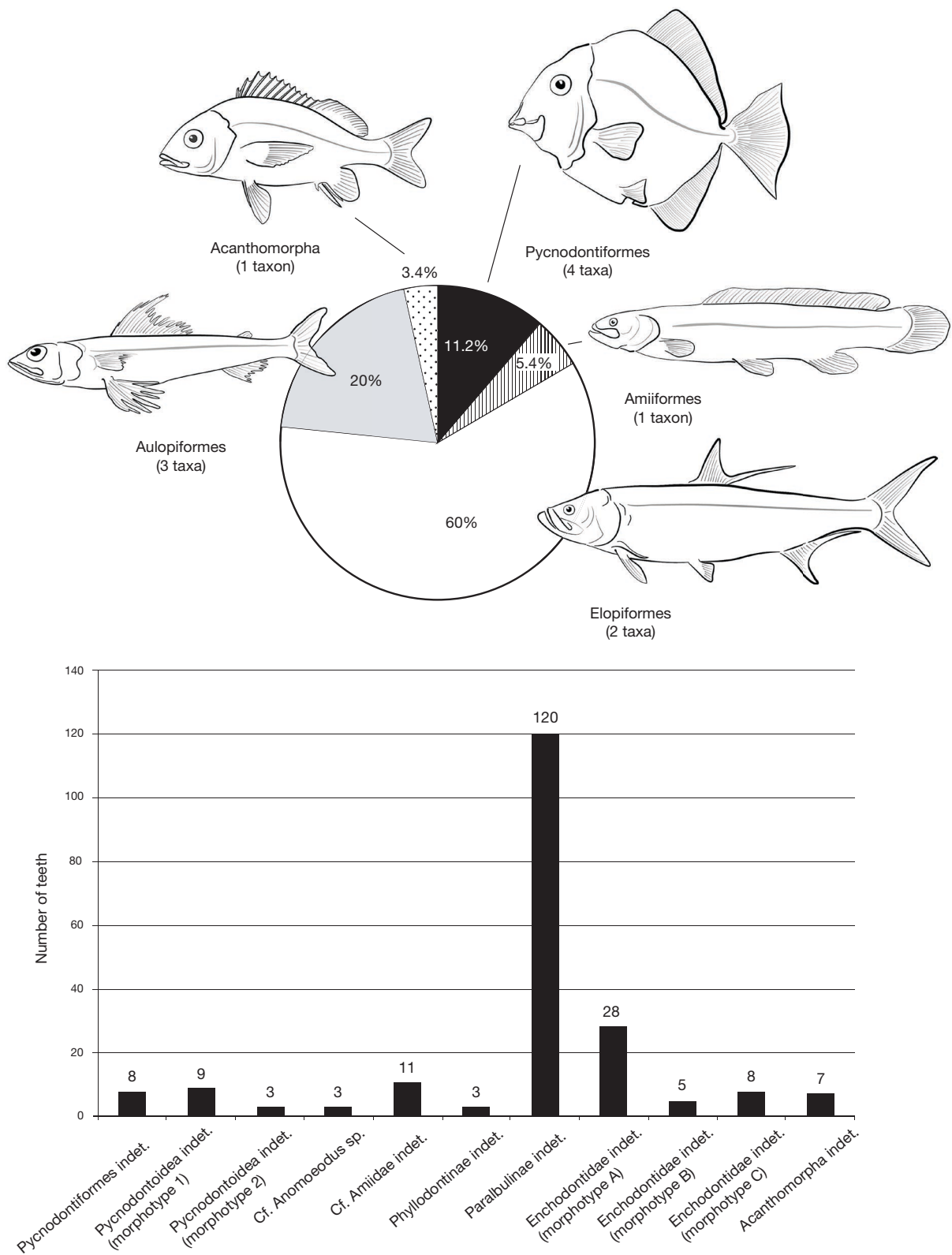


FIG. 12. — Percent relative abundance of teeth identified from the major actinopterygian morphotypes in the assemblage QLO2 (above); number of elements identified to taxon (below), recovered from the site as shown in Table 3. Fish drawings adapted from Nelson (2006) and own research (F.J.P.-A.); drawings depict a member of the group (not to scale).

