Middle-Late Triassic chondrichthyans remains from the the Betic Range (Spain)

Restos de condrictios del Triásico Medio-Superior de la Cordillera Bética (España)

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Abstract

Purpose.- In the present study, we described, for first time, the chondrichthyan fauna from several Middle-Late Triassic sections in the Betic Domain and compare it with other recent described coeval faunas from the Iberian Ranges.

Methods.- Specimens were retrieved after the dissolution (with 10% acetic acid) of carbonate rocks.

Results.-The assemblage comprises of seven species belonging to six genera (*Hybodus plicatilis, Omanoselache bucheri* comb. nov.*, Omanoselache contrarius* comb. nov.*, Lonchidion derenzii, Lissodus* aff*. L. lepagei* and cf. *Rhomaleodus budurovi*)*,* most of them non-nesoselachian. Chondrichthyans remains occur in levels dating from Ladinian to Carnian according with bivalves, ammonoids and conodonts.

Conclusions.-The findings are comparable, in taxonomical terms, to the chondrichthyan fauna from the Ladinian of the Iberian Range that was recently described, although chondrichthyans seems noticeably less abundant in the Betic Domain. Most of the species found occur also in the Iberian Range, with the exception of *Lonchidion* *derenzii* and cf *Rhomaleodus. budurovi*, which occur in the Boyar Section, dated as Carnian. The small size of all teeth recovered, belonging probably to young specimens, suggest that the very shallow epicontinental environments recorded in Middle-Upper Triassic rocks from the Betic Domain could be used as nursery areas.

Keywords: Chondricthyans, Ladinian, Carnian, Palaeocommunities, Betic Range

Resumen

Objetivo.- En el presente estudio describimos por primera vez, la fauna de condrictios de diversas secciones del triásico Medio-Tardío en el Dominio Bético y lo comparamos con otras faunas parecidas descritas recientemente en la Cordillera ibérica.

Metodología.- los ejemplares fueron recuperados después de la disolución (con ácido acético al 10%) de rocas carbonatadas.

Resultados.- La asociación se compone de siete especies pertenecientes a seis géneros (*Hybodus plicatilis*, *Omanoselache bucheri* comb. nov., *Omanoselache contrarius* comb.nov, *Lonchidion derenzii*, *Lissodus* aff. *L. lepagei*, *Pseudodalatias henarejensis* y cf. *Rhomaleodus budurovi*), la mayoría de ellos no neoseláceos. Los niveles donde aparecen los restos de condrictios datan del Ladiniense hasta el Carniense según la saosciaciones de bivalvos, amonoideos y conodonts.

Conclusiones.- Estos hallazgos son comparables, en términos taxonómicos, a la fauna de condrictios del Ladiniense de la Cordillera Ibérica que fue descrita recientemente, aunque éstos parecen ser menos abundantes en el Dominio Bético. Muchas de las especies encontradas aquí también aparecen en la cordillera Ibérica, con las excepciones de *Lonchidion derenzii* y cf. *Rhomaleodus budurovi* que aparecen en la sección Boyar,

datada como Carniense. El pequeño tamaño de los dientes recuperados, pertenecientes a individuos juveniles, sugieren que los ambientes epicontinentales someros registrados en las rocas del Triásico Medio-Superior del Dominio Bético podrían haber sido usadas como zonas de cría.

Palabras clave: Condrictios, Ladiniense, Carniense, Paleocomunidades, Cordillera Bética.

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1. Introduction

A number of recent studies in the Middle Triassic of the Iberian Range (Spain) have evidenced the presence of a rich and diverse chondrichthyan fauna (Botella et al. 2009; Pla et al. 2009, 2013; Ferrón et al. 2014; Escudero-Mozo et al. 2015), changing the inaccurate previous perception that chondrichthyans are rare, or even completely absent, in the Triassic marine sediments of the Iberian Peninsula (e.g. Chrzastek 2008; Fortuny et al. 2011). These works revealed the presence of a paleobiogeographically heterogeneous chondrichthyan association, which includes components of Middle

Triassic faunas of northern Europe, together with species only previously known in North America and China with some additional “Iberian” endemic taxa.

In order to increase our understanding of the chondrichthyan diversity in the epicontinental shallow marine environments of eastern Iberia during Triassic times, we have extended our investigations to other “classical” Middle-Late Triassic basins of the Iberian Peninsula (see López-Gómez et al. 2002). The present study focuses on the Middle and Late Triassic chondrichthyan remains recovered in four sections of the Betic Domain, located on the South-Eastern parts of the Iberian Peninsula (Fig. 1A). As in the Iberian Range, Middle-Upper Triassic rocks of the Betic Domain have been extensively studied, so it exists a great amount of literature about fossils groups such as bivalves (López-Gómez et al. 1994; Márquez-Aliaga et al. 1999; Márquez-Aliaga and Márquez 2000), ammonoids (Goy and Pérez-López 1996; Goy et al. 1996; Pérez-Valera, 2016), foraminifera (Pérez-López et al. 2003, 2005) and conodonts (Plasencia 2009 and references therein). This provides an excellent stratigraphic and palaeoenvironmental framework for the study of the shark fauna.

