



Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: http://www.tandfonline.com/loi/ujvp20

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To cite this article: Cristina Pla, Ana Márquez-Aliaga & Héctor Botella (2013) The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain), Journal of Vertebrate Paleontology, 33:4, 770-785, DOI: 10.1080/02724634.2013.748668

To link to this article: https://doi.org/10.1080/02724634.2013.748668

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Published online: 25 Jun 2013.



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ARTICLE

THE CHONDRICHTHYAN FAUNA FROM THE MIDDLE TRIASSIC (LADINIAN) OF THE IBERIAN RANGE (SPAIN)

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ABSTRACT—Here we present for the first time a detailed taxonomic study of a diverse chondrichthyan fauna from the Middle Triassic of the Iberian Range (Spain). The assemblage consists of isolated remains of seven species of five non-neoselachian shark genera (*Palaeobates, Hybodus, Pseudodalatias, Prolatodon,* gen. nov., and *Lissodus*), including a new species of hybodontiform shark, *Hybodus bugarensis*, sp. nov. In addition, a new homalodontid genus, *Prolatodon*, sp. nov., is erected for the taxa '*Polyacrodus' bucheri* and '*Polyacrodus' contrarius*. The chondrichthyans of the Iberian Range represent a heterogeneous group from a paleogeographic point of view made up of common components of Middle Triassic shark faunas of northern Europe (*Hybodus plicatilis* and *Palaeobates angustisimus*) together with species only known previously from North America and China (*Prolatodon bucheri*, comb. nov., and *Prolatodon contrarius*, comb. nov.), as well as several 'endemic' taxa (*Pseudodalatias henarejensis*, *Hybodus bugarensis*, sp. nov., and *Lissodus* aff. *L. lepagei*). This fauna demonstrated adaptation for a wide diversity of feeding strategies, implying that non-neoselachian sharks dominated among the predator community of Middle Triassic coastal ecosystems of Iberia. The co-occurrence with bivalves, ammonoids, and conodonts allows us to date the chondrichthyan assemblage as 'Longobardian' (upper Ladinian).

INTRODUCTION

Paleontological studies in Middle Triassic marine sediments of the Iberian Range have been carried out for several decades. As a result, lithostratigraphy and fossil content are well known. Several groups of fossils have been studied in detail—including bivalves (see Márquez-Aliaga and López-Gómez, 1989; Márquez-Aliaga and Martínez, 1996; Márquez-Aliaga et al., 2002; Márquez-Aliaga, 2010, and references therein), ammonoids (Goy, 1995; Goy and Rodrigo, 1999), conodonts (e.g., Hirsch et al., 1987; Márquez-Aliaga et al., 2000; Plasencia et al., 2004, 2007, 2010), and brachiopods (Márquez-Aliaga et al., 1999, 2007)—enabling the setting of the correlation of the different lithological units of the Hispanic Muschelkalk.

The presence of chondrichthyan microremains has been named in several of these studies; however, the diversity of the chondrichthyan fauna from the Middle Triassic of the Iberian Range has never been studied in detail. This fact may lead to the mistaken perception that in the Triassic of Spain chondrichthyans are rare or even completely absent (as suggested by Chrząstek, 2008). More recently, Pla et al. (2009) presented a preliminary study of chondrichthyan teeth of the Bugarra section and Botella et al. (2009) described a new species of pseudodalatiid from the Henarejos section (both sections are located in the southeast of the Iberian Range, see below). Now, we present here a comprehensive taxonomic study of a diverse chondrichthyan fauna found in several Middle Triassic sections located in different areas of the Iberian Range (Spain). The new material reported here includes a new species of hybodont, Hybodus bugarensis, nov. sp., and necessitates the erection of Prolatodon, nov. gen., including two species-Prolatodon bucheri (Cuny, Rieppel, and Sander, 2001), comb. nov. (= Polyacrodus bucheri

Cuny, Rieppel, and Sander, 2001), and *Prolatodon contrarius* (Johns, Barnes, and Orchard, 1997), comb. nov. (= *Polyacrodus contrarius* Johns, Barnes, and Orchard, 1997)—not previously reported from the Triassic in Europe. This new shark association from Spain increases our understanding on the great diversity, paleobiogeographic dispersion, and ecological dominance that non-neoselachian sharks reached during this period.

GEOGRAPHIC AND GEOLOGIC SETTINGS

During Middle Triassic times, the Iberian Plate was mainly composed of an old Variscan massif to the west (the Iberian Massif) surrounded by the extending Tethys Sea. The Middle Triassic sediments in eastern Iberia comprise limestones and dolomites that represent epicontinental shallow marine environments. These sediments were part of the western-most area of the Tethys margin and represent the so-called Muschelkalk facies. Sedimentary characteristics of these deposits exhibit clear differences when compared with the Muschelkalk of Central Europe. Moreover, in the eastern part of Iberia it is possible to differentiate zones that clearly correspond to different paleogeographic environments.

The Middle Triassic (Anisian–Ladinian Muschelkalk) of the Iberian Range has two carbonate intervals interpreted as prograding carbonate ramps, related to shallow marine environments of epicontinental character. From bottom up: (1) a lower carbonate unit with bioclastic limestones, algal mats and marls, (lower Muschelkalk) of 70–120 m thick (Anisian); (2) a middle red siliclastic–evaporitic interval of variable thickness, up to several hundred meters; and (3) an upper carbonate unit with bioclastic and oolitic limestones, algal buildups, and shallowing-upwards marl-limestone sequences, (upper Muschelkalk) 100–140 m thick (Ladinian).

The upper Muschelkalk corresponds to the second and the most important marine transgression of the Middle Triassic

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FIGURE 1. A, map of the Iberian Peninsula showing the location of studied sections (Calanda, Henarejos, Moya, Bugarra, Montserrat, Macastre, and Jarafuel) and **B**, the biostratigraphic column of each section with indication of levels that yielded the material described in this work.

in the southeast area of the Iberian range (meridional sector). López-Gómez and Arche (1992) have formally described the Dolomites and Limestones of Cañete (CDL) Formation for the upper Muschelkalk units of this area. Our specimens have been recovered from seven sections of this Formation of the Aragonese and Castillian branches of the Iberian Ranges (see Fig. 1).

The Calanda section is located 2 km to the south of Calanda village (Teruel) in the meridional Aragonese branch of the Iberian Range. The Triassic material belongs to the core of the 'Mesozoic Calanda Anticlinal' and were studied by many authors because of the relatively good fossil record of this region. Middle Triassic bivalve and ammonoid assemblages are cited by Márquez-Aliaga et al. (1987, 1994) and Ladinian conodonts were studied by Plasencia et al. (2004). The Henarejos section is located 1 km southeast of the village of Henarejos (Cuenca). This section has one of the best fossil records of the studied area but with a covered part in the top. Several Ladinian molluscs have been cited by Márquez-Aliaga (1985) and López et al. (1987). The Moya section is located near Landete village (Cuenca). This section is very close to that of Henarejos, with very similar lithological units and fossil records, mainly brachiopods (Márquez-Aliaga et al., 2007). The Bugarra section is located very near Bugarra village (Valencia) and the upper Muschelkalk is well established as part of the Ladinian transgression. Márquez-Aliaga et al. (1984) studied for the first time the stratigraphical and paleontological aspects of this section. The other studied sections, Montserrat, Macastre, and Jarafuel, are very close to the localities of Valencia from which they take their names. These are the most meridional Triassic outcrops of the Iberian Range and their materials belong to the same lithological units (CDL).