The biogeographical relationships from the western Pyrenees elasmobranch faunae to the south-eastern Pyrenees elasmobranchs, which are roughly coeval areas in northern Iberia, are still poorly known. Elasmobranchs are represented by myliobatiform teeth in the lower Maastrichtian strata of the eastern Pyrenees. Blanco (2019) have recently reported the ray *Igdabatis marmii* from the Fumanya Member of the Tremp Group and Kriwet *et al.* (2007) described a faunule of small rays from Fontllonga-6 site within the Tremp Formation, including the taxa *Rhinobatos ibericus* and *Igdabatis indicus*. The low diversity probably resulted from the type of sedimentary setting (very near coastal/lagoonal marine environments with a western opening to the sea).

The significant differences should not be related to some geographical barriers preventing faunal interchange between these two regions, as the distribution of *Igdabatis* is indicative of a dispersal route between Europe and the Gondwanan continents through the northern and western continental margins of Iberia according to Blanco (2019). Thus, the faunal dissimilarity observed in the Maastrichtian formations located at the western and eastern ends of the Pyrenees could be conditioned by different depositional settings and by the poor representation of early Maastrichtian depositional sequences in the Basque-Cantabrian Region.

CONCLUSIONS

Diverse shallow depositional settings developed during the latest Cretaceous to early Paleogene in the Castilian Ramp (southern part of the Basque-Cantabrian Basin), ranging from inner shelf to coastal and, even, continental environments (Floquet 1991; Pluchery 1995). The Valdenoceda Fm, which is one of the Maastrichtian formations named for exposures of dolomitized limestone with rudist bivalves in the Villarcayo Syncline, is unconformably bounded below by an erosion surface representing an eastward progradation of the deltaic system (Rioseco Member) (Floquet 1991; Berreteaga 2008). This basal discontinuity, upon which a fossiliferous conglomeratic lag deposit occurs, is a transgressive ravinement surface that can be correlated with the basal boundary of the depositional T-R cycle DC12 – one of the many T-R cycles defined by Floquet (1998). On the other hand, the carbonate beds at the base of the Valdenoceda Fm represent an increasing influence of marine conditions in the system (i.e., the transgressive phase of T-R cycle DC12).

The Valdenoceda Fm exposed at Quintanilla la Ojada is also significant, as it has yielded many isolated teeth and skeletal parts of marine fishes (elasmobranchs and actinopterygians), although fossil remains of mosasaurids and dinosaurs also occur. The fossil assemblage QLO2 is represented by a rich selachian and actinopterygian diversity (Berreteaga *et al.* 2011; Corral *et al.* 2015b) and reflects a sublittoral (shallow coastal) environment connected with open sea, physically harsh for associated invertebrate organisms, as the latter are represented in a very low number (contrary to the Albaina marine ecosystem that includes baculitid ammonites, bivalves and gastropods; J.-C.C., pers. obs.).

In terms of species diversity, the elasmobranch assemblage QLO2 of the Valdenoceda Fm at Quintanilla la Ojada is similar to that of the Torme Formation at Albaina described by Cappetta & Corral (1999), being dominated by a wide diversity of small nekto-benthic rays and active coastal pelagic sharks usually inhabitants of temperate to subtropical shallow environments. Other coeval elasmobranch records in southern Europe are circumscribed to the eastern and western parts of the French Pyrenees (Gheerbrant *et al.* 1997; Cappetta & Odin 2001) and the Spanish eastern Pyrenees (Kriwet *et al.* 2007).

Finally, the Quintanilla la Ojada vertebrate assemblages (QLO 1 and QLO 2) are considered to be relatively older than those of Albaina on the basis of their stratigraphical position within the Valdenoceda Fm, as this unit lies directly below the Sobrepeña Formation. In this regard, it may be recalled that final depositional cycle DC13 of the Maastrichtian is poorly represented across the northern limb of the Villarcayo Syncline (Floquet 1991; Pluchery 1995; Berreteaga 2008).

The Maastrichtian vertebrate assemblages of the slightly younger Torme Formation at Albaina (Treviño County, Basque-Cantabrian Region) constitute the other only noticeable marine faunae in the Iberian Peninsula to compare. These two fossil sites record the most diverse Maastrichtian assemblages of marine vertebrates in southwestern Europe.

Acknowledgements

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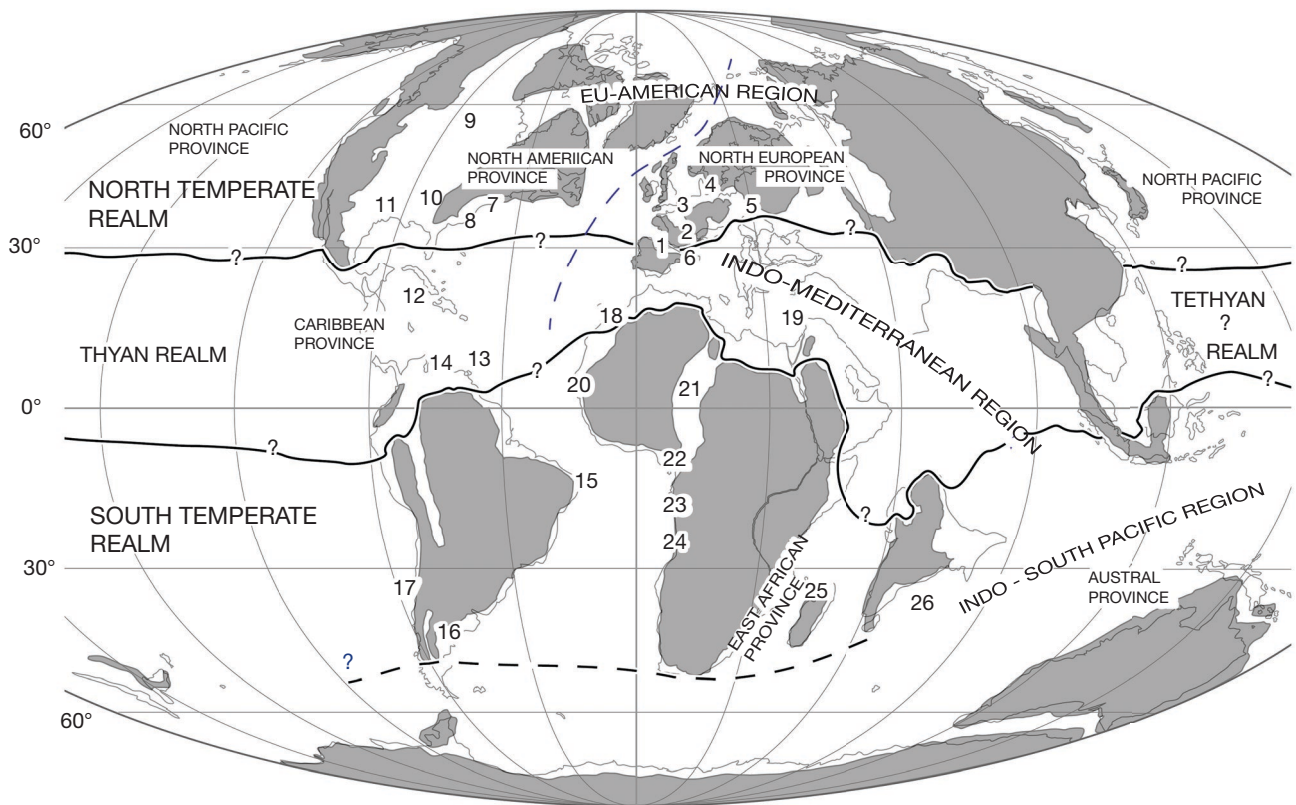


FIG. 13. — The Earth during the Maastrichtian times with the main selachian sites indicated (modified from Corral 2018; see this publication for the references): 1, Basque-Cantabrian Region, Spain; 2, Southern France; 3, Netherlands and Franco-Belgian basins; 4, Denmark; 5, Bulgaria; 6, North Catalonia, Spain; 7, New Jersey, USA; 8, North Carolina, United States; 9, Western Interior, South Dakota, United States; 10, Arkansas, United States; 11, Texas, USA; 12, Jamaica; 13, Trinidad; 14, Venezuela; 15, Brazil; 16, Argentina; 17, Chile; 18, Morocco; 19, Libya, Egypt, Jordan, Syria, and Israel; 20, Senegal; 21, Niger; 22, Nigeria; 23, DR Congo; 24, Angola; 25, Madagascar; 26, India. Palaeogeographical map redrawn from Smith *et al.* (1984) and biogeographical units after Kaufmann (1973).

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APPENDICES

APPENDIX 1. — List of figured actinopterygian elements transferred from the University of the Basque Country (UPV/EHU, Leioa) to the Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa (MCNA, Vitoria-Gasteiz). Figuration in Berreteaga *et al.* (2011).

TABLE 1. — The known vertebrate taxa of the Maastrichtian Valdenoceda Formation found at Quintanilla la Ojada (Basque-Cantabrian Region).

Class CHONDRICHTHYES Huxley, 1880	Class OSTEICHTHYES Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838	Subclass Actinopterygii Cope, 1887
Superorder Galeomorphii Compagno, 1973	Infraclass Neopterygii Regan, 1923 sensu Poyato-Ariza, 2015
Order Carcharhiniformes Compagno, 1973	Order Pycnodontiformes Berg, 1937
Family Triakidae Gray, 1851	Pycnodontiformes indet.
Genus <i>Palaeogaleus</i> Gurr, 1962	Suborder Pycnodontoidei Nursall, 1996
<i>Palaeogaleus faujasi</i> (Geyn, 1937)	Superfamily Pycnodontoidea Agassiz, 1833 sensu Poyato-Ariza & Wenz, 2002
Order Lamniformes Berg, 1958	<i>Pycnodontoidea</i> indet. Morphotype 1
Family Anacoracidae Casier, 1947	<i>Pycnodontoidea</i> indet. Morphotype 2
Genus <i>Squalicorax</i> Whitley, 1939	Family Pycnodontidae Agassiz, 1833 sensu Nursall, 1996
<i>Squalicorax kaupi</i> (Agassiz, 1843)	Genus <i>Anomoeodus</i> Forr, 1887
<i>Squalicorax pristodontus</i> (Agassiz, 1843)	cf. <i>Anomoeodus</i> sp.
<i>Squalicorax</i> sp.	Division Halecostomi Regan, 1923 sensu Poyato-Ariza, 2015
Family Odontaspidae Müller and Henle, 1839	Order Amiiformes Hay, 1929 sensu Grande & Bemis, 1998
Genus <i>Carcharias</i> Rafinesque, 1810	Family Amiidae Bonaparte, 1838
<i>Carcharias heathi</i> Case & Cappetta, 1997	cf. Amiidae indet.
<i>Carcharias</i> sp.	Subdivision Teleostei Müller, 1846 sensu Patterson & Rosen, 1977
Family Otodontidae Glikman, 1964	Order Elopiformes Greenwood, Rosen, Weitzman & Myers, 1966
Genus <i>Cretolamna</i> Glikman, 1958	Superfamily Albuloidea Greenwood, Rosen, Weitzman & Myers, 1966
<i>Cretolamna</i> aff. <i>appendiculata</i> (Agassiz, 1843)	Family Phyllodontidae Sauvage, 1875 sensu Estes, 1969
Family Serratolamnidae Landemaine, 1991	Subfamily Phyllodontinae Sauvage, 1875 sensu Estes, 1969
Genus <i>Serratolamna</i> Landemaine, 1991	Phyllodontinae indet.
<i>Serratolamna serrata</i> (Agassiz, 1843)	Subfamily Paralbulinae Estes, 1969
Order Orectolobiformes Applegate, 1972	Paralbulinae indet.
Family Ginglymostomatidae Gill, 1862	Order Aulopiformes Rosen, 1973
Genus <i>Plicatoscyllium</i> Case & Cappetta, 1997	Family Enchodontidae Lydekker in Nicholson & Lydekker, 1889
<i>Plicatoscyllium lehneri</i> (Leriche, 1938)	Enchodontidae indet. Morphotype A
Superorder Batomorphii Cappetta, 1980	Enchodontidae indet. Morphotype B
Order Rajiformes Berg, 1940	Enchodontidae indet. Morphotype C
Suborder Rhinobatoidei Fowler, 1941	Superorder Acanthopterygii Klein, 1885 sensu Johnson & Patterson, 1993
Family Rhinobatidae Müller & Henle, 1838	Clade Acanthomorpha Rosen, 1973 sensu Johnson & Patterson, 1993
Genus <i>Rhinobatos</i> Link, 1790	Acanthomorpha indet.
<i>Rhinobatos echavei</i> Cappetta & Corral, 1999	
<i>Rhinobatos ibericus</i> Cappetta & Corral, 1999	
<i>Rhinobatoidei</i> incert. fam.	
Genus <i>Vascobatis</i> Cappetta & Corral, 1999	
<i>Vascobatis albaitensis</i> Cappetta & Corral, 1999	
Suborder Sclerorhynchoidei Cappetta, 1980	
Family Sclerorhynchidae Cappetta, 1974	
Genus <i>Ganopristis</i> Arambourg, 1935	
<i>Ganopristis leptodon</i> Arambourg, 1935	
Order Myliobatiformes Compagno, 1973	
Superfamily Dasyatoidea Whitley, 1940	
Dasyatoidea incert. fam.	
Genus <i>Coupatezia</i> Cappetta, 1982	
<i>Coupatezia fallax</i> (Arambourg, 1952)	
Superfamily Myliobatoidea Compagno, 1973	
Family Rhombodontidae Cappetta, 1987	
Genus <i>Rhombodus</i> Dames, 1881	
<i>Rhombodus binkhorsti</i> Dames, 1881	
<i>Rhombodus</i> sp.	
	CLASS REPTILIA Laurenti, 1768 (sensu Modesto & Anderson, 2004)
	Order Squamata Oppel, 1811
	Family Mosasauridae Gervais, 1852
	Subfamily Mosasaurinae Gervais, 1852
	Genus <i>Mosasaurus</i> Conybeare, 1822
	<i>Mosasaurus</i> sp.
	Subfamily Plioplatecarpinae Dollo, 1884
	Genus <i>Prognathodon</i> Dollo, 1889
	<i>Prognathodon</i> sp.
	Superorder Dinosauria Owen, 1842
	Order Ornithischia Seeley, 1887
	Suborder Ornithopoda Marsh, 1881
	Family Hadrosauridae Cope, 1869
	Hadrosauridae indet.

TABLE 2. — Relative abundance of selachian species at Quintanilla la Ojada site. Percentage values are based on a sample of 180 teeth. Relative abundance ranges: abundant (>30% teeth in total assemblage); common (10–30% teeth in total assemblage); uncommon (5–10% teeth in total assemblage); rare (4–5% teeth in total assemblage); extremely rare (1–4% teeth in total assemblage).

Order	Species	Relative abundance	no.	%
Orectolobiformes	<i>Plicatoscyllium lehneri</i> (Leriche, 1938)	extremely rare	3	1.67
Lamniformes	<i>Carcharias heathi</i> Case and Cappetta, 1997	uncommon	15	8.33
–	<i>Carcharias</i> sp.	extremely rare	3	1.67
–	<i>Cretolamna</i> sp. aff. <i>C. appendiculata</i> (Agassiz, 1843)	extremely rare	1	0.56
–	<i>Serratolamna serrata</i> (Agassiz, 1843)	common	23	12.78
–	<i>Squalicorax kaupi</i> (Agassiz, 1843)	uncommon	12	6.67
–	<i>Squalicorax pristodontus</i> (Agassiz, 1843)	uncommon	11	6.11
–	<i>Squalicorax</i> sp.	extremely rare	4	2.22
Carcharhiniformes	<i>Palaeogaleus faujasi</i> (Geyn, 1937)	extremely rare	3	1.67
Rajiformes	<i>Ganopristis leptodon</i> Arambourg, 1935	extremely rare	6	3.33
–	<i>Rhinobatos echavei</i> Cappetta & Corral, 1999	extremely rare	3	1.67
–	<i>Rhinobatos ibericus</i> Cappetta & Corral, 1999	extremely rare	1	0.56
–	<i>Vascobatis albatensis</i> Cappetta & Corral, 1999	uncommon	14	7.78
Myliobatiformes	<i>Coupatezia fallax</i> (Arambourg, 1952)	extremely rare	6	3.33
–	<i>Rhombodus binkhorsti</i> Dames, 1881	abundant	61	33.89
–	<i>Rhombodus</i> sp.	uncommon	14	7.78

TABLE 3. — Relative abundance of the actinopterygian taxa at Quintanilla la Ojada site. Percentage values are based on a sample of 205 teeth (modified from Berreteaga *et al.* 2011). Relative abundance ranges as in Table 2.

Order/Clade	Taxon	Relative abundance	no.	%
Pycnodontiformes	Pycnodontiformes indet.	extremely rare	8	3.90
	Pycnodontoidea indet. (morphotype 1)	rare	9	4.39
	Pycnodontoidea indet. (morphotype 2)	extremely rare	3	1.46
	Cf. <i>Anomoeodus</i> sp.	extremely rare	3	1.46
Amiiformes	Cf. Amiidae indet.	uncommon	11	5.37
Elopiiformes	Phyllodontinae indet.	extremely rare	3	1.46
	Paralbulinae indet.	abundant	120	58.54
Aulopiformes	Enchodontidae indet. (morphotype A)	common	28	13.66
	Enchodontidae indet. (morphotype B)	extremely rare	5	2.44
	Enchodontidae indet. (morphotype C)	extremely rare	8	3.90
Acanthomorpha	Acanthomorpha indet.	extremely rare	7	3.41