Chondrichthyan microremains studied in this paper, were derived from conodont residues supplied by Dr. Pablo Plasencia (Plasencia 2009) with more microvertebrate material recovered from resampling of selected levels.

2. Geographical and geological setting

Middle-Upper Triassic rocks are well preserved in the south of the Iberian Peninsula and show different facies related to different transgressive-regressive cycles during the Triassic times (López et al. 2002). In the Betic Range, two large geologic zones have been differentiated: External Zones and Internal Zones. The External Zone exposes

Mesozoic and Tertiary sediments deposited in the continental margin in the south of the Iberian Peninsula, with two main domains spanning in an ENE direction: the Subbetic and the Prebetic domains. The oldest outcrops are Triassic, since the Paleozoic rocks belong to the basement. The Internal Zones consisting of basement and cover rocks, mostly metamorphic, which constitute,during the Mesozoic, a more southern domain (i.e. the Alboran domain) independent from the Southern Iberian Paleomargin (García-Dueñas and Balanyà 1986; Pérez-López 1998). All the sections studied here are located in the External Zones of the Betic Range (Fig. 1 a) and belong to the Prebetic Domain (Calasparra, Canara and Esperejas section) and the Subbetic Domain (Boyar section). Rocks from these zones record tidal flats and shallow platforms of an epicontiental sea, but in some cases, they are continental in origin (López-Gómez et al. 2002).

2.1. *Espejeras Section* (Fig. 1 b)

This section is located near the city of Elda (0º 39’ 10” N 38º 23’ 55” O). This column has a total of 144.5 m. The section has yielded fossils of bivalves and foraminifera, which dated the section as Ladinian (López-Gómez et al. 1994).

2.2. *Calasparra Section* (Fig. 1 b)

This section is in in the province of Murcia near the city of Calasparra (38º 12’ 30” N 1º 38’ 10”O). The section was divided in five units, it is the richest of all the studied sections of this paper, and it has an important fossil record that has been studied previously (Pérez-Valera 2005 and references therein). It is dated as Anisian? to upper Ladinian based on the ammonoids found in the section (Pérez-Valera 2016 see also Pérez-Varela 2005).

2.4. Canara section (Fig. 1 b)

This section is located between the cities of Canara and Cehegín (in the province of Murcia) (38º 07' 49"N 1º 46' 28"O). This column has a total of 150 meters, it is divided into four units and it has been dated as Anisian to upper Ladinian (Pérez-Valera 2005), although the top of the section belongs to the Keuper facies.

2.3. *Boyar Section* (Fig. 1 b)

It is situated near the cities of Ubrique and Grazalema, in the province of Cádiz, southern Spain. The section is located in the southwest part of the Betic Ranges (36º 44' 49" N 5º 25' 12" O). The Boyar Section is subdivided into 4 main units comprising strata belonging to the upper Muschelkalk and Keuper facies (Fig. 1B), and it has been dated as Carnian (Late Triassic) in age on the basis of the contained bivalve, conodont and pollen assemblages (Martín-Algarra et al. 1995).

3. Systematic paleontology

The carbonate rocks from the four sections were dissolved using 10 per cent acetic acid and screened with sieves meshes of 2, 0.125 and 0.063 mm, respectively. Subsequently, the microremains were picked up under a binocular microscope. The photographs were taken with the HITACHI 4100 Electronic Microscope from SCSIE from the University of Valencia. The achieved specimens are mainly isolated teeth and fragments, housed in the Geological Museum of the University of Valencia (MGUV), Spain.

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Cohort Euselachii Hay 1920

Order Hybodontoformes Zangerl 1981

Superfamily Hybodontoidea Owen 1846

Family Hybodontidae Owen 1846

Genus *Hybodus* Agassiz 1837

Type Species—*Hybodus reticulatus* Agassiz 1837.

Hybodus plicatilis Agassiz 1843

(Fig. 2 a-c)

Material—Two almost complete tooth and more than 20 incomplete teeth from Calasparra section, level CPR-46(+5m) (MGUV-35896); Canara section, level CNI-02-2(MGUV-35897, MGUV-35898); Espejeras section, level ESP-29 (MGUV-35899); and Boyar section, level 92-A-40 (MGUV-35900).

Description—Most of the material consists of broken cusps. Only two of the teeth are almost complete. Their sizes vary from 2.816 mm in mesiodistal length and 2.421 mm in height in the smaller specimen (Fig. 2 c-d), to 4.518 mm in length and 2.031 mm in height in the biggest specimen (Fig. 2 a-b). The central cusp is flanked by up to two pairs of cusplets (Fig 2 a-d), all aligned and ornamented with rectilinear ridges. The base presents the random foramina characteristic of hybodonts. In the biggest specimen (Fig. 2 a-b) is straighter than the base of the smaller specimen, which has a more arched shape (Fig. 2 c-d).

Remarks—It is widely accepted that the genus *Hybodus*, as used actually, is broadly polyphyletic (Rees 1998; Underwood and Rees 2002; Rees and Underwood 2008; Ginter 2010; Cappetta 2012) and do not correspond to a biological group. A taxonomical revision is required, which surely will lead to the division of the species currently included in *Hybodus* into different genera. This taxonomical revision is beyond the aim of this work, but all the morphological and vascular characteristics shared with teeth of the *Hybodus* type species, *H. reticulatus*, (e.g. high and slender cusp, with a circular cross-section. and accessories lateral cusplets orates with vertical ridges) recommend maintaining, for the meantime, the generic epithet for *H. plicatilis* until hybodont taxonomy will be resolve. Teeth of the *Hybodus plicatilis* are the largest teeth recovered from the Betic Range, as happens in the Iberain Range (Pla et al. 2013).

Ocurrence—Muschelkalk, Middle Triassic of Schwenningen, Germany (Agassiz 1843); Muschelkalk, Middle Triassic of Monte Giorgio, Switzerland (von Meyer 1849; Rieppel 1981); Muschelkalk, Middle Triassic of Luxemburg (Delsate 1992, 1993); Middle Triassic of the Iberian Range, Spain (Pla et al. 2013), Middle-Late Triassic of the Betic Range.

Family Lonchidiidae

Genus *Lissodus* Brough 1935

Type specie—*Hybodus africanus* Broom 1909

Lissodus aff. *L. lepagei*

(Fig. 2 e-g)

Material—Two complete crowns from the Calasparra section, level CPR-46 (+5m) (MGUV-35901, MGUV-35902).

Description—The tooth crowns found in the material from the Betic Range have a characteristic "boomerang" shape with the labial side larger than the lingual (Fig. 2 g-h). A well-marked occlusal crenulated crest separates both faces. A main low central cusp is flanked by two cusplests on each mesial and distal side. In both specimens, the cusplets show signs of wear (Fig. 2 e, g). They present a faint labial peg with a poorly developed cusplet near the crown shoulder and under the central cusp. No bases are preserved, but when observed in basal view all teeth indicated the presence of a sulcus in the crown/base junction.

Remarks—Betic specimens present no significant morphological differences, when compared with the teeth described by Pla et al. (2013) as *Lissodus* aff. *L. lepagei* from the Iberian Range. Thus, we suggest that they belong to the same species; however, the scarcity of the material does not allow for the formal description of a new species, so it is left as *Lissodus* aff. *L. lepagei*.

Ocurrence—Middle Triassic of the Iberian Range, Spain (Pla et al. 2013), Middle Triassic of the Betic Range.

Lonchidion Estes 1964

Type Species—*Lonchidion selachos* Estes 1964, Maastritchian, Lance Formation, Eastern Wyoming, U.S.A.

Lonchidion derenzii Manzanares, Pla, Martínez-Pérez, Ferrón, Botella 2016

(Fig. 2 i-l)

Material—10 teeth from the Boyar section, level 92-A-40, Spain. (MGUV- 27.744 to MGUV-27.748)

Description— These minuscule teeth are elongated and gracile, measuring 0.5 to 0.4 mm mesiodistally, 0.3 to 0.2 mm apicobasally, and 0.3 to 0.2 mm labiolingually. The crown has a very distinctive “whale tail”-shape in labial view (Fig. 2 j, l). The main central cusp is small, rounded to triangular in shape and labially inclined; flanked by 2–3 pairs of lateral cusplets (Fig. 2 k-l). The main cusps and the lateral cusplets appear very abraded. A very prominent labial peg with one small accessory cusplet is situated above the crown-root junction (Fig. 2 i-l). The crown/root junction is very constricted and only in one specimen half of the base is preserved (Fig. 2 j).

Remarks—These specimens were recovered only from the level 92-A-40 of the Boyar section. The presence of pollen in this level has been interpreted as evidence in favour of the entire sequence being deposited in very shallow waters in close proximity to continental areas.

Occurrence—Late Triassic of the Betic Range.

Order incertae sedis

Family Homalodontidae Mutter, De Blanger and Neuman 2008

Genus *Omanoselache* Koot, Cuny, Tintori and Twitchett 2013

Remarks— Genus *Omanoselache* Koot, Cuny, Tintori and Twitchett, 2013 was erected by Koot et al. (2013) to include several new forms (*Omanoselache hendersoni*, *Omanoselache angiolinii*) found the Middle Permian of central eastern Oman. In parallel Pla et al. (2013) described new material of "*Polyacrodus" contrarius* Johns, Barnes and Orchard, 1997 and '*P.' bucheri* Cuny, Rieppel and Sander, 2001 from the upper Ladinian of the Iberian Range, Spain, and erected the new genus *Prolatodon* Pla, Márquez-Aliaga and Botella, 2013 for the re-accommodation of this two species (see also Mutter et al (2007)). Recently Koot et al. (2015) have suggested that *Omanoselache* and *Prolatodon* are synonyms genus, and, in fact, the diagnostic characteristics defined for both genus match to a large degree match to a large degree. Although both taxa were erected in 2013, *Omanoselache* (March) takes priority over *Prolatodon* (Juny). Thus, Koot et al. (2015) refers *Prolatodon contrarius* and *Prolatodon bucheri* to *Omanoselache*.

Here we follow the taxonomical proposal of Koot et al. (2015). The Spanish material refered to "*Prolatodon*" fits perfectly within *Omanoselache*, and *Prolatodon* is accepeted as a junior synonym of *Omanoselache*.

Type specie—*Omanoselache henedrsoni* Koot, Cuny, Tintori and Twitchett 2013

Omanoselache bucheri comb. nov. (Cuny, Rieppel, Sander 2001)

(Fig. 2 m-r)

Material— Three complete and more than 20 incomplete teeth from the Boyar section, level 92-A-40 (MGUV-35903, MGUV-35904, MGUV-35916); Espejeras section, level Esp-29 (MGUV-35905, MGUV-35917); and Calasparra section, level CPR-46(+5m) (MGUV-35906).

Description—Most of the teeth are broken, specially near the main cusp. Teeth are labiolingually compressed and elongated mesiodistally; measuring between 2.322 and 1.811 mm mesiodistally, 0.696-0.606 mm in height and 0.957-0.682 mm labiolingually. All teeth present only a main pyramidal cusp with an occlusal crest that covers the crown teeth mesiodistally with undulated vertical ornamentation ridges appearing on labial and lingual sides. Two of the teeth (Fig. 2 p-q) has a clear pyramidal shape and shows a bigger size than the other specimens, which are more elongated and compressed labiolingually (Fig. 2 m-o). A well-developed sulcus is located in the crown/base junction. A lingual peg is easily recognizable and placed under the main cusp. The base has a size comparable to the crown and it is also labiolingually compressed. Vascularization consists of a row of well-developed foramina in both labial and lingual walls.

Remarks—Teeth assigned to *"P." bucheri* from the Iberian Range (about 170 specimens) show a great variation in morphology and shape that has been interpreted as evidence of (at least) monognatic heterodonty (Pla et al. 2013). Thus, minute specimens were assigned to symphyseal positions (Pla et al. fig:3A, B); possible messial teeth present one main cusp and are arched, which gives them a "boomerang"- shape (Pa et al. fig:3C-F); and latero-distal teeth are blunt and display a reduced main cusp (Pla et al. fig: 3G). The small number of teeth recovered in the Betic Range (around 25 partially complete specimens) does not reflect all the morphological variation present in the specie. Almost all of the elements recovered belong probably to latero-distal teeth (Fig. 2 m-o), whereas two complete teeth (and few fragment) (Fig. 2 p-r), which have a more pyramidal shape and a more evident central cusp, could probably occupied symphyseal positions.

Occurrence—Middle Triassic, northwest of Nevada (Cuny et al. 2001; Rieppel et al. 1996); Middle Triassic, Iberian Range of Spain (Pla et al. 2013), Middle-Late Triassic of the Betic Range.

Omanoselache contrarius comb. nov. (Cuny, Rieppel, Sander 2001)

(Fig. 3 a-e)

Material—4 complete teeth and more than 10 incomplete teeth from the Boyar section, level 92-A-40 and 92-A-35E (MGUV-35907, MGUV-35908, MGUV-35909); and Calasparra section, level CPR-46(+5m) (MGUV-35910, MGUV-35918).

Description—The found specimens are labiolingually compressed, measuring 1.092 mm mesiodistally, 0.474 in height and 0.293 mm labiolingually (Fig. 3 a-e). A crenulated crest extends across the whole tooth from the distal to the mesial side, in most of the specimens this crest is worn (Fig. 3 c-e). A main pyramidal cusp placed in the center of the tooth is flanked by a few pairs of cusplets (Fig. 3 a-b). Vertical sinuous ridges, which originated radially from the apex of the main cusp, ornate the crown of the teeth. This is more evident in those specimens that present less wear (Fig. 3 a-b). *P. contrarius* presents labial and lingual pegs, both at the same level of the tooth and flanking the main cusp.

Occurrence—Middle Triassic of British Columbia, Canada (Johns et al. 1997); Middle–Late Triassic of Yang Liu Jing, China (Chen et al. 2007); Middle Triassic from the Iberian Range of Spain (Pla et al. 2013), Middle-Late Triassic of the Betic Range.

Order incertae sedis

Family Pseudodalatiidae Reif 1978

Genus *Pseudodalatias* Reif 1978

Type Species—*Pseudodalatias barnstonensis* Sykes 1971.

Pseudodalatias henarejensis Botella, Plasencia, Márquez-Aliaga, Cuny, Dorka 2009

(Fig. 3 f-g)

Material—Four incomplete crowns from the Calasparra section, level CPR-46(+5m) (MGUV-35914, MGUV-35915).

Description—. All the crown teeth are broken and there are no bases. The lower jaw teeth present the typical spearhead-like, sharp and slightly net towards the apex; with a few coarse denticles that are directed upwards present in the cutting edges, most of them damaged in our material (Fig. 3 f-g).

Remarks—Although the teeth of *P. henarejensis* can be clearly separated into two different morphologies, assuming dignathic heterodonty (Botella et al. 2009) only the teeth from the lower jaws are recovered in the Betic Range.

Occurrence—Middle Triassic from the Iberian Range, Spain (Pla et al. 2013), Middle Triassic of the Betic Range.

Subcohort Neoselachii Compagno 1977

Superorder Selachimorpha Nelson 1984

Order incertae sedis

Family incertae sedis

Genus *Rhomaleodus* Andreev and Cuny 2012

Type specie—*Rhomaleodus budurovi* Andreev and Cuny 2012

cf. *Rhomaleodus budurovi*

(Fig. 3 h-j)

Material—3 complete and several incomplete teeth from Boyar section; levels 92-A-40 (MGUV-35911, MGUV-35912, MGUV-35919) and 92-A-38 (MGUV-35913).

Description— Teeth of small sizes and very well preserved. They present a massive triangular main cusp flanked by a pair of lateral cusplets (Fig. 3 h-i). All the cusp and cusplets are lingually inclined, and it is possible to see the vertical ridges that descend from the apex of each cusp in the lingual side (Fig. 3 h-j). The root is compact and has a trapezoidal outline in basal view (Fig. 3 j), with a prominent lingual torus penetrated by a single row of large foramina (Fig. 3 h).

Remarks— The specimens show clear morphological similarities with teeth form the Middle and Upper Triassic of Bulgaria assigned to *Rhomaleodus budurovi* (Andreev and Cuny, 2012), including the presence of a prominent lingual torus penetrated by a single row of large foramina and the triangular main cusps flanked by one pair of smaller cusplets, all of them inclined lingually. *Rhomaleodus budurovi* has been reported to have three different morphologies (A, B and C) by Andreev and Cuny (2012). By the moment, all the teeth found in the Betic Range belong to the type B. Andrew and Cuny (2012) realized a surface study of the enamaloid layer of *Rhomaleodus budurovi* and found the presence of a Parallel Bundle Enameloid (PBE) layer, which led them to include this species as a basal selachimorpha. We also have realized ground sections of one of the speciemns found in the Betic Range, but the study has not yield any satisfactory results. More histological studies of the enameloid layer would clarify the enameloid layer of this species.

Occurrence— Middle and Upper Triassic of Bulgaria (Andreev and Cuny 2012); Late Triassic of the Betic Range.

4. Discussion

This paper report a diverse shark fauna from the Betic Range, confirming the presence of chondrichthyans as an important component in the shallow marine environments of the Iberian Peninsula during Middle-Late Triassic times. The assemblage found in the Betic Range comprises of six genera and seven species belonging to five families, all of them belonging to non-nesoselachian, with the only probable exception of cf. *Rhomaleodus budurovi*. This assemblage is taxonomically comparable to that described by Pla et al. (2013) from the Ladinian of the Iberian Range, although chondrichthyans become visibly less abundant in the Betic Domain. Five of the seven species found in the Betic basin (i.e. *Hybodus plicatilis, Omanoselachae bucheri* comb. nov., *Omanoselache contrarius* comb.nov., *Pseudodalatias henarejensis* and *Lissodus* aff. *L. lepagei*) occur as well in the Iberian Ranges. Among these, *Pseudodalatias henarejensis* and *Lissodus* aff. *L. lepagei* are endemic of the Middle Triassic of the Iberian Peninsula. Two species, *Lonchidion derenzii* and cf. *R. budurovi* appear in the Betic Range but not in the Iberian Range.

The chondrichthyan assemblage from the Iberian Range, studied in Pla et al (2013), was dated as Longonbardian (late Ladinian) based on the presence of the conodonts *Sephardiella mungoensis* and *Pseudofurnishius murcianus* (see Pla et al. 2013, fig 1). Sections studied in the Betic Range, however, exposed sediments from Anisian to Carnian. The species *Pseudodalatias henarejensis* and *Lissodus* aff. *L. lepagei* appear only in level CPR-46(+5m) of the Calasparra section, which can be dated as Longonbardian due to the presence of the same conodont taxa, already mentioned above (Plasencia, 2009). In the same sense *Lonchidion derenzii* and cf. *Rhomaleodus budurovi*, only appear in levels of the Boyar section, dated as Carnian by Martín-Algarra et al. (1995). In contrast, *Hybodus plicatilis*, *Omanoselache bucheri* comb. nov.and *Omanoselache contrarius* comb. nov. appear in all the sampled sections, including the Boyar section, so their stratigraphic record in the Betic Domain range is from the Ladininan to Carnian. With this new data, the upper stratigraphic range of the species *H. plicatilis* and *Omanoselache bucheri* comb.nov. extends to the Upper Triassic. In addition, the occurrence of *H. plicatilis, O. bucheri* comb. nov. and *O. contrarius comb.nov.*, *L. derenzii* and cf. *Rhomaleodus budurovi* in levels of the Boyar section represents the first record of late Triassic direct vertebrate remains in the South-East of the Iberian Peninsula (see Fortuny et al. 2011).

Based on the tooth morphology, most of the taxa found in this study present grasping-crushing dentitions, adapted, potentially, to moderate durophagous diets containing by example, crustaceans, ostracods and even small bivalves and gasteropods, which are abundant in the shallow near-coastal facies of the Betic Domain. According to López-Gómez et al. (2002, and references therein), carbonate rocks of the Betic Domain were deposited in the shallow platform and tidal flats of an epicontinental sea connected to the Tethys. It would offer a number of restricted and protected areas from open seas, which could have been a perfect place for development and growth of juvenile sharks. It is known that females of extant sharks migrate to these kinds of environments to deposit their eggs or give birth and the juvenile specimens live there until they reach maturity (Castro 1993; Grubbs 2010; Matich and Heithaus 2015).

An exception to this grasping-crushing pattern is found in *Pseudodalatias henarejensis*. This species, exhibit a peculiar clutching-cutting dentition analogous to that present in some recent Dalatiidae, which feed excising bites of flesh from larger animals (i.e marine mammals, other sharks, etc). In this sense, remains of large reptiles and bony fishes have been discovered in Ladinian rocks on nearby sites of the Betic Range deposited in a marine setting near the shoreline (Niemeyer 2002; Fortuny et al. 2011).

As said above, chondrichthyans remains seem considerably less abundant in the Betic Domain than in the Iberian Range. To be exact, in most of the studied sections in the Iberian Ranges by Pla et al. (2013, see their fig. 1), the chondrichthyans are abundant in several levels dated as Longobardian. In contrast, in the Longobardian units of Espejeras, Canara and Calasparra from the Betic Range shark remains only appear in two punctual levels (CPR 46 (+5) and ESP-29, Fig. 1) despite some of the studied sections were sampled in detail for conodont studies (Plasencia 2009). In fact, a large number of samples were processed, being that a great majority of them is sterile for chondrichthyans (Fig. 1). Moreover, some other Triassic sections from the Betic Domain (i.e. Arroyo Hurtado, Salmerón, Valdepeñas de Jaén and Cabo Cope sections) were sampled in detail in that study but do not yield shark remains, and they have not been considered in the present study (but see Plasencia 2009 for more information).

7. References

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Figure captions

Fig. 1- a) Geologic setting and location of the Betic Range. b) Stratigraphic section of Espejeras, Canara, Calasparra and Boyar. The levels from where the microremains were recovered are indicated by the shark outlines. Modified from Plasencia (2009) and Pérez-Valera (2016).

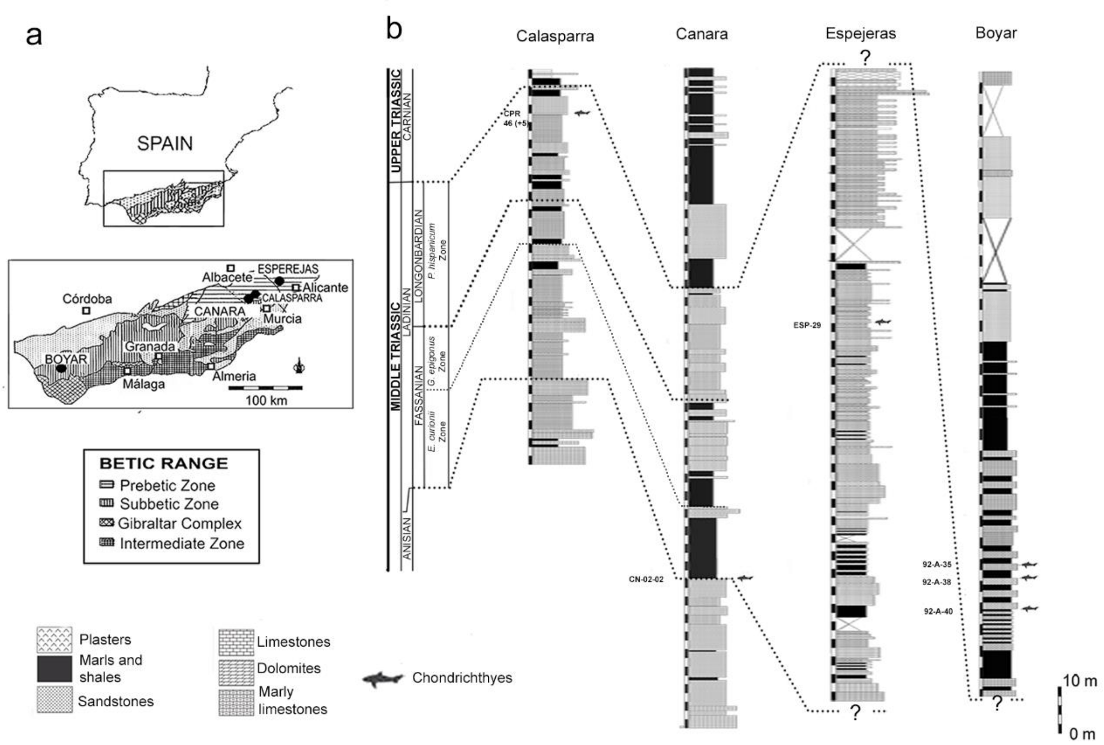


Fig. 2- a-d) *Hybodus plicatilis,* scale bar 600 µm; a-b) MGUV-35896, c-d) 35897*;* e-h) *Lissodus* aff. *lepagei*, scale bar 200 µm, e-f) MGUV- 35901, g-h) MGUV- 35902); i-l) *Lonchidion derenzii*, modified from Manzanares et al. (2016), i-j), MGUV-27744, k-l) MGUV 27745; m-r) *Omanoselache bucheri* comb. nov., m-n), scale bar 400 µm, MGUV-35904; o) scale bar 100 µm, MGUV-35916, p-q), scale bar 200 µm, MGUV-35903; r) scale bar bar 100 µm, MGUV-35917.

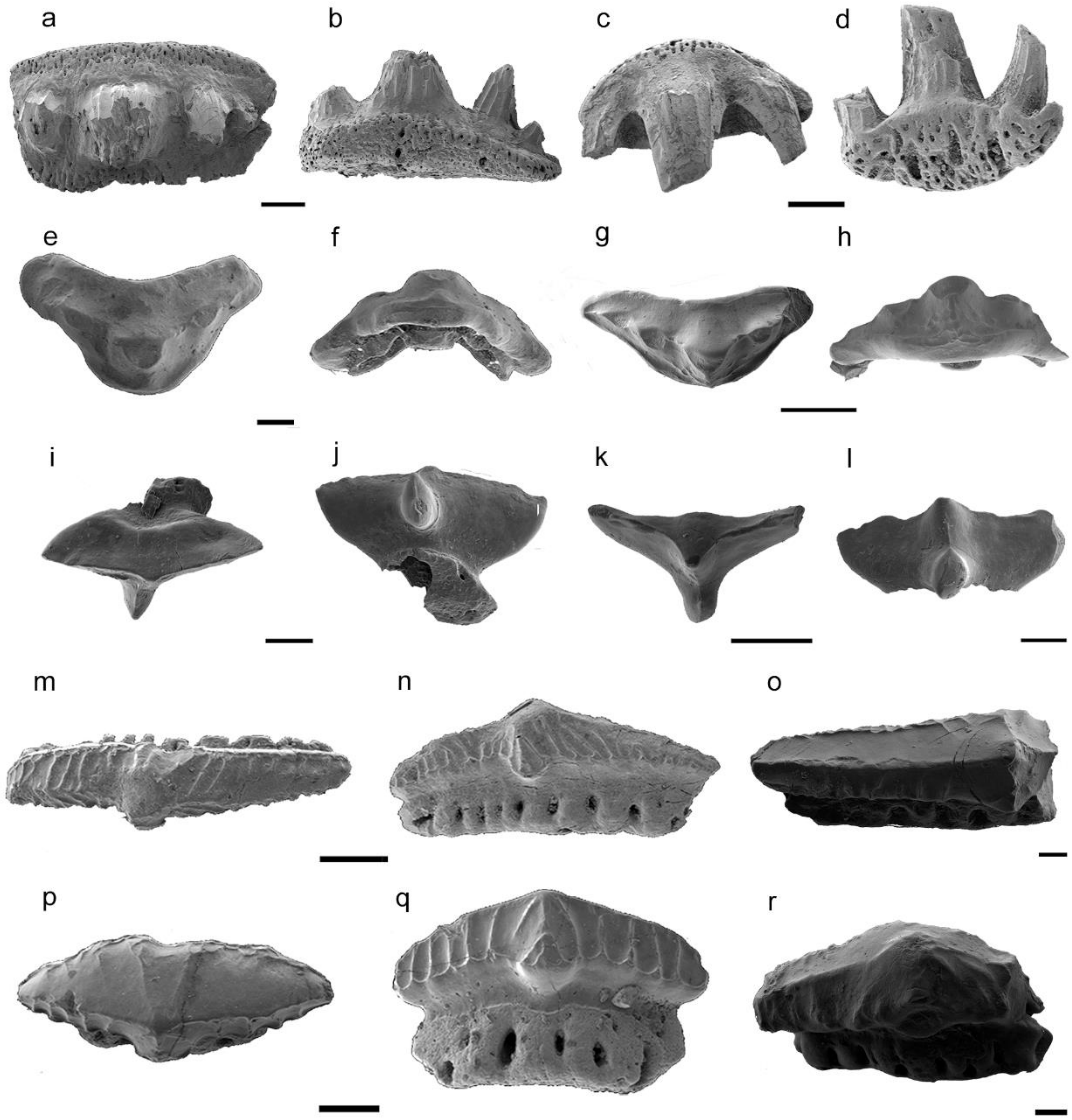
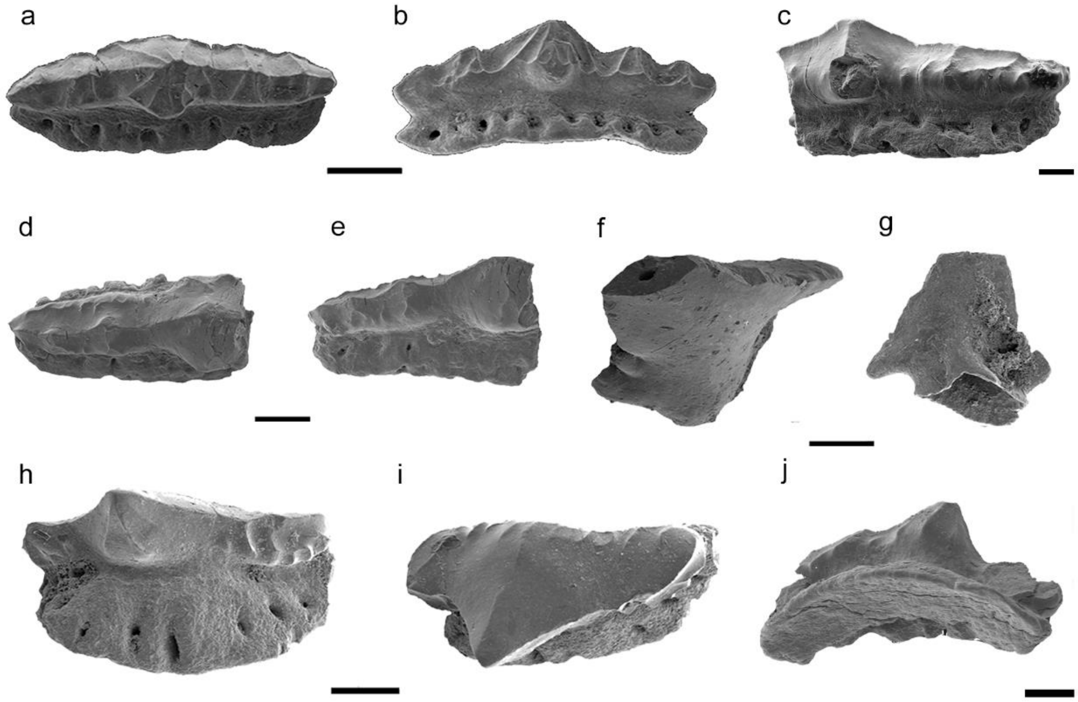


Fig. 3- a-e) *Prolatodon contrarius*, scale bar 200 µm, a-b) MGUV-35905; c) scale bar 100 µm, MGUV-35918; d-e) MGUV-35908; f-g) *Pseudodalatias henarejensis*, scale bar 200 µm; MGUV-35914; h-j) cf. *Rhomaleodus budurovi*, h-i) scale bar 200 µm, MGUV-35909; j) scale bar 100 µm, MGUV-35919.



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