SYSTEMATIC PALEONTOLOGY

The material described below is composed of isolated teeth, resulting from the dissolution of carbonate rocks with 10% acetic acid. The terminology used to describe the teeth in the present paper follows tooth terminology of Cappetta (1987) and Rees and Underwood (2002). All specimens are housed in the Geological Museum of Valencia University (MGUV), Spain.

Class CHONDRICHTHYES Huxley, 1880 Subclass ELASMOBRANCHII Bonaparte, 1838 Cohort EUSELACHII Hay, 1902 Order HYBODONTIFORMES Zangerl, 1981 Superfamily HYBODONTOIDEA Owen, 1846 Family ACRODONTINAE Casier, 1959 Genus PALAEOBATES Meyer, 1849

Type Species—Strophodus angustissimus Agassiz, 1838.

PALAEOBATES ANGUSTISSIMUS (Agassiz, 1838) (Fig. 2A, B)

Material—One fragmented tooth, MGUV 25791, from the Bugarra section (level Bu1-26).

Description—Tooth is broken in three parts but reconstructed almost completely (Fig. 2A). It is enlarged and labiolingually compressed, measuring 7 mm mesiodistally and 2 mm labiolingually. The crown is flat, asymmetrical-i.e., in occlusal view, one lateral edge is trapezoidal whereas the opposite one has a pointed-diamond shape—and is blunt in outline (Fig. 2A). The ornamentation of the crown is complex and reticulated. The tooth is covered with irregular granulations composed of small, oval hollows on its central part, from which originate a dense network of ridges. Close to the shoulder the reticulated ornamentation becomes a series of ridges extending parallel to each other reaching the edge of the shoulder of the crown, but never reaching the base. The aspect of the crown is rugged (Fig. 2B). The lingual and labial shoulders are convex (Fig. 2A). There are no crests or cusps. A peg is absent, but underneath the edges of the whole tooth there is a flat face implying the presence of a sulcus. The base is not preserved.

Remarks—The elongated labiolingually compressed shape of the tooth with a crenulated, low, flat crown enables us to include the Iberian specimens in the *Palaeobates* genus. The typical grooves on the crown surface fit the teeth of *P. angustissimus*, abundant in the upper Muschelkalk bone beds of north Europe.



However, it is known that *P. angustissimus* usually possesses a transverse crest, which is sometimes absent (e.g., Cappetta, 1987; Diedrich, 2009), as in *P. angustissimus* from the Iberian Range. Also, the Iberian tooth of *P. angustissimus*, in contrast to those teeth figured by Cappetta (1987) and Diedrich (2009), possesses a lower number of hollows than the latter ones, and the transverse section of the Iberian tooth of *P. angustissimus* is a bit larger than the transverse sections of the teeth figured by Cappetta (1987) and Diedrich (2009), which could be due to the position of the tooth along the jaw.

The Iberian tooth possesses a very similar ornamentation to those of *P. angustissimus* from the southwest of Poland (Chrząstek, 2008:fig. 4f–j), although in those teeth the number of hollows is more numerous and the hollows have a more oval section. Among other *P. angustissimus* records based on crown fragments such as those of Dorka (2001), we emphasize the close similarity of the reticulated ornamentation, even if the lack of ridges extending parallel to each other in the crown shoulder of the latter fragments can be noticed. Cuny et al. (2000) described some crown fragments that are very similar to ours, although there is a longitudinal crest mentioned, which is lacking in the Iberian teeth.

P. angustissimus teeth can be clearly differentiated from *P. polaris* Stensiö, 1921, because of the ornamentation, which is more *Acrodus*-like, with more striations than crenulations in the whole surface of the crown, and with a transverse crest and numerous folds more or less perpendicular to it. In addition, *P. shastensis* (Bryant, 1914) differs from *P. angustissimus* in the presence of developed radiating striations, which is unknown in Iberian specimens. The crown shoulder vertical ridges are very poorly developed in *P. shastensis*. Also, Iberian specimens differ from *P. reticulatus* Duffin, 1998, in size, the latter being the smaller species. Furthermore, *P. reticulatus* teeth are distinct from *P. angustissimus* in their absence of a tendency of the reticulations to elongate towards the crown shoulder.

The angular edges present in MGUV 25791 exhibit an interdigitated distribution on the dentition, which is in accordance with Rieppel (1981) and does not support the interpretation of Romano et al. (2010), where an arrangement of the dentition files in series for the whole genus is proposed: they consider it a diagnostic feature to differentiate the genus *Palaeobates* from *Acrodus* and *Asteracanthus*.

Occurrence—Upper Rhaetian and Muschelkalk of Jena, Germany (Schmidt, 1928); lower Muschelkalk of Wolica, Poland (Liszkowski, 1973); Middle Triassic of Switzerland (Rieppel, 1981); middle Muschelkalk of Göttingen, Germany (Schultze and Möller, 1986); lower, middle, and upper Muschelkalk of the Opole region, Poland (Liszkowski, 1993); Rhaetian and lower Muschelkalk of the north Sudetic Basin, southwest Poland (Chrząstek and Niedźwiedzki, 1998); Muschelkalk, Middle Triassic of Lunéville, eastern France (Delsate and Duffin, 1999; Chrząstek, 2002); Triassic of lower Saxony, Germany (Dorka, 2001); Middle Triassic of the Iberian Range, Spain.

Family HYBODONTIDAE Owen, 1846 Genus HYBODUS Agassiz, 1837

Type Species—Hybodus reticulatus Agassiz, 1837.

HYBODUS BUGARENSIS sp. nov. (Figs. 2C–J, 4A, B)

Etymology—Named in honor of the locality of Bugarra where the first specimen of the species was discovered.

Holotype—MGUV 25831 from the Henarejos section, level He-18.

Material—Six isolated teeth. MGUV 23239 and 25834–35 from the Bugarra section (levels Bu1-26 and Bu-pl) and MGUV 25831–33 from the Henarejos section (levels He-18 and He-19).

Diagnosis—Teeth of *Hybodus* characterized by their minute size (0.7–2 mm) do not evince any type of heterodonty. They have multicusped crowns with central main cusps and between four and six lateral cusps and these are fully separated from one another at the base. Cusps lack ornamentation and are labiolingually compressed, with lateral cutting edges especially in the central most cusps. There are no lingual or labial pegs present. The base is markedly low and overhangs laterally towards mesial and distal edges. Vascularization is anaulacorhize, with numerous small foramina randomly arranged and a row of four or five larger foramina present on the lingual wall. The enameloid is single crystallite enameloid (SCE) with randomly oriented, rodshaped crystallites.

Description-Minute teeth, measuring less than 2 mm of mesiodistal length and 1.3 mm of maximum height. The crown is multicusped with five or seven cusps. All of them are pointed, slender, and perfectly aligned inwardly, differentiating from each other at the base, but in the case of the seven cusps, the last pair of them is fused in the mesial and distal edges (Fig. 2G, H). The main central cusp measures 0.8 mm in height. Cusplets decrease gradually in height moving away from the main cusp to the mesial and distal ends (Fig. 2C, D, G, I, J). All cusps have a labiolingual compression, with an oval transversal section. Cusps placed at the mesial and distal ends display a more spherical transversal section (Fig. 2E, F, H). The crown is smooth and all cusps and cusplets lack ornamentation, although the main cusps of some specimens have one or two gentle rectilinear ridges. These ridges can be observed in both faces of the cusp, originating in the crown/base junction at the middle height of the cusp and never reaching the apex (Fig. 2C, D, G). The whole crown is strongly arched towards the lingual face (Fig. 2E, F, H). Cusplets of the distal edge of the teeth are also slightly distally arched (Fig. 2C, D, G, H), which indicates a lateral position in the dentition pattern. The absence of this distal bow and the presence of straight cusplets instead could indicate a symphyseal position (Fig. 2I, J). There is no lingual or labial peg, and no sulcus is present either.

The base is lightly mesiodistally longer than the crown (Fig. 2C–E, G, I, J). It is not very deep, around 0.1–0.2 mm, and it exhibits a lenticular transversal section. It is projected to the lingual face in a subperpendicular plane to the crown (Fig. 2F).

The labial outline is convex and the lingual contour is slightly concave. The basal face of the base is flat, and there is a slight arching in this area in most of the specimens (Fig. 2C, D). Vascularization is of an anaulacorhize type (following Casier, 1947; Cappeta, 1987), with the presence of small foramina randomly

[←] FIGURE 2. **A**, **B**, *Palaeobates angustissimus* (Agassiz, 1838). MGUV 25791, tooth crown, Bugarra section, occlusal view of the reconstructed crown tooth, and detail of the crown tooth to appreciate the reticulated ornamentation. **C**–**J**, *Hybodus bugarensis*, sp. nov. **C**–**F**, holotype, MGUV 25831, lateral tooth, Henarejos section (He-18), lingual, labial, occlusal, and lateral views; **G**, **H**, MGUV 25833, lateral tooth, Henarejos section (He-19), lingual and occlusal views; **I**, **J**, MGUV 25834, symphyseal tooth, Bugarra section (Bu-pl), lingual and labial views. **K**–**O**, *Hybodus plicatilis* Agassiz, 1843. **K**, MGUV 25842, lateral tooth, Bugarra section (Bu-pl), lingual and labial views. **K**–**O**, *Hybodus plicatilis* Agassiz, 1843. **K**, MGUV 25842, lateral tooth, Henarejos section (He-14), lingual view; **L**, MGUV 25843, tooth, Henarejos section (He-19), lingual view; **M**, MGUV 26460, symphyseal tooth, Henarejos section (He-14), lingual view; **N**, **O**, MGUV 25837, symphyseal tooth, Bugarra section (Bu-14), lingual view; **R**, **S**, MGUV 25858, lateral tooth crown, Bugarra section (Bu1-26), occlusal and labial view; **U**, MGUV 25854, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **T**, MGUV 25865, lateral tooth crown, Bugarra section (Bu1-26), occlusal view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra section (Bu1-26), lingual view; **V**, MGUV 25856, lateral tooth crown, Bugarra sect

oriented in the labial and lingual walls; a feature that keeps the porous appearance of the base. However, there are a few well-developed foramina in the lingual wall organized in a row (Fig. 2C, G).

Due to preservational conditions, the material is sometimes broken, especially in the labial wall of the base, which hinders a complete study of vascularization. On the other hand, it is interesting to note the well-preserved nature of the cusps even though they look very fragile.

A fine capping layer of single crystallite enameloid (SCE) 10 μ m thick (Fig. 4A) is present at the cusp. The ultrastructure of this SCE layer is composed of randomly oriented, rod-shaped crystallites whose size is approximately 1 μ m (Fig. 4B).

Remarks—*Hybodus bugarensis*, sp. nov., displays typical features of the genus *Hybodus* with well-defined slender cusps with lateral cusplets decreasing in height inclined laterally, and a fairly shallow base lingually offset from the crown underside (see Maisey, 1987; Duffin, 1993; Ginter et al., 2010). Based on the characteristics mentioned above, we included our new species in this genus. Nevertheless, it is necessary to point out that several authors have recently claimed that the genus *Hybodus* is in need of revision (e.g., Rees, 2008; Rees and Underwood, 2008; Ginter et al., 2010).

The general morphology of teeth of H. bugarensis, sp. nov., is very similar to that of the type species H. reticulatus and other multicusped species of Hybodus (see characteristics above). However, H. bugarensis, sp. nov., differs in the lack of ornamentation of its cusps, whereas species of Hybodus usually have ridges along the cusps. H. bugarensis, sp. nov., also differs in the usually minute size of its teeth compared with species of Hybodus. It must be mentioned that juvenile (minute) teeth of some species of Hybodus lack ornamentation, although it is present in the teeth of adults. Therefore, the possibility that the minute teeth assigned here to H. bugarensis, sp. nov., belong to juvenile specimens of an already known species of Hybodus cannot be completely excluded. However, differences listed below appear to favor the erection of the new species: (1) the cusps of H. bugarensis, sp. nov., decrease gradually in height, whereas other species of Hybodus usually present cusplets that vary from being very small elevations to reaching only one quarter of the central cusp (Rees, 1998); (2) cusplets of H. bugarensis, sp. nov., are not fused at their bases and the cross-section of cusps in H. bugarensis, sp. nov., is strongly oval; and (3) the vascularization, which is of anaulacorhize type, always has a lingual row of four to five well-developed foramina (Fig. 2C, G), which is missing in some species of Hybodus. In addition, the fact that juvenile teeth of H. plicatilis (another species of Hybodus found in the Iberian Range) show a well-developed striated ornamentation (see below), and the fact that teeth such as those here assigned to H. bugarensis, sp. nov., have never been described in association with teeth of other species of Hybodus, also supports the erection of the new species.

The multicusped tooth crowns of *H. bugarensis*, sp. nov., seem functionally similar to those of several Palaeozoic phoebodonts (see Ginter et al., 2010:figs. 26–33, and references therein) or Cretaceous to present Clamydoselachidae (see, e.g., Consoli, 2008, and references therein) with a number of slender and delicate cusps that present fine cutting edges and rather modest (or absent) ornamentation. These teeth are typical grasping (or clutching sensu Capetta, 1987:fig. 22A) type teeth adapted for taking, holding, and stabilizing small prey (usually soft-bodied), which sharks will generally swallow whole.

Occurrence—Middle Triassic of the Iberian Range, Spain.

HYBODUS PLICATILIS Agassiz, 1843 (Figs. 2K–O, 4C, D)

Material—One hundred roughly damaged teeth and more than one hundred (103) isolated cups and fragments. MGUV 23238,

23243, 25836–42, and 25852–53 from the Bugarra section (levels Bu1-25, Bu1-26, Bu1-33, and Bu-pl); MGUV 22837, 25843–48, and 25850–51 from the Henarejos section (levels He-14, He-18, He-19, and He-20); and MGUV 25849 from the Moya section (level Moya II-8).

Description-Most of the specimens are damaged, mainly lacking one or more cusps, and only a small number of them are complete. The size of teeth varies from 3 mm in mesiodistal length and 2.5 mm in height in smaller specimens, to up to 5 mm in mesiodistal length and 4 mm in height in larger ones. An exceptionally large tooth 10 mm in length has also been found (Fig. 2M). The crown is characterized by a large pointed central cusp usually flanked by two, sometimes three, pairs of cusplets (Fig. 2N, O). Cusplets placed at the mesial and distal ends are always more rounded than the central ones. All cusps are aligned (Fig. 2K, N, O), with an oval transversal section lightly compressed labiolingually and slightly inclined to the lingual side (Fig. 2O). Additionally, the orientation of most lateral cusplets is mesial and distal, and in the transversal section they are less oval and more spherical. Ornamentation is striated, by way of rectilinear ridges covering the whole cusp (Fig. 2K, L, N, O). However, the main cusps occasionally do not have ornamentation in their apical parts.

There is no 'sulcus' or peg between the crown and the base. The base is deeper in large specimens, and slightly projected to the lingual side (Fig. 2K, M), increasing in depth from the labial to the lingual wall. In basal view, the lingual outline of the base is convex, whereas labial and lateral edges (mesial and distal) are straight (Fig. 2L). Vascularization is anaulacorhize with a large number of randomly distributed foramina, which give a porous aspect, especially at the labial face of the base (Fig. 2O). Occasionally, there is a row of three to four well-developed foramina in the lingual wall (Fig. 2K, N).

Enameloid analysis reveals a 10- μ m-thick monolayered SCE formed by single crystallites (Fig. 4C) of a slender rod shape (Fig. 4D) and they can be differentiated directly from each other. They are randomly oriented; there are no packages, bundles, or fibres (Fig. 4D).

Remarks-All morphological, vascular, and histological characters of these specimens (Fig. 2K-O) agree with their assignment to Hybodus plicatilis (Agassiz, 1837:pl. 189, pl. 24, figs. 10, 13), and are similar to those figured from several other geographical areas (Agassiz, 1837, 1843; Meyer, 1849; Stefanov, 1966; Scheinpflug, 1984; Delsate, 1992, 1993) characterized by the multicusped crown with highly ornamented cusps and porous base (Rees, 2008). An important feature of this species is the presence of a deep base. Within the material of the Iberian Range assigned to Hybodus plicatilis, the largest teeth (similar in size to Hybodus plicatilis from other localities) show this characteristic deep base (Fig. 2M), and smaller teeth, probably from juveniles, present fewer deep bases that increase in depth from the labial to the lingual side (Fig. 2K, L, N, O). This suggests that in H. plicatilis tooth bases become deeper during ontogeny (i.e., crown and base grow allometrically). The bases of smaller teeth are similar to those of H. similis Oertle, 1984, displaying an ellipticalrounded semicircle form of a robust base. Nevertheless, crowns of H. similis are clearly different because lateral cusplets are lower (compared with the main cusp) than in *H. plicatilis*, where the first pair of lateral cusplets is higher than half the height of the main cusp. Additionally, the main cusp of H. plicatilis is slender, whereas in *H. similis* the main cusp is wider.

Rieppel (1981:fig. 1a, b) reported the presence of *Hybodus* cf. *plicatilis* in Mte. San Giorgio (Switzerland). *Hybodus* cf. *plicatilis* from San Giorgio shares some features with the described teeth. These features are vertical ridges extending along the cusp and cusplets, but not reaching the apex of the central one and a base that becomes deeper from the lingual to the labial wall, and the presence of several vertical grooves in the lingual view of the

base (Fig. 2L). Furthermore, specimens from Iberia are similar to those described as *Hybodus* aff. *H. plicatilis* from Saudi Arabia (Vickers-Rich et al., 1999). However, *Hybodus* aff. *H. plicatilis* possesses five cusplets and a lenticular cross-section of the base, which is separated by a broad groove from the crown; this latter feature differs from the specimens from Iberia.

H. plicatilis is clearly different from *H. bugarensis*, sp. nov. (Fig. 2C–J), mainly because of its size, because the latter species is tiny compared with *H. plicatilis*. *H. bugarensis*, sp. nov., also presents an oval cross-section of the cusps that lack vertical ridges by means of ornamentation, in contrast to *H. plicatilis*. The lingual row of well-developed foramina, which is always present in *H. bugarensis*, sp. nov., is not as pronounced in *H. plicatilis* (Fig. 2K, L).

Occurrence—Muschelkalk, Middle Triassic of Schwenningen, Germany (Agassiz, 1843); Muschelkalk, Middle Triassic of Monte Giorgio, Switzerland (Meyer, 1849; Rieppel, 1981; Scheinpflug, 1984); Muschelkalk, Middle Triassic of Luxemburg (Delsate, 1992, 1993); Middle Triassic of the Iberian Range, Spain.

> Family incertae sedis Genus *LISSODUS* Brough, 1935

Type Species—*Hybodus africanus* Broom, 1909.

LISSODUS aff. L. LEPAGEI (Figs. 2P–V, 4E, F)

Material—Twenty teeth and 27 fragments. MGUV 25854–60 and 25865–66 from the Bugarra section (levels Bu1-26 and Bu1-33); MGUV 25861–62 from the Henarejos section (levels He-14 and He-19); MGUV 25864 from the Macastre section (level Mac-25); and MGUV 25863 from the Jarafuel section (level Jaraf-3).

Description—Only the crowns of the teeth are preserved (see below), but these are generally well preserved. The crown teeth are labiolingually compressed. The mesiodistal length is usually around 1-2 mm, but some minute teeth measure less than 1 mm in length. The labial face is wider than the lingual face, and they are separated by a main occlusal crenulated crest that passes from the mesial edge to the distal edge (Fig. 2R, T–V). The occlusal crest separates a wide labial side from the lingual one. Crown ornamentation is composed of some faint to conspicuous ridges in both faces, which originate in the occlusal crest and do not reach the shoulders. There is a main low central cusp flanked by one or, more commonly, two cusplets on each mesial and distal side (Fig. 2R, T-V). In several specimens, the central cusps and lateral cusplets are worn. A labial peg is present (Fig. 2P, R-T, V), containing a small, poorly defined cusplet near the crown shoulder, although this small cusplet is absent in several specimens. A pair of moderate ridges originates in the apex of the main cusp and covers the labial peg (Fig. 2R, T, V). A developed rim extends along the occlusal tooth outline above the shoulder height of the crown (Fig. 2R, S, U, V). In lingual or labial view, crown teeth are 'boomerang' shape (Fig. 2U). Some teeth are smaller (less than 1 mm long), more rounded, lack the circumferential rim, and have more pronounced cusps (Fig. 2P, Q). These teeth probably came from symphyseal-mesial positions, indicating a monognathic heterodonty.

Although the bases are not preserved, tooth crowns indicate the presence of a sulcus in the crown/base junction in evidence in some specimens (Fig. 2S). There is only one specimen where the base is preserved, but this is broken and highly altered. The height of the base is 0.6 mm, approximately the same as the crown. Due to bad preservation, the vascularization cannot be studied.

Enameloid analysis reveals a thick layer—without any kind of differentiation—of SCE, which reaches up to 30 μ m in some ar-

eas of the tooth (Fig. 4E). Crystallites are rod-shaped and can be differentiated, each measuring less than 1 μ m (Fig. 4F).

Remarks—The specimens have been included in the genus *Lissodus* on account of their being domed teeth with low central cusp and cusplets, and having wide occlusal crests, triangular labial protuberances, and weak folds for ornamentation (see emended diagnosis and revision of the genus provided by Rees and Underwood, 2002, and Rees, 2008).

Our material shows clear morphological similarities with teeth from the Upper Triassic of Luxembourg assigned to L. lepagei Duffin, 1993, including the same small size (measuring mesiodistally about 1 mm), an occlusal crenulated crest with a low central cusp flanked by cusplets (Fig. 2R, T-V), and a labial peg with ornamentation ridges confined to the upper part of the crown (Fig. 2R, T, V). In addition, Duffin (2001) describes a longitudinal ridge that extends around the crown shoulder; this ridge must be the same as the rim we identified in the specimens described in this paper. However, there are some important differences that prevent us from including our specimens in the species of L. lepagei, leaving its assignment to Lisodus aff. L. lepagei. Thus, teeth of Lissodus lepagei typically possess several pairs of minute cusplets (up to three; Duffin, 1993:fig. 3), whereas teeth from Spain usually present only one pair of larger cusplets. The well-developed cutting edges present in Lissodus lepagei are not present in this material, in which edges are more rounded. Additionally, Lissodus aff. L. lepagei never shows the very strongly developed labial peg present in several teeth of L. lepagei. Finally, the circumferential rim seems to be more continuous and rounded in Lissodus aff. L. lepagei. Besides these morphological differences, L. lepagei has been found only in the Upper Triassic.

However, given that bases are still unknown in the teeth from Spain, and all the crowns are highly worn, probably due to functional wear (see below), together with the fact that specimens of Lisodus lepagei hardly figure in the literature-just in schematic drawings (Duffin, 1993:fig. 3) and only one scanning electron microscopy (SEM) picture (Cuny et al., 1998:fig. 5a, b)-we prefer to maintain the taxonomic assignment of the specimens from Spain as Lisodus aff. L. lepagei, and wait for some better-preserved teeth to make a compare with teeth of Lisodus lepagei from Luxembourg. It should be noted that teeth of L. lepagei from the Upper Triassic of Grozon (Cuny et al., 1998) are very similar to L. aff. L. lepagei, both exhibiting only one pair of well-developed lateral cusplets (compare Fig. 2R, T-V with Cuny et al., 1998:fig. 5a, b). L. aff. L. lepagei clearly differs from other Lissodus coeval species (synthesized in Duffin, 1993), for example, L. angulatus (Stensiö, 1921) and L. africanus (Broom, 1909), in the absence of the labial peg cusplet. The latter species also differs from L. aff. L. lepagei by the fact that it lacks cusplets, a longitudinal ridge around the crown shoulder and vertical ridges. In addition, the teeth of L. angulatus present cusplets on the labial face of the crown unknown in L. aff. L. lepagei. Among other Triassic species, L. nodosus (Seilacher, 1943) lacks the longitudinal ridge around the crown shoulder of the teeth and measures up to 5 mm, whereas L. aff. L. lepagei is smaller, with a longitudinal ridge on the crown shoulder. Besides this, L. nodosus possesses teeth differing from those of L. aff. L. lepagei with the presence of labial (anterior teeth) and lingual nodes (in lateral teeth), which are absent in L. aff. L. lepagei. The teeth of L. aff. L. lepagei are distinct from L. sardiniensis Fisher, Schneider, and Ronchi, 2010, in the absence of vertical striations, secondary cusplets between the main cusp and the mesial and distal edges, and a longitudinally crenulated occlusal crest. Moreover, L. sardiniensis lacks a longitudinal ridge around the crown shoulder and possesses a pair of cusplets placed on top of both edges (mesial and distal) arched towards the central cusp. This type of cusplet is absent in L. aff. L. lepagei.

The phylogenetic affinities of the genus *Lissodus* have long been discussed (see Duffin, 1985, 2001; Cappeta, 1987; Rees and



Underwood, 2002, and references therein). Recent cladistic analysis on interrelationships of hybodont sharks placed *Lissodus* outside Lonchidiidae (as a monophyletic group) and placed it as the sister group of the family Hybodontidae (Rees, 2008:fig. 1). Due to controversial phylogenetic interpretations, we maintain *Lissodus* here without family assignment.

Occurrence-Middle Triassic of the Iberian Range, Spain.

Order incertae sedis Family HOMALODONTIDAE Mutter, De Blanger, and Neuman, 2008 Genus *PROLATODON*, gen. nov. (Figs. 3A–P, 4G–J)

Type Species—*Polyacrodus bucheri* Cuny, Rieppel, and Sander, 2001.

Etymology—After 'prolato-', Latin, elongated; and '-odon', Greek, tooth. In allusion to the characteristic narrow and elongated lateral teeth.

Included Species—*Prolatodon bucheri* (Cuny, Rieppel, and Sander, 2001), comb. nov. = *Polyacrodus bucheri* Cuny, Rieppel, and Sander, 2001; *Prolatodon contrarius* (Johns, Barnes, and Orchard, 1997) = *Polyacrodus contrarius* Johns, Barnes, and Orchard, 1997.

Diagnosis—Prolatodon, gen. nov., is a genus known only from isolated teeth, which show evidence of gradational monognatic heterodonty. Teeth are labiolingually compressed and mesiodistally elongated with a main pyramidal cusp; a longitudinalocclusal crest flanked by vertical 'nerve-shaped' ridges ranging perpendicularly or radially from the apex of the cusp towards the tooth shoulder. Ridges never reach the crown/base junction. The sulcus is located in the crown/base junction. It has a welldeveloped lingual peg and circumferential rim. Presumed mesial teeth are smaller and display reminiscent cusplets; lateral teeth are more elongated than mesial ones, with a reduced main cusp. The vascularization of the base is highly specialized, consisting of a lingual row of large foramina and one or two foramina rows in the labial wall. The upper labial row, if present, is positioned in the sulcus underneath the crown, holding minute foramina. The single crystallite enameloid is organized in two layers; crystallites of the outer layer are more compact than crystallites from the inner one; crystallites of the inner layer are arranged in loosely packed bundles.

Remarks—Mutter et al. (2007) erected the family Wapitiodidae to include a new genus (*Wapitiodus*) of Lower Triassic elasmobranchs based on articulated specimens from Canada. Wapitiodidae and *Wapitiodus* were later replaced by the names Homalodontidae and *Homalodontus* (Mutter et al., 2008) because the generic name was already in use for the conodont *Wapitiodus* Orchard, 2005. Mutter et al. (2007, 2008) also included two species from the genus *Polyacrodus*, '*Polyacrodus*' bucheri and '*Polyacrodus*' contrarius, in the family Homalodontidae. The shared characters of these taxa—essentially a monognathic heterodonty consisting of cusped mesial and blunt distal teeth with singlelayered enameloid-are discussed by these authors who have also noted the necessity of a thorough revision of the genus Polyacrodus (see also Rees, 2008). In fact, a currently widely accepted opinion (e.g., Rees and Underwood, 2002; Mutter et al., 2007; Rees, 2008) recommends the rejection of the family Polyacrodontidae. This family united two genera (Polyacrodus and Paleobates) on the basis of a single histological character: the orthodont tooth structure. However, tooth histology has proven not to be useful in assessing the phylogenetic affinities of hybodontiforms (see Maisey, 1987; Błazejowski, 2004). Moreover, the orthodont structure in teeth of Polyacrodus and Paleobates is considered a plesiomorphy (Maisey, 1987; Rees and Underwood, 2002; Maisey et al., 2004). Rees (2008) has tentatively included the genus Paleobates in the family Acrodontidae, whereas he has held Polyacrodus as nomen dubium and proposed that species currently included in the genus must be relocated to other genera. In agreement with this proposal, and with the suggestion of Mutter et al. (2007) to place 'Polyacrodus' bucheri and 'Polyacrodus' contrarius within the Homalodontidae (accepted also by other authors, e.g., Chen et al., 2007), we formally propose here the erection of a new genus Prolatodon to place 'Polyacrodus' bucheri and 'Polyacrodus' contrarius. These species share a number of characteristics (listed below) that distinguish them from those of the genus Homalodontus, consequently we consider the erection of a new homalodontid genus more accurate than including them in Homalodontus. Note that because neither 'Polyacrodus' bucheri nor 'Polyacrodus' contrarius is the type species of the genus, the generic name cannot be retained.

Homalodontus and Prolatodon, gen. nov., differ in (1) the length of the ornamentation ridges, which reach the base in Homalodontus but not in Prolatodon, gen. nov., where ornamentation ridges terminate at the crown shoulder (Mutter et al., 2007:fig. 2); (2) the size of the distal teeth, which is wider and smaller in Homalodontus than in Prolatodon, gen. nov.; (3) the lineal organization of the foramina of Prolatodon, gen. nov., at the base (Fig. 3D, G, H, J-L, N); (4) the main cusp is always present in Prolatodon, gen. nov.-although it is extremely small in some specimens (Fig. 3G), in distal teeth of Homalodontus it can be absent (Mutter et al., 2007:table 1); (5) the absence of lateral cusplets in Homalodontus but not in Prolatodon, gen. nov. (Fig. 3A, K, N, P); (6) the presence of a well-developed lingual peg and a circumferential rim in Prolatodon, gen. nov. (Fig. 3B, C, E-G, I-K, M-P), which is absent in Homalodontus (Mutter et al., 2007:figs. 5, 15); and (7) the two-layered enameloid of the Prolatodon, gen. nov. (Fig. 4H, J), which has not been studied in Homalodontus at this time.

PROLATODON BUCHERI (Cuny, Rieppel, and Sander, 2001), comb. nov. (Figs. 3A–F, 4G, H)

[←] FIGURE 3. **A–G**, *Prolatodon bucheri* (Cuny, Rieppel, and Sander, 2001), comb. nov. **A**, **B**, MGUV 25796, symphyseal tooth, Bugarra section (Bu1-26), labial and lingual view; **C**, MGUV 25802, mesial tooth, Bugarra section (Bu1-26), occlusal-lingual view; **D**, MGUV 25803, mesial tooth, Bugarra section (Bu-18), distal view; **F**, MGUV 23229, mesial tooth, Henarejos section (He-18), occlusal view; **G**, MGUV 25801, distal tooth, Macastre section (Mac-33), lingual view; **H**–**P**, *Prolatodon contrarius* (Johns, Barnes, and Orchard, 1997), comb. nov. **H**, MGUV 25822, symphyseal tooth, Henarejos section (He-14), labial view; **I**, MGUV 23227, mesial tooth, Bugarra section (Bu1-26), occlusal view; **J**, MGUV 25826, mesial tooth, Macastre section (Mac-37), occlusal view; **K**, MGUV 25819, mesial tooth, Bugarra section (Bu1-26), labial view; **L**, MGUV 25836, mesial tooth, Bugarra section (Bu1-26), labial view; **K**, MGUV 25817, distal tooth, Bugarra section (Bu1-26), labial view; **N**, MGUV 25830, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25817, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25830, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25818, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25817, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25830, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25818, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25818, distal tooth, Bugarra section (Bu1-26), lingual view; **Q**, MGUV 25818, distal tooth, Bugarra section (Bu1-26), labial view; **R**, MGUV 25637, lower tooth crown, Macastre section (Mac-33), lateral view; **R**, MGUV 25637, lower tooth crown, Macastre section (Mac-27), lingual view; **S**, MGUV 25648, lower tooth crown, Henarejos section (He-18), labial view; **T**, MGUV 25642, lower tooth crown, Macastre section (Mac-27), lingual view; **S**, MGUV 25869, upper complete tooth, Henarejos section (He-14), lingual view. Scale bar equals 200 µm.



Material—One hundred and thirty teeth and thirty-six fragments. MGUV 22834–35, 23226, 23228, 23229, 23230–34, 23236, 25795–803, and 25810–12 from the Bugarra section (levels Bu1-13, Bu1-26, Bu-pl, and Bu1-33); MGUV 25707 from the Calanda section (level CLD-7); MGUV 23229, 25804–25807, and 26460 from the Henarejos section (levels He-14, He-18, and He-19); MGUV 25793–94 from the Jarafuel section (levels Jaraf-27 and Jaraf-30); MGUV 25624–25, 25635, 25681–83, and 25699 from the Macastre section (levels Mac-25, Mac-27, Mac-33, and Mac-39); MGUV 25808 from the Montserrat section (level Ms-55); and MGUV 25809 from the Moya section (level F-3).

Description—Teeth of *Prolatodon bucheri*, comb. nov., are some of the most commonly found and well-preserved specimens in the material from the Iberian Range.

The cusps are covered by an occlusal crest in the mesiodistal direction. Both sides (labial and lingual) are ranged by undulated vertical ornamentation ridges. Ridges originate from the occlusal crest reaching the shoulder (Fig. 3A-G). Ornamentation ridges, which originate from the cusp, range radially towards the shoulder. They extend parallel to each other along the crown. All ridges bifurcate in a 'V' shape at the crown shoulder height and tail off without reaching the crown/base junction (Fig. 3A, D-G). This bifurcation produces an anastomosing, outstanding rim present at the shoulder height. Ridges rise when they reach the occlusal crest. There are no cusplets, with the exception of small teeth assigned to symphyseal positions (Fig. 3A, B). The labial and lingual outlines of the crown are usually convex in occlusal view. All teeth possess a relatively well-developed lingual peg. The lingual peg is placed at the same level as the cusp, and is subperpendicular to the occlusal main crest overhanging from the base (Fig. 3B–C, E–F). The lingual peg is ranged by a main ridge, which originates at the apex of the cusp and divides it into three, although mainly two, pairs of secondary ridges on its way to reaching the shoulder of the tooth. The ridges do not reach the base. There is no labial peg. Teeth possess a well-developed 'sulcus' around the whole crown/base junction (Fig. 3A, B, D-G).

A presumed monognatic heterodonty has been noticed due to the variation of the specimens, which range from (1) minute (0.5–1 mm) specimens cusped with one pair of the reminiscent cusplets flanking the main central cusp assigned to symphyseal positions (Fig. 3A, B); to (2) presumed mesial teeth larger than symphyseal ones, with a mesiodistal measurement of 2–4 mm and 1–1.5 mm in depth, unicusped, symmetric, and lightly to strongly arched, resembling a 'boomerang' (Fig. 3D) in lateral view (Fig. 3C–F); to (3) supposed lateradistal teeth are the largest ones, with a mesiodistal measurement of 2–4 mm and 1–1.5 mm in depth. These teeth are elongated and blunt, displaying a reduced main cusp (Fig. 3G). Both symmetric and asymmetric lateral teeth are present. Interestingly, many of the symmetric teeth are strongly arched in lateral view, whereas all the asymmetric teeth are flat (Fig. 3G). This variation is probably related to the position of the teeth along the jaw. In a small number of very elongated specimens, the peg is much reduced (Fig. 3G).

The base size is comparable to the crown. The base is labiolingually compressed and the lowermost part is lingually projected (Fig. 3B, C). The lingual wall is deeper than the labial wall. Vascularization consists of well-developed rows of foramina in both labial and lingual walls. There are two rows of foramina in the labial face (upper and lower). The upper row is placed immediately below the crown/base junction, and possesses foramina with a smaller diameter than the ones from the lower row (Fig. 3D). The lingual face displays only one row of foramina, which are oval and are usually larger than the foramina in the labial face (Fig. 3B, G). Due to the poor preservation of some bases, or even the minute size of the foramina, these two labial rows (see above) are normally intercalated. Furthermore, the foramina in the upper row are sometimes slit-like and may fuse with the foramina in the lower row, making them appear like only one row (Fig. 3D).

The enameloid is composed of single crystallites. Crystallites are easily differentiable and organized in two different layers. The outer layer is 10 μ m thick and is more densely compacted than the inner layer (Fig. 4H). The orientation of its crystallites is radially perpendicular to the surface. The thickness of the inner layer is 20 μ m (Fig. 4H). The crystallites are more loosely organized into 'bundles' with variable orientation, but are predominantly perpendicular to the enameloid dentine junction. All the crystallites within a bundle have the same orientation (Fig. 4H). The SCE is thicker at the level of the main cusp (Fig. 4G).

Remarks-Teeth of Prolatodon bucheri, comb. nov., are abundant and well preserved (more than 170 specimens), in comparison with the material reported by Cuny et al. (2001) and Rieppel et al. (1996; assigned to Polyacrodus sp. B) from the Anisian of northwestern Nevada (17 incomplete teeth). In general, the specimens from the Iberian Range are similar to those from Nevada, characterized by a unicusped, low crown with a well-developed lingual peg together with a circumferential rim and a specialized ornamentation consisting of vertical ridges reaching from the main occlusal crest to the crown shoulders. Thus, some of the teeth here assigned to mesial position (Fig. 3C, E) are identical to the holotype of the species (figured by Cuny et al., 2001:fig. 3H–I). In addition, teeth figured by Rieppel et al. (1996:fig. 3d, e), assigned by Cuny et al. (2001) as anterior teeth of 'Polyacrodus' bucheri, are also similar to Iberian symphyseal morphologies (Fig. 3B). However, part of the morphological variability found in Spain was unknown in the Nevada material. Thus, neither large specimens assigned here to lateradistal positions (Fig. 3G) nor strongly arched lateradistal teeth (Fig. 3D, F) have been found in Nevada, probably because of the small number of teeth found in this locality. As a consequence, the new material from the Iberian Range provides a more complete understanding of the variability in the heterodont dentition of Prolatodon bucheri, comb. nov.

Strongly arched teeth such as those present in *Prolatodon* bucheri, comb. nov., have been reported in some species of

[←] FIGURE 4. **A**, **B**, *Hybodus bugarensis*, sp. nov. MGUV 25835, complete tooth etched 6 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section (Bu1-26); (**A**) occlusal view of the tooth, scale bar equals 100 μ m, and (**B**) a detail of its SCE ultrastructure, scale bar equals 1 μ m. **C**, **D**, *Hybodus plicatilis* Agassiz, 1843. MGUV 2582, transversal section of the tooth cusp etched 4 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section (Bu1-26); (**C**) enameloid general view, scale bar equals 100 μ m, and (**D**) the detail of its SCE ultrastructure. Scale bar equals 10 μ m. **E**, **F**, *Lissodus* aff. *L. lepagei*. MGUV 25865, longitudinal section of the tooth crown at the main cusp etched 4 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section (Bu1-26); (**E**) enameloid general view, scale bar equals 50 μ m, and (**F**) the detail of its SCE ultrastructure, scale bar equals 2 μ m. **G**, **H**, *Prolatodon bucheri* (Cuny, Rieppel, and Sander, 2001), comb. nov. MGUV 25810, transversal section of the tooth etched 4 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section of the tooth etched 4 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section (Bu1-33); (**G**) enameloid general view, scale bar equals 100 μ m, and (**H**) the detail of its enameloid, showing the bundles, scale bar equals 10 μ m. **I**, **J**, *Prolatodon contrarius* (Johns, Barnes, and Orchard, 1997), comb. nov. MGUV25830, longitudinal section of the tooth etched 4 seconds in 10% HCl; uppermost member of CDL Formation, Bugarra section (Bu1-13); (**I**) enameloid general view, scale bar equals 20 μ m, and (**J**) the detail of its enameloid showing the bundles, 2009. MGUV 25885, fresh transversal section of the tooth etched 6 seconds in 10% HCl; uppermost member of CDL Formation, Henarejos section (He-14); (**L**) enameloid general view, scale bar equals 20 μ m, and (**M**) the detail of its SCE ultrastructure, scale bar equals 20 μ m, and (**M**) the detail of its compacted ul

Acrodus (e.g., Mutter, 1998a). However, in species of Acrodus the lingual contour in occlusal view is concave, as noted by Cappetta (1987:32), "this concavity lodges the labial protuberance of the next tooth in the same file." (See also Mutter, 1998b.) In contrast, all the different teeth of *Prolatodon bucheri*, comb. nov., lack this labial protuberance but possess a well-developed lingual peg (absent in species of Acrodus). Furthermore, Acrodus teeth exhibit a narrow sulcus, whereas teeth assigned to Prolatodon bucheri have a deep sulcus. Besides these two diagnostic characters (i.e., lingual peg and deep sulcus), all teeth assigned to Prolatodon bucheri, comb. nov., share important features such as (1) similar crown ornamentation; (2) the vascularization consisting of well-developed rows of foramina in both labial and lingual walls; and (3) an identical enameloid ultrastructure. All the dental types occur together in the same stratigraphical levels, supporting their assignment to the single species of Prolatodon bucheri, comb. nov.

On the other hand, Vickers-Rich et al. (1999) reported a Middle Triassic vertebrate assemblage from Saudi Arabia where some chondrichthyan teeth are included. Some of these teeth (tentatively assigned to Acrodus sp. by Vickers-Rich et al., 1999:fig. 2c) show some clear morphological similarities with teeth of Prolatodon bucheri, comb. nov., such as the presence of a main low pyramidal cusp, a well-developed lingual peg and circumferential rim, and the characteristic ornamentation of ridges, which branch at the crown shoulders. Furthermore, some other specimens classified as Acrodus sp. by Vickers-Rich et al. (1999:fig. 2d, e) are very similar to our presumed symphyseal teeth. The range in size of Arabian teeth assigned to Acrodus sp. (0.9-3.8 mm in mesiodistal length) is also similar to that of Prolatodon bucheri, comb. nov. (0.5-4 mm), and finally, although Vickers-Rich et al. (1999) do not describe any special organization of foramina, some of the specimens have a lingual row of large foramina (Vickers-Rich et al., 1999:fig. 2c-e). Notwithstanding these similarities, the material figured from Saudi Arabia is limited and it must be studied in detail before its definitive assignment to Prolatodon bucheri, comb. nov.

Occurrence—Middle Triassic, northwest of Nevada (Cuny *et al.*, 2001; Rieppel et al., 1996); Middle Triassic from the Iberian Range of Spain.

PROLATODON CONTRARIUS (Johns, Barnes, and Orchard, 1997), comb. nov. (Figs. 3H–P, 4I, J)

Material—Seventy-three teeth and seven more fragments. Figured as MGUV 22836, 23225, 23227, 23240–41, 25813–25820, and 25829–30 from the Bugarra section (levels Bu1-33, Bu1-26, and Bu-pl); MGUV 25821–25 from the Henarejos section (levels He-14, He-18, and He-19); MGUV 25827 from the Moya section (level Moya II-8); MGUV 25826 from the Calanda section (level CLD-5); and MGUV 25636 and 25828 from the Macastre section (levels Mac-27 and Mac-33).

Description—Teeth are labiolingually compressed, measuring between 1 and 2 mm mesiodistally, 0.4–0.7 mm in height, and 0.3–0.5 mm labiolingually. The crown has a crenulated crest, which extends across the whole tooth from the distal to the mesial edge and is often lightly displaced lingually (Fig. 3I). The low main pyramidal cusp is usually placed in the center of the tooth and flanked by no to several pairs of cusplets (Fig. 3K, N, P). The variation in size, symmetry, and the number of cusplets illustrates a gradational monognathic heterodonty. This variability ranges from smaller presumed symphyseal teeth, which are roughly symmetrical and cusped with a main pyramidal central cusp and small or reduced lateral cusplets (Fig. 3H), to larger mesial (Fig. 3I–L) and lateradistal (Fig. 3M–P) teeth, which are more elongated, consistently asymmetrical, and usually possess up to two pairs of lateral cusplets.

Crown ornamentation is striated, consisting of vertical sinuous ridges, which originate radially from the apex of the main cusp, and extend perpendicular to the occlusal crest, reaching the shoulders of the tooth (Fig. 3I–L, N–P). It is rare that ridges do not extend to the shoulder (Fig. 3H, M). Ornamentation ridges never reach the crown/base junction; they are strongly marked and more numerous on the lingual than on the labial face. Presumed lateradistal teeth show faint ridges of ornamentation in the occlusal labial face (Fig. 3M). Normally, ridges bifurcate at the shoulders displaying a reticulous aspect of the circumferential rim. In addition, this bifurcation of the ridges often displays nodes, presenting a crenulated outline from an occlusal view (Fig. 3I, J).

Both labial and lingual pegs are present at the same level of the tooth length, flanking the main cusp. Pegs are arranged perpendicular to the occlusal crest, displaying the tooth as a cross when viewed occlusally (Fig. 3I, J). The labial peg is regularly smoother than the lingual one, which is raised and prominent. From an occlusal view, the tooth outline forms a characteristic sinuous shape at the mesial and distal edges (Fig. 3I, J). The labial peg is ornamented by up to three vertical crests, which bifurcate at the points at which they reach the shoulders of the tooth (Fig. 3I, J). The lingual peg is ranged by one main crest that divides into two pairs of ridges (Fig. 3N, P). The lower face of the crown, between the shoulder and the crown/base junction, is depressed and flat. It ends in a depression that is situated at the crown/base junction (Fig. 3H, K–P).

The base is lingually projected and deeper in the lingual wall (Fig. 3I, J, O). The labial face of the base is reduced and slightly convex (Fig. 3K, L), whereas the lingual one is enlarged and concave (Fig. 3H, M, N, P).

Vascularization is anaulacorhize, consisting of large foramina roughly organized in a single row in both labial and lingual faces (Fig. 3H, K–N, P). In the labial wall foramina are circular and sometimes they are basally enlarged (Fig. 3K, L). In some specimens, smaller isolated foramina can be identified in the middle part of the labial wall (Fig. 3K). In the lingual wall, foramina are often more elongated—perpendicular to the crown—and sometimes reach the basal surface (Fig. 3H, K–N, P).

In addition to the morphology described above, we have found two very minute teeth—from 400 to 700 μ m—in level He-14 of the Henarejos section, where teeth of *Prolatodon contrarius*, comb. nov., are very abundant, which we tentatively assