A new actinopterygian fauna from the latest Cretaceous of Quintanilla la Ojada (Burgos, Spain)

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ABSTRACT

We describe a new actinopterygian fauna from the uppermost Cretaceous of Quintanilla la Ojada (Burgos, Spain), in the Villarcayo Sinclynorium of the Basque-Cantabrian Region. It consists mostly of isolated teeth of pycnodontiforms (cf. *Anomoeodus* sp., Pycnodontoidea indet.), amiiforms (cf. Amiidae indet.) and teleosteans (elopiforms: Phyllodontinae indet., Paralbulinae indet.; aulopiforms: Enchodontidae indet., plus fragmentary fin spines of Acanthomorpha indet.). Paralbulinae teeth are the most abundant elements in the fossil assemblage. All the remains are disarticulated and show intense post-mortem abrasion. The fossil association has been found in dolomite sandstones that are laterally correlated with the Valdenoceda Formation (Lower to basal Upper Maastrichtian) of the Castilian Ramp. The observed taphonomic features are coherent with the sedimentological interpretation of the fossiliferous beds as coastal deltaic deposits.

KEY WORDS
Osteichthyes,
Pycnodontiformes,
Amiiformes,
Elopiformes,
Aulopiformes,
Acanthomorpha,
Maastrichtian,
Iberian Peninsula,
Basque-Cantabrian
Region.

RÉSUMÉ

Une nouvelle faune d'actinoptérygiens du Crétacé supérieur de Quintanilla la Ojada (Burgos, Espagne).

Une nouvelle faune d'actinoptérygiens du Crétacé supérieur de Quintanilla la Ojada (Burgos, Espagne), localité située dans le Synclinorium de Villarcayo dans la région basco-cantabrique, est décrite ici. La plupart du matériel correspond à des dents isolées de pycnodontiformes (cf. *Anomoeodus* sp., Pycnodontoidea indet.), d'amiiformes (cf. Amiidae indet.) et de téléostéens (Elopiformes : Phyllodontinae indet., Paralbulinae indet. ; Aulopiformes : Enchodontidae indet., ainsi que des fragments d'épines d'Acanthomorpha indet.). Les dents de Paralbulinae sont les éléments les plus abondants de l'association fossile. Tous les restes sont désarticulés et ont subi une abrasion post-mortem intense. Les fossiles ont été trouvés dans des dolomies sableuses qui sont corrélées latéralement avec la Formation Valdenoceda (Maastrichtien inférieur à base du Maastrichtien supérieur) de la Rampe Norcastillane. Les caractéristiques taphonomiques observées sont cohérentes avec l'interprétation sédimentologique des couches fossilifères comme ayant été déposées dans un milieu deltaïque côtier.

MOTS CLÉS
Osteichthyes,
Pycnodontiformes,
Amiiformes,
Elopiformes,
Aulopiformes,
Acanthomorpha,
Maastrichtian,
péninsule Ibérique,
région basco-cantabrique.

INTRODUCTION

Upper Cretaceous marine localities that have yielded actinopterygian remains are presently rather scarce in the sedimentary basins of Spain (see Poyato-Ariza *et al.* 1999a). One of the most important known sites is Albaina, located in the Laño quarry (Condado de Treviño; area situated within the Basque Country but administered by the province of Burgos), where pycnodontiform and teleostean fossils have been found in Upper Maastrichtian marine levels (Poyato-Ariza *et al.* 1999b). In the same quarry, the Upper Campanian to lowermost Maastrichtian fluviatile deposits of the Laño site have yielded scarce lepisosteiform and teleostean remains (Cavin 1999). Thus, the osteichthyan fossils of the Laño quarry occur at two distinct stratigraphic horizons and were accumulated in quite different circumstances; both Albaina and Laño are part of the Miranda-Treviño Synclinorium (Baceta *et al.* 1999). Recently, additional marine fish-bearing localities of Late Cretaceous age have been discovered in the Basque-Cantabrian Region (López-Horgue & Poyato-Ariza 2005, work in progress). The fossil association of the Maastrichtian locality of Quintanilla la Ojada (Burgos) is composed of actinopterygian, selachian, and reptile remains (Berreteaga *et al.* 2010, work in progress). The present paper aims to describe the actinopterygian fauna that occurs in this new vertebrate site, which consists mostly of teeth of pycnodontiforms, amiiforms, elopiforms, and aulopiforms, plus fragmentary acanthomorph spines.

MATERIAL AND METHODS

The vertebrate fossil remains of Quintanilla la Ojada (Burgos) have been collected since 2002. Some teeth were picked up in the field (or extracted from the matrix after bulk rock processing), but most of the remains were obtained by screen-washing of the sediment. About 300 kg of sediment were washed through 2 mm, 1 mm and 0.5 mm stainless steel meshes with running water in order to search for microremains. The fine fraction was washed again using a hand sieve of 0.25 mm. The sorting of the teeth and other microremains was made by means of stereomicroscopes. The material is housed in the laboratory of the Departamento de Estratigrafía y Paleontología of the Universidad del País Vasco/Euskal Herriko Unibertsitatea (Bilbao) (EHUEP). About 200 actinopterygian isolated teeth and a few fin spine fragments are known.

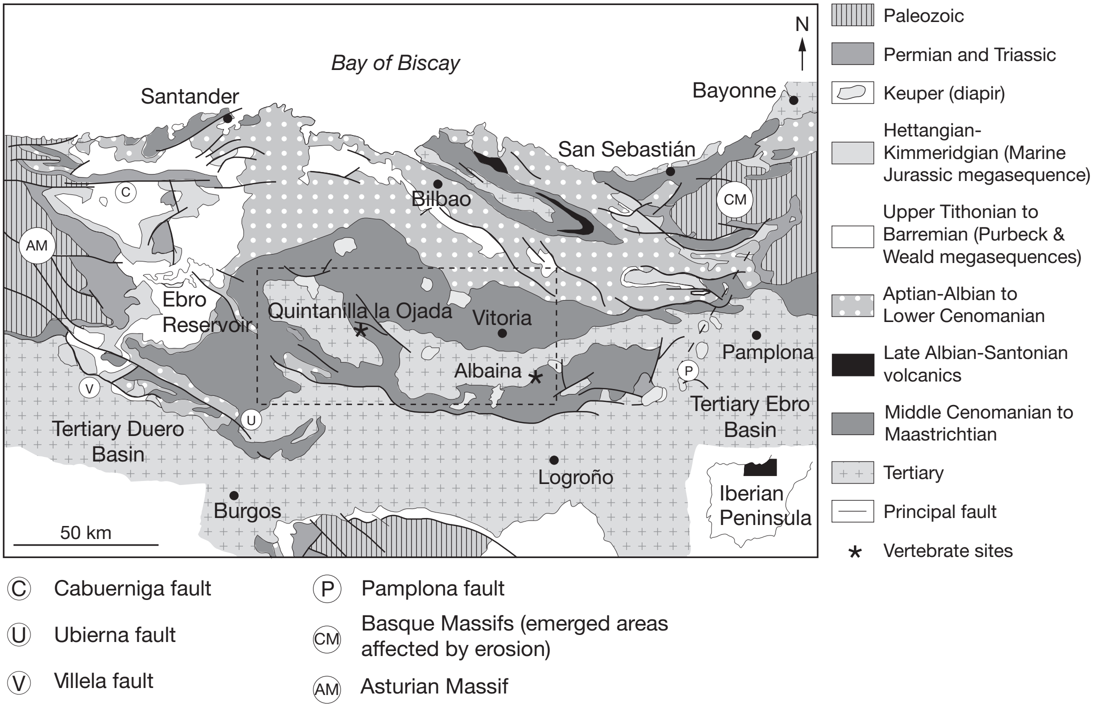

Fig. 1. — Geological map of the Basque-Cantabrian Region showing the location of the actinopterygian sites mentioned in the text.

LOCATION AND GEOLOGICAL SETTING

Quintanilla la Ojada is located in the northern part of Burgos province (Losa Valley), approximately 22 km east and 14 km northeast of Villarcayo and Trespaderne localities, respectively. Geologically, it is situated in the northern limb of the Villarcayo Synclinorium, in the northern part of the Basque-Cantabrian Region. Actinopterygian remains have been found in a quarry near the village of Quintanilla la Ojada.

The Villarcayo and Miranda-Treviño synclinoria belong to the southern part of the Basque-Cantabrian Basin (Fig. 1). During the Late Cretaceous and Early Paleogene, the sedimentation throughout the study area comprised varied depositional environments ranging from inner self to coastal and even continental ones (Floquet 1991; Pluchery 1995). In Campanian-Maastrichtian time interval the regression trend in the Basque-Cantabrian Basin resulted in the progradation of deltaic siliciclastic systems and the development of shallow marine environments, inhabited by a fauna rich in chondrichthyans and osteichthyans (López-Horgue & Poyato-Ariza 2005, work in progress).

The Cretaceous-Tertiary deposits in the northwest limb of the Villarcayo Synclinorium show several hundred meters of siliciclastic and carbonate materials arranged in transgressive-regressive cycles (Floquet 1991, 1998; Berreteaga 2008). Time-equivalent materials in the Miranda-Treviño Synclinorium are also arranged in comparable transgressive-regressive cycles (Baceta 1996; Baceta *et al.* 1999). The Maastrichtian deposits of both synclinoria have yielded abundant actinopterygian remains.

FACIES DESCRIPTION

The lower part of the Quintanilla la Ojada section consists of bioclastic calcarenites that include: bivalves, gastropods, brachiopods, green and red algae, sponges, oysters, echinoderms, bryozoans, serpulids, foraminifers, ostracods, and crustaceans (Floquet 1991). These calcarenites correspond to the top of the Tubilla del Agua Formation, as defined by Floquet *et al.* (1982).

This formation is dated from the final Santonian to probably early Campanian by foraminifera and ammonites (Floquet 1991, 1998; Gräfe 2005).

The Tubilla del Agua Formation shows a gradual facies-transition to the overlaying siliciclastic unit. The latter is nearly 60 m in thickness in the Quintanilla la Ojada site; it consists of well-rounded conglomerates and sandstones of mainly quartz composition arranged in meter-scale tabular sets with troughs cross-stratification, alternating with thin (cm thick) levels of laminated greenish siltstones. This siliciclastic unit shows important thickness variations across the Villarcayo Synclinorium, decreasing their thickness towards the North-West and the South. It reaches its maximum thickness (70-80 m) in the Quintanilla la Ojada and the Rioseco sections. The unit, named Rioseco Member, is laterally equivalent to the Moradillo de Sedano, Quintanaloma, and Sedano formations, which have been ascribed to the Campanian-Lower Maastrichtian and even basal Upper Maastrichtian (Floquet *et al.* 1982; Floquet 1991, 1998; Berreteaga 2008). In the study area, these three formations show minor lithological changes that are hardly noticeable because the zone corresponds to the area with the highest sedimentation rates of the Rioseco delta (Floquet 1991; Pluchery 1995; Berreteaga 2008).

The Rioseco delta sediments are overlain by lutites or coarse gravel sized conglomerates containing abundant vertebrate fossils. Both lithologies are only 50 cm thick and are overlain by sandy dolomites and organic-matter rich clays. These materials (dolomites and clays) are organised in metre-scale upward thinning sequences. These sequences are overlaid by a 30-40 m thick massive dolomite body. The sequences and overlaid dolomite body are regarded as laterally equivalent to the Valdenoceda Formation (Floquet *et al.* 1982; Floquet 1991; Berreteaga 2008). Moreover, the type of the sequences is characteristic of the Valdenoceda Formation. The vertebrate fossils occur in the lower part of the Valdenoceda Formation, in the two first meters, immediately above and closely related to the boundary between the Rioseco Member and the Valdenoceda Formation (Berreteaga *et al.* 2008b).

Finally, after a gradual increase in the clay content of the dolomites, there are nearly 30 m of variegated clays corresponding to a coastal plain environment (Sobrepeña Formation, Floquet 1991; Berreteaga *et al.* 2008a) (Fig. 2).

Facies interpretation

The Rioseco Member is interpreted as an easterly progradational deltaic system (Floquet 1991; Berreteaga 2008). The boundary between the Rioseco Member and the Valdenoceda Formation is an erosive surface defined by conglomerates, and is interpreted as a *ravinement* surface with conglomeratic transgressive *lag* deposits. This surface is correlated with the basal discontinuity of the DC12 depositional cycle (Fig. 2). This is one of the depositional transgressive-regressive cycles defined in the North-Castilian Ramp by Floquet (1998). The base of the Valdenoceda Formation represents the increasing influence of marine conditions in the system. The stratigraphical position of the Valdenoceda Formation suggests an Early to basal Late Maastrichtian age (Floquet 1991; Berreteaga 2008; Berreteaga *et al.* 2010).

Time-equivalent transgressive-regressive cycles formed in similar conditions outcrop in the Miranda-Treviño Synclinorium (Pluchery 1995; Baceta 1996). In the Albaina site (Condado de Treviño), vertebrate fossils have not been discovered related to the DC12 depositional cycle, but near the base of the DC13 depositional cycle (Fig. 2). The shallow marine calcarenites of Albaina are laterally equivalent to the Torme Formation (Pluchery 1995; Cappetta & Corral 1999; Berreteaga 2008). In Albaina, vertebrate fossils also occur associated with a transgressive surface (Intra-Maastrichtian Unconformity of Baceta *et al.* 1999) (Fig. 2). This discontinuity is correlated with the cycle boundary of CB13 (*sensu* Floquet 1998). The Albaina site is regarded as Upper Maastrichtian (Baceta *et al.* 1999); the selachian association indicates a Late but not latest Maastrichtian age (Cappetta & Corral 1999).

Taphonomic observations

The fact that only isolated teeth and fin spines have been unearthed from Quintanilla la Ojada obviously indicates the occurrence of total disarticulation of the individuals, and, very probably, intense selective transport as well. This is supported by recurrent observation of noticeable, substantial abrasion facets (e.g., Figs $3C_1$, D_2; $4A_1$, D_2). On the teeth,

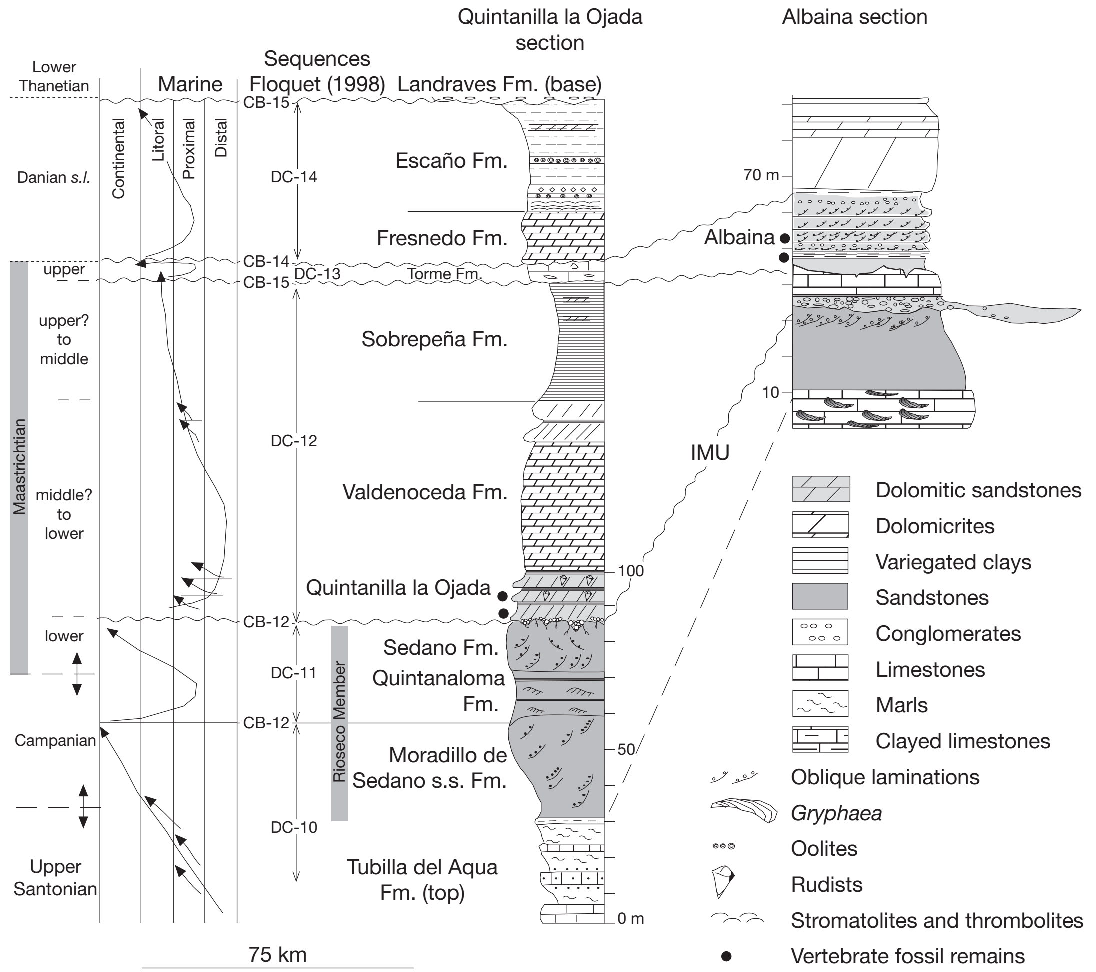

FIG. 2. — Correlation of transgressive-regressive depositional cycles from the Late Cretaceous sections in Villarcayo Synclinorium (based on the Quintanilla la Ojada section) and Miranda-Treviño Synclinorium (based on the Albaina section). The Upper Cretaceous interval shows stratigraphical units, actinopterygian fossil-bearing units and transgressive-regressive depositional cycles. The cycles described from the Upper Santonian until the end of the Cretaceous are DC10-13, all of them are included in a transgressive-regressive megacycle called LTC4 by Floquet (1998). Abbreviation: **IMU**, Intra-Maastrichtian Unconformity.

post-mortem abrasion facets are distinguishable from anatomic wearing facets during lifetime of the individual by: a) the aspect of their surface, which is, respectively, rough rather than smooth; b) the size of each facet in relation to the total surface of the tooth, which is extensive rather than limited, respectively; c) their pattern of distribution, which is regular rather than irregular, and d) their situation, which occurs on mechanical contact surfaces rather than on anatomical contact surfaces.

Following the abrasion categories described by Vullo (2007), 95% of the studied actinopterygian teeth show moderate to advanced abraded stage, indicating heavy transport. Such heavy transport must have been biostratinomic, since the results of geochemical analysis (e.g., distribution of rare earth elements) in vertebrate fossils of Quintanilla la Ojada allow us to reject the hypothesis of reelaborated bones in this site (Berreteaga 2008).

SYSTEMATIC PALAEONTOLOGY

The osteichthyan fish remains from Quintanilla la Ojada are represented by isolated actinopterygian teeth mostly, plus a few specimens of fin spines. In general, isolated actinopterygian teeth provide limited taxonomic information, and usually present considerable parataxonomic problems. In this particular locality, the abrasion of the material is yet another limitation for this type of study, as it often rubs out significant taxonomic characters such as crests, ridges, pits, and so on. For these reasons, the taxonomic assessments in the present paper are to be taken with precaution, and are made mostly at higher-rank level. Lower-rank assignments are proposed only in the cases were the assessment is reasonably reliable and parataxonomic problems are limited. In addition, the teeth are also classified according to morphotypes, as this classification can be very useful for palaeoecological comparisons with other fossil assemblages (e.g., Buscalioni *et al.* 2008).

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Division HALECOSTOMI
Regan, 1923 *sensu* Patterson 1973
Order PYCNODONTIFORMES Berg, 1933
Pycnodontiformes indet.

Morphotype 1: molariform teeth – type A
(Fig. 3A, B)

MATERIAL EXAMINED. — Eight molariform teeth (EHUEP Q1-Q8).

DESCRIPTION

Molariform teeth presenting a low crown, very enlarged, with great development of enamel, and especially of dentine; the basal part, which is devoid of dentine, is consistently lost, as it remains inside the bone when the tooth is disarticulated. EHUEP Q7 is a very broken and heavily transported tooth, probably originally oval in shape (Fig. 3A); there are also three teeth with oval contour in occlusal view and heavy abrasion facets, 1.6 to 2.5 mm in major axis length. Three other teeth have subcircular contour in occlusal view, 2.0 to 3.1 in major axis length; EHUEP Q8 is the biggest one, 7.3 × 5.7 mm, with the occlusal side flattened by abrasion (Fig. 3B).

DISCUSSION

Molariform teeth *sensu* Poyato-Ariza (2005a) are typical of pycnodontiforms, and are always present on the vomer and the prearticular of this neopterygian order. Both oval and subcircular molariform teeth are broadly present among Pycnodontiformes (Poyato-Ariza & Wenz 2002), so that they cannot be assessed to any particular taxon within this group. As for diversity, both morphologies are often present on a single individual (e.g., Poyato-Ariza & Wenz 2002: figs 21A, 22C; Poyato-Ariza 2003: fig. 1C, D), so they do not necessary indicate the presence of two distinct taxa. The molariform teeth of the Pycnodontidae are relatively higher in lateral view than those of the Sparidae, which have been cited to occur in the Late Cretaceous (e.g., Buffetaut *et al.* 1996), and whose crowns are much more flattened.

Suborder PYCNODONTOIDEI Nursall, 1996
Superfamily PYCNODONTOIDEA
Agassiz, 1833 *sensu* Poyato-Ariza & Wenz 2002
Pycnodontoidea indet.

Morphotype 2: incisiform teeth
(Fig. 3C-E)

MATERIAL EXAMINED. — Nine incisiform teeth (EHUEP Q9-Q17).

DESCRIPTION

Incisiform teeth present a high crown, enlarged and flattened, with labial side more or less convex, lingual side markedly concave, and occlusal border quite narrower than the base (labio-lingual dimension). See also Nursall (1996a), Poyato-Ariza & Wenz (2002) and Poyato-Ariza (2005a) for further details. In contrast with molariform teeth, incisiform teeth usually exhibit at least part of their base together with their crown. In

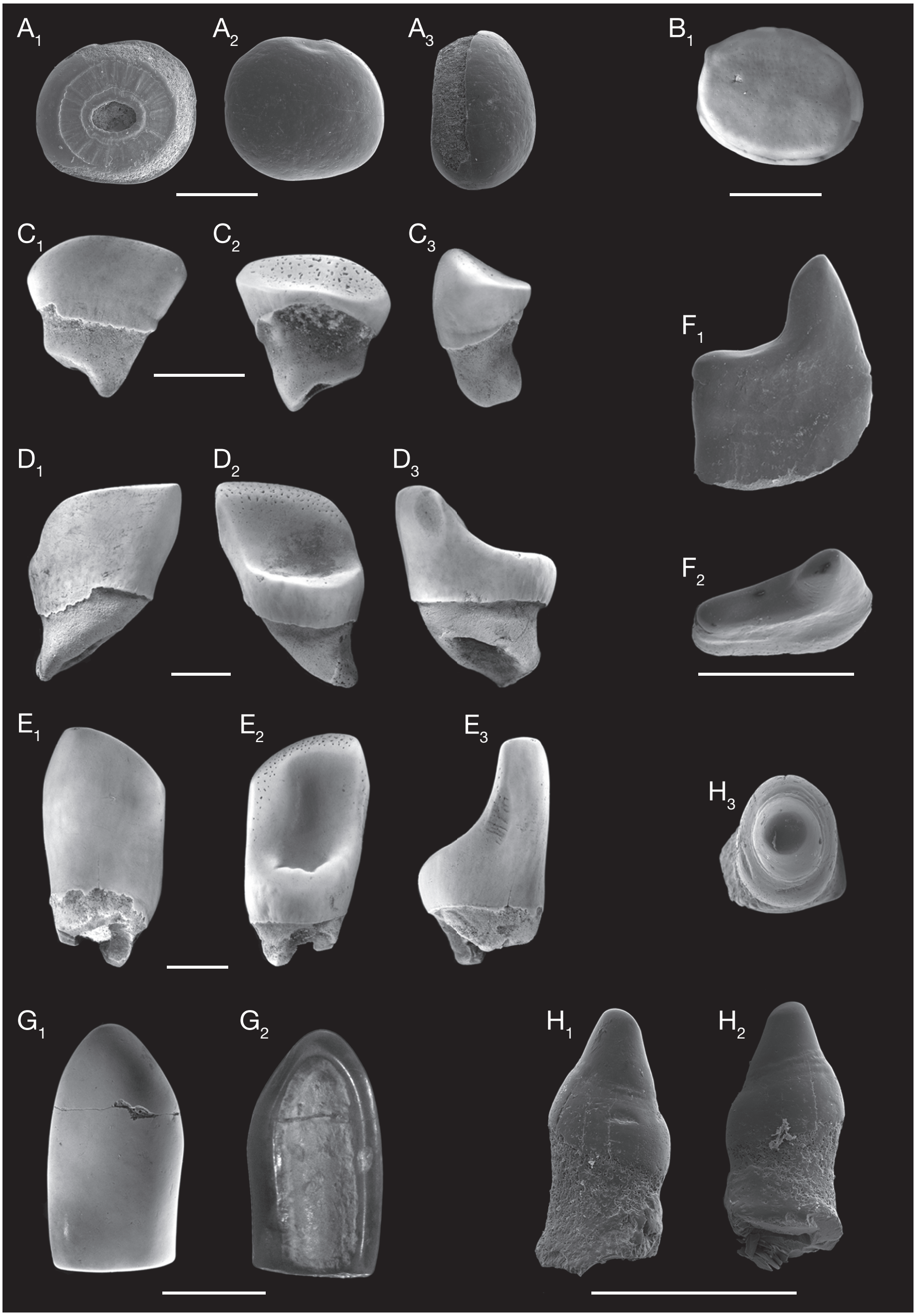

FIG. 3. — Pycnodontiforms and amiiforms from Quintanilla la Ojada (Burgos): **A**, **B**, Pycnodontiformes indet., molariform teeth EHUEP Q7 in basal (**A$_1$**), occlusal (**A$_2$**) and lateral (**A$_3$**) views and EHUEP Q8 in occlusal (**B$_1$**) view; **C**-**E**, Pycnodontoidea indet., incisiform teeth EHUEP Q14, Q16, Q15 in labial (**1**), lingual (**2**) and mesiodistal (**3**) views; **F**, Pycnodontoidea indet., branchial tooth EHUEP Q20 in lateral (**F$_1$**) and apical (**F$_2$**) views; **G**, cf. *Anomoedus* sp., molariform tooth EHUEP Q23 in occlusal (**G$_1$**) and basal (**G$_2$**) views; **H**, cf. Amiidae indet., conic-styliform tooth EHUEP Q26 in mesiodistal (**H$_1$**), (**H$_2$**) and occlusal (**H$_3$**) views. Scale bars: A, H, 1 mm; B, G, 4 mm; C-F, 2 mm.

Quintanilla la Ojada, incisiform teeth present intense abrasion, which has considerable reduced their original size, and even veiled their original morphology (e.g., Fig. 3C). The parallel canals of the dentine layer are often clearly visible. The bigger tooth (Fig. 3E) is 7.6 mm high (crown is 5.5 mm high), 4.2 mm in maximum width, and 5.2 mm in labiolingual dimension; the smallest teeth are about 1.2 mm in height and maximum width.

DISCUSSION

The inclination of the occlusal border from the horizontal plane (Fig. 3D_1, D_2, E_1, E_2) was most likely caused by wearing during life time of the individual (FJPA, pers. obs. on articulated pycnodontoid specimens; for a list of taxa and material, see Poyato-Ariza & Wenz 2002, 2004), but the uniform, intense abrasion observed is post-mortem (see criteria above). The presence of fully incisiform premaxillary and dentary teeth is a typical diagnostic character of the Pycnodontoidea (Poyato-Ariza & Wenz 2002). Although it is reverted in some members of the Pycnodontoidea, such as *Nursallia* Blot, 1987 (Poyato-Ariza & Wenz 2002) and *Akromystax* Poyato-Ariza & Wenz, 2005, and is therefore not an autapomorphy, it is not known in any taxon outside this superfamily; it is therefore a synapomorphy of this group, and consequently a reliable taxonomic character.

Pycnodontoidea indet.

Morphotype 3: branchial teeth
(Fig. 3F)

MATERIAL EXAMINED. — Three branchial teeth (EHUEP Q18-Q20).

DESCRIPTION

These branchial teeth are hook-shaped, pedicellate, and very flattened, markedly laterally compressed; they present a wide base and a conspicuous, stout anterior process (Fig. 3F). They are usually higher than long, but they can also be wider than high; one of these three teeth is 1.0 mm wide and 0.6 mm high. In this locality, they are scanter than other pycnodont teeth, and range in size from 0.6 to 2.8 mm in maximum dimension.

DISCUSSION

This tooth morphotype has for a long time been assessed to "*Stephanodus*" Zittel, 1883, but this is clearly a parataxon, and must not be used in formal taxonomy until its in-depth revision is accomplished. This tooth morphotype is found in the branchial chamber of a number of Pycnodontoidea, and is not known outside the superfamily (Kriwet 1999; Poyato-Ariza & Wenz 2002, 2005; FJPA, pers. obs.), so that their occurrence in this locality does not necessarily indicate the presence of another distinct taxon of this superfamily. Although elongated branchial teeth have been reported outside the Pycnodontoidea, the type of broad pharyngeal tooth herein reported has never been found in non-pycnodontoid pycnodontiforms. Similar pharyngeal teeth have been, nonetheless, found in other groups, such as Semionotiformes (e.g., Thies 1989). Since they are associated to pycnodont teeth, and since remains of other candidate groups are absent, they are more confidently assessable to pycnodontoids than to other groups.

Family PYCNODONTIDAE
Agassiz, 1833 *sensu* Nursall 1996b
Genus *Anomoeodus* Forir, 1887
cf. ***Anomoeodus*** sp.

Morphotype 4: molariform teeth – type B
(Fig. 3G)

MATERIAL EXAMINED. — Three broken and incomplete teeth (EHUEP Q21-Q23).

DESCRIPTION

Molariform teeth whose major axis, in occlusal view, is about three times longer than the minor axis; their medial edge is tapering, and the general outline, in occlusal view, is curved and sort of drop-shaped. The occlusal surface is eroded, so that it is smooth, and the presence of crests, ridges, or any other kind of ornamentation cannot be estimated. The biggest preserved fragment (Fig. 3G) is 5.1 mm wide and 9.8 mm long (preserved portion).

DISCUSSION

This crown morphology, only found in prearticular teeth, is described in detail and compared with other molariform shapes in Poyato-Ariza & Wenz (2002: 174, 175). Only two pycnodont genera, reliably identifiable from articulated remains, bear this type of molariform, tapering-edged teeth (Poyato-Ariza & Wenz 2002). One of them is *Ichthyoceros* Gayet, 1984, from the Cenomanian of the Lebanon, but the size of these teeth in this genus is significantly smaller than the teeth from Quintanilla la Ojada. The other genus where this type of teeth is known, and for which are typical, is *Anomoeodus*, known from the Early Cretaceous of Uña (Kriwet 1999) and from the Late Cretaceous of the Netherlands and England (e.g., Poyato-Ariza & Wenz 2002: 143). In both cases, the teeth are ornamented, with a central ridge and/or light to strong crenulations (Kriwet 1999; Poyato-Ariza & Wenz 2002). The teeth from Quintanilla la Ojada are devoid of any ornamentation, but this is probably due to abrasion during the fossilization process. In addition, the specimens are broken and incomplete, so their assessment to cf. *Anomoeodus*, based on the general morphology combined with their relatively big size, is to be taken with precaution.

Order AMIIFORMES
Hay, 1929 *sensu* Grande & Bemis 1998
Family AMIIDAE Bonaparte, 1838
cf. Amiidae indet.

Morphotype 5: conic-styliform teeth
(Fig. 3H)

MATERIAL EXAMINED. — 11 teeth (EHUEP Q24-Q34).

DESCRIPTION

Small, conic-styliform teeth with pointed, well-defined enameloid, glossy crown, straight to slightly curved in lateral view. The crown presents no striae, lateral crests, projections, or processes whatsoever. The enamel is thin, smooth, and translucid. Most specimens are broken, yet they do not show heavy abrasion facets. This type of teeth is relatively rare in this locality. The only complete known tooth measures 1.2 mm of total height and 0.4 mm of maximum diameter; the glossy crown is 0.6 mm high (Fig. 3H). Other teeth are more or less fragmentary: the preserved part of the biggest one is 1.9 mm high (glossy crown, maybe incomplete), so that its total height would be at least 3.8 mm, as estimated from comparison of crown height to total height in the complete tooth just described.

DISCUSSION

Small conic-styliform teeth of this kind are typical of small to medium-sized fishes with ichthyofagous diet and predatory habits. When compared with other geographically close ichthyofagous forms, they appear to be typical of the family Amiidae (e.g., Grande & Bemis 1998), which includes both marine and freshwater fossil forms plus the Recent *Amia calva* Linnaeus, 1766, which is an abundant freshwater North American species. The teeth of other typical small- to medium-sized ichthyofagous fishes from the Late Jurassic-Cretaceous, such as the Aspidorhynchidae, Ionoscopidae or Allothrissopidae, are quite different in curvature, height to diameter ratio, morphology of the occlusal end of crown, etc. (e.g., Thies & Mudroch 1996; Brito 1997). Other ichthyofagous Mesozoic fishes, such as the Ichthyodectidae, bear much bigger teeth. Other similar teleostean teeth seem to present a not so glossy and traslucid crown (Martín-Abad & Poyato-Ariza pers. obs.). Pending a thorough revision of this type of teeth from a reliable sample of articulated material, it is herein considered as cf. Amiidae indet.

Subdivision TELEOSTEI Müller, 1846
sensu Patterson & Rosen 1977
Order ELOPIFORMES
Greenwood, Rosen, Weitzman & Myers, 1966
Superfamily ALBULOIDEA
Greenwood, Rosen, Weitzman & Myers, 1966

Family Phyllodontidae Sauvage, 1875
sensu Estes 1969
Subfamily Phyllodontinae Sauvage, 1875
sensu Estes 1969
Phyllodontinae indet.

Morphotype 6: flattened teeth
(Fig. 4A)

Material examined. — Three teeth (EHUEP Q35-Q37).

Description

These teeth are somewhat similar to molariform teeth because their single crown is robust, stout, and subcircular in occlusal view (Fig. $4A_1$). But this morphotype is much more flattened, so that their thickness, measured as their occluso-basal dimension, is less than one third of their diameter in occlusal view (Fig. $4A_3$), quite lower than that of molariform teeth (Fig. $3A_3$). Their dentine and enamel are less developed than those of molariform teeth, and they lack the small central cavity that all molariform teeth exhibit when observed in basal view (Figure $4A_2$ *versus* Figure $3A_1$, respectively). In Quintanilla la Ojada, flattened teeth are very rare and only three specimens are known. Specimen EHUEP Q35 measures 2.3 × 2.9 mm in occlusal view, and 0.9 mm thick in occluso-basal dimension. It shows life-wearing facets, indicating that it was probably a functional rather than a replacement tooth, and also strong transport facets, with loss of the whole central region. Specimen EHUEP Q36 (Fig. 4A) is the biggest one, as it measures 6.6 × 4.7 mm in occlusal view, and 1.9 mm in occluso-basal dimension. This specimen is more irregular in contour, with concave occlusal surface and convex basal surface. It shows abrasion facets, but apparently no life-wearing surfaces, suggesting it was a replacement, non-functional tooth. Finally, specimen EHUEP Q37 measures 5.0 × 4.1 mm, and is heavily eroded by abrasion. In all three cases, abrasion prevents from observing any tooth ornamentation; the irregular exposures (Fig. $4A_1$) correspond to the inner tissular structure.

Discussion

Phyllodont teeth, unlike pycnodont teeth, grow as replacement sets (e.g., Estes 1969). In phyllodontines, the replacement sets grow very closely arranged, hence the remarkable flatness of each individual tooth. However, no complete phyllodont dentitions are known from this locality (unlike Albaina: Poyato-Ariza *et al.* 1999b). Although the individual tooth morphology of this type of tooth is consistent with that of the genus *Phyllodus* Agassiz, 1839, generic assessments within this group are mostly based on characters of complete tooth plates, and therefore, isolated teeth can only be assessed, with the necessary precautions, to the Phyllodontinae.

Subfamily Paralbulinae Estes, 1969
Paralbulinae indet.

Morphotype 7: globular teeth
(Fig. 4B, C)

Material examined. — 122 teeth (EHUEP Q38-Q160).

Description

High, robust teeth of globular shape in overall morphology, circular in occlusal view and nearly circular in lateral view, except for their insertion base. They present a well-developed basilar foramen with strong, striated borders (Fig. $4C_2$). The enamel is thick, heavy, opaque, and blackened. These teeth are, by far, the most abundant actinopterygian remains in Quintanilla la Ojada. They usually show life-wearing facets, and especially transport facets; whenever accessible to observation (some teeth with less intense wearing and abrasion), certain ornamentation can be observed in form of faint, diverging crests with tiny intercalated tubercles (Fig. $4B_1$). These teeth range from 0.6 to 2.3 mm in diameter, although the majority of them measures around 1.5 mm.

Discussion

Paralbulinae teeth, like Phyllodontinae teeth, grow as replacement sets, although the sets, and

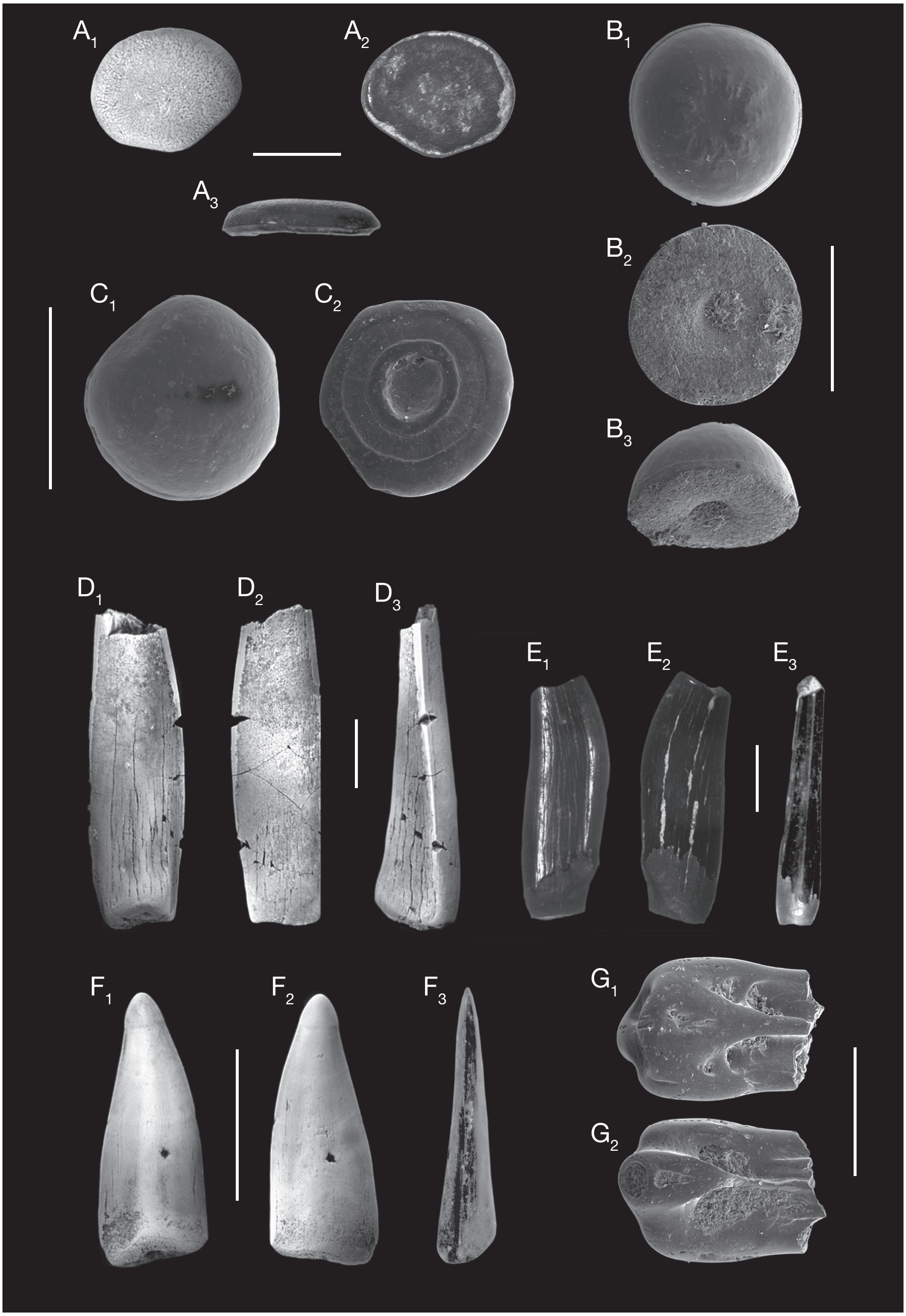

FIG. 4. — Teleosteans from Quintanilla la Ojada (Burgos): **A**, Phyllodontinae indet., flattened tooth EHUEP Q36 in occlusal (**A1**), basal (**A2**) and lateral (**A3**), views; **B**, **C**, Paralbulinae indet., globular teeth EHUEP Q61-62 in occlusal (**1**), basal (**2**) and inclined lateral (**3**) views; **D**-**F**, Enchodontidae indet.; **D**, caniniform teeth EHUEP Q175 (morphotype A); **E**, EHUEP Q186 (morphotype B); **F**, EHUEP Q193 (morphotype C) in labial (**1**), lingual (**2**) and mesiodistal (**3**) views; **G**, Acanthomorpha indet., fragmentary fin spine EHUEP Q200 in posterior (**G1**) and anterior (**G2**) views. Scale bars: A, D-F, 4 mm; B, G, 1 mm; C, 2 mm.

consequently the teeth, are quite different in morphology and arrangement, much less compact than phyllodontine sets (e.g., Estes 1969), and, consequently, individual teeth are quite higher, nearly spherical. As for phyllodontine teeth, no complete paralbuline dentitions are known from this locality (unlike, again, Albaina). Although the individual tooth morphology is consistent with that of the genus *Paralbula* Blake, 1940, including the development of the basilar foramen, generic assessments, within this group as well, are greatly based on characters of complete tooth plates. Consequently, these isolated teeth can only be assessed, with the necessary precautions, to the Paralbulinae.

Order AULOPIFORMES Rosen, 1873
Family ENCHODONTIDAE Lydekker, 1889
Enchodontidae indet.

Morphotype 8: caniniform teeth – type A
(Fig. 4D)

MATERIAL EXAMINED. — 28 teeth (EHUEP Q161-Q183, Q205-Q209).

DESCRIPTION

Enchodontidae material from this locality is quite fragmentary and very worn out. The term caniniform is used for teeth that are stout, strong, very elongated, and laterally compressed, presenting cutting edges and pointed to slightly blunt occlusal end. Those of this locality present a base that is not expanded, but is well marked, bearing tiny pits. The contour of the crown seems more or less straight in labial and lingual views, and slightly curved backwards in mesial and distal views. Their incompleteness and bad state of preservation, though, prevent from knowing their precise degree of curvature, or possible sigmoid shape when complete. The lingual side is always quite flatter than the labial side, which is rather convex. Some better preserved remains (Fig. 4D) exhibit sharp crests developed on their cutting edges (mesial and distal). These crests are also slightly curved, although the incompleteness of the specimen prevents from knowing their precise shape (simply curved or sigmoid). Wearing would prevent from observing striae, had these been present. The material is too fragmentary to provide accurate size range estimations: the preserved part of the biggest specimen (Fig. 4D) is 18.9 mm; its maximum width at about the mid-length of the preserved part of the crown.

DISCUSSION

As for molariform and incisiform teeth above, the term caniniform is used as a descriptive and ecomorphological term only, and does not have any kind of taxonomic or phylogenetic implication on itself. This type of caniniform teeth, so strong and elongated, is typical of the Enchodontidae, who present surprisingly big teeth with this morphology on their dentary, dermopalatine, and ectopterygoid bones (e.g., Goody 1969; Chalifa 1996; Poyato-Ariza *et al.* 1999b). Assessment of these teeth to a particular genus within the Enchodontidae is not reliable, since key characters such as size ranges, degree of elongation, and complete lateral profile are not accurately observable in this material, and it is only the combination of these characters, together with the presence of crests on the cutting edges (Poyato-Ariza *et al.* 1999b) that allows consistent assessment to *Enchodus* Agassiz, 1835 (or to any other particular genus). These teeth are therefore considered as Enchodontidae indet.

Morphotype 9: caniniform teeth – type B
(Fig. 4E)

MATERIAL EXAMINED. — Five teeth (EHUEP Q184-Q188).

DESCRIPTION

Unlike caniniform teeth of type A, the contour of the crown in caniniform teeth type B is clearly sigmoid in labial and lingual views (Fig. 4E), instead of straight, and they are straight in mesial and distal views instead of slightly curved backwards (Fig. 4E_3). In addition, both sides, lingual and labial, are relatively flat, rather than convex.

The biggest specimen, 15.1 mm preserved high and 5.4 mm of maximum width (Fig. 4E); all specimens are fragmentary, incomplete. Crests on its cutting edges are not observable, but this may be due to abrasion.

Discussion

See above for caniniform teeth – type A.

Morphotype 10: caniniform teeth – type C
(Fig. 4F)

Material examined. — Eight teeth (EHUEP Q189-Q197).

Description

These teeth are scarcer and quite similar in general shape, although relatively less elongated, that is, comparatively larger, than those of type A and B; unlike type A and B, the maximum width occurs at the base of the tooth. Type B teeth are also apparently smaller. The contour of type C teeth is clearly sigmoid in labial and lingual views (Fig. 4F_1, F_2), and straight in mesial and distal views (Fig. 4F_3). The only complete tooth of this (and the other enchodontid) type is 7.0 mm high and 2.9 mm in maximum width (Fig. 4F).

Discussion

The three different types of caniniform teeth probably represent at least two distinct taxa, as the difference in meso-distal contour (sigmoid in B and C here *versus* straight in type A) might be significant at specific, and even generic level (in combination with other characters that are not observable in this material). In contrast, type C might correspond to younger individuals of the same taxon than type B, or even to smaller teeth of the same individual: it is typical of enchodontids to present the first (most anterior) tooth remarkably big and elongated on the dentary, dermopalatine, and ectopterygoid bones. As a consequence, the occurrence of a third morphotype is not necessarily an indication of the presence of a third distinct taxon within the Enchodontidae of this locality.

Superorder ACANTHOPTERYGII Klein, 1885
sensu Johnson & Patterson 1993
Clade ACANTHOMORPHA Rosen, 1973
sensu Johnson & Patterson 1993

Acanthomorpha indet.
(Fig. 4G)

Material examined. — Seven fragments of spines (EHUEP Q197-Q203).

Description

The fragments of fin spines are very partial: only the basal parts are preserved. They are apparently fragile, and quite worn out. The widest fragment measures 2.4 mm in maximum base width. When better preserved, the base of these fin spines shows: one pair of well-developed basal processes; one pair of large, comparatively bigger lateral processes; and a small anterior median process (Fig. 4G). They seem to present one single median cavity on their posterior side. The visible ornamentation consists of one pair of big, deep basal grooves.

Discussion

This is the only fish material other than teeth known from Quintanilla la Ojada. Johnson & Patterson (1993) affirm that true fin spines, that is, azygous, unsegmented, and laterally fused, are a diagnostic character of the Acanthomorpha (i.e. all Acanthopterygii excluding the Atherinomorpha). Their ornamentation, crests, processes, cavity, and general morphology are quite different from polypteriform or siluriform fin spines. The precise morphology, variability, and taxonomic distribution of the fin spines among Cretaceous acanthomorphs are at present very poorly understood, and consequently the scarce material from this locality is referred to Acanthomorpha indet.

DISCUSSION

Osteichthyan fishes are, in general, potentially misleading palaeoenvironmental indicators (Poyato-Ariza *et al.* 1998), so that the mere presence of any particular taxon is not a necessary indication of any particular environment. Not even the presence of pycnodontiform remains is a necessary indication of a marine palaeoenvironment, since these fishes are also known from continental palaeoenvironments (Nursall 1996b; Poyato-Ariza *et al.* 1998; Poyato-Ariza 2005a-c). Only the ensemble of the community, studied in combination with all other fauna and flora, and especially in combination with sedimentological and geochemical data, is palaeoecologically reliable. This especially applies to the fish material of this locality, where the remains are so partial that most of them cannot be assessed to any low rank taxon.

In overall, there are 10 different tooth morphotypes known from Quintanilla la Ojada. This number of different morphotypes, nonetheless, does not necessarily correspond to the same number of distinct taxa. The number of pycnodont taxa (4 morphotypes) can be estimated in a minimum of 2, but no certainty of additional diversity can be provided (see particular discussions above). There are probably no more than two distinct taxa of Enchodontidae indet. (see above). Consequently, this accounts for a reliable estimated diversity of 7 taxa, as inferred from these 10 tooth morphotypes. With the addition of the fin spines, which belong to a totally different taxon altogether, the whole actinopterygian diversity for Quintanilla la Ojada is estimated in a minimum of 8 different taxa. These correspond to 5 major taxa, order or higher. Two of these high rank taxa are non-teleostean ones: corresponding to 3 lower rank taxa, and the other three are teleostean ones, corresponding to 5 lower rank taxa.

The better assemblage comparisons (with the precautions explained above) are made with the geographically and temporally close locality of Albaina (Poyato-Ariza *et al.* 1999b). The higher rank taxa present in both localities are the same (with the exception of the Amiiformes, only known in Quintanilla la Ojada), although this is obviously a reflection of their similar taphonomic bias, in addition to their obvious ichthyofaunal similarities. That is, they have the same high rank taxa in common, but other actinopterygians that certainly must have formed part of the corresponding original communities (e.g., small teleosts with villiform or absent teeth), are not preserved due to destruction during taphonomic processes. But as far as they can be compared with the necessary precautions, the actinopterygian assemblages from Quintanilla la Ojada and Albaina are very similar in composition, and even in relative abundance (Table 1). For instance, phyllodontine teeth are rare, much scarcer than the extremely abundant paralbuline teeth in both localities. However, whenever the taphonomic bias and the state of preservation allow observation of significant characters, some differences in lower rank taxa can be found. For instance, the generic assessments that can be made for pycnodonts are different in both localities (cf. *Anomoeodus* sp. from Quintanilla la Ojada, also reported from Uña [Kriwet 1999]; cf. *Paramicrodon* sp. from Albania). Interestingly, the most derived forms present in both Quintanilla la Ojada and Albaina are different low rank taxa of the same high rank taxon (Acanthomorpha). The base of the acanthomorph fin spines from Quintanilla la Ojada, with their big pair of lateral processes and smaller anterior median process, are quite different from the Albaina acanthomorph fin spines, which show very faint lateral processes and comparatively bigger median process (Poyato-Ariza *et al.* 1999b: fig. 5C). The visible ornamentation, consisting of one pair of big, deep basal grooves, is also quite different from the small, shallow wavy grooves of the Albaina material. This means that the corresponding acanthomorph forms of both localities, although not identifiable at present, are clearly distinct taxa. There are, then, at least a couple of significant differences at low rank level within the general similarity at high rank level.

The assemblage of actinopterygian remains from Quintanilla la Ojada, as that of Albaina and other localities of comparable age, shows a larger diversity and greater abundance of teleostean taxa, within the mixture of primitive, non-teleostean and derived teleostean taxa that is characteristic to all of them. The most reliable ecomorphotype for ichthyofaunal comparisons is the durophagous one. The teeth with this function are heavy, stout, dense, and extremely resistant, and are consequently the best, more consistently, and more abundantly preserved in this kind of isolated-remains assemblages biased by strong, differential transport during the biostratinomic and/or fossil-diagenetic processes. In Quintanilla la Ojada, this ecomorphotype includes both non-teleosts (pycnodonts: morphotypes 1 and 4) and teleosts (phyllodonts: morphotypes 6 and 7), but teleosts (especially Paralbulinae) are largely dominant in number, by far, over non-teleosts.

This is interesting because Cretaceous ichthyofaunas from the Iberian area, in general, are characterized by this mixture of non-teleostean forms, mostly relicts from Jurassic times, and teleostean forms, which are in the process of replacing them. This replacement is especially remarkable and intense during the Late Cretaceous, by the end of which teleosts are experiencing the huge evolutionary radiation that would eventually make them the dominating fish forms, by far, in any aquatic environment from this time on. Pycnodonts, which are the dominating durophagous actinopterygians during the Jurassic and the Early Cretaceous, saw their geographic distribution progressively reduced during the Late Cretaceous, and became extinct after the Eocene/Oligocene, leaving no known relatives (see Poyato-Ariza 2005a for further details). Semionotiformes, another group that includes typically durophagous forms, consistently present in Early Cretaceous fish communities, are totally absent in Quintanilla la Ojada (and Albaina, for that matter). The actinopterygian remains of Quintanilla la Ojada, with their mixture of dominating teleostean forms plus relict, non-teleostean forms, is a nice example of this in-process ichthyofaunal replacement that would radically change the actinopterygian composition of the aquatic ecosystems in the Iberian area during the Late Cretaceous.

CONCLUSIONS

Brackish vertebrate fossil remains, most of them isolated teeth, found in the latest Cretaceous of Quintanilla la Ojada (Burgos, northern Spain) correspond to actinopterygians, selachians, and marine reptiles. Actinopterygians are mainly represented in number of specimens by teleosts (paralbulines, enchodontids, and in lesser extent phyllodontines and acanthomorphs), but pycnodonts and amiids are also present. Different tooth morphotypes (i.e. molariform, incisiform, branchial, conic-styliform, flattened and globular teeth) are known. The actinopterygian diversity for this locality is estimated in a minimum of 8 different taxa. The fossil association of Quintanilla la Ojada (Villarcayo Synclinorium) is similar to that discovered in Albaina (Miranda-Treviño Synclinorium), both located in the Basque-Cantabrian Region. The actinopterygian-bearing beds of Quintanilla la Ojada are closely related to a transgressive *lag* at the base of the Valdenoceda Formation, which is attributed to the Lower Maastrichtian to basal Upper Maastrichtian on the basis of the regional stratigraphy. The Albaina unit is laterally equivalent to the Torme Formation, which is considered to be Upper but not uppermost Maastrichtian on the basis of the selachian association. These Cretaceous Iberian ichthyofaunas are characterized by a mixture of dominating teleosteans and relict, non-teleostean forms (such as pycnodonts), and constitute an example of replacement process of the actinopterygian composition in the aquatic ecosystems during the Latest Cretaceous.

TABLE 1. — Actinopterygian taxonomic distribution from the Maastrichtian localities of Albaina (Miranda-Treviño Synclinorium) and Quintanilla la Ojada (Villarcayo Synclinorium). The table indicates the number of specimens (mainly isolated teeth) by taxon and/or morphotype. For more details about the actinopterygian fauna of Albaina see Poyato-Ariza *et al*. (1999b).

	Quintanilla la Ojada	**Albaina**
Pycnodontiformes indet.	8	15
Pycnodontoidei indet. A		1
Pycnodontoidei indet. B		14
Pycnodontoidea indet. (morphotype 1)	9	
Pycnodontoidea indet. (morphotype 2)	3	
Cf. *Anomoeodus* sp.	3	1
Cf. *Paramicrodon* sp.		29
Cf. Amiidae indet.	11	
Cf. Elopiformes indet.		2
Phyllodontinae indet.	3	
Phyllodus sp.		6
Paralbulinae indet	~120	
Paralbula sp.		559
Enchodontidae indet. (morphotype A)	28	
Enchodontidae indet. (morphotype B)	5	
Enchodontidae indet. (morphotype C)	8	
Enchodus sp. A		15
Enchodus sp. B		146
Acanthomorpha indet.	7	8
Cf. "*Stephanodus*" sp.		2
Total specimens	**205**	**798**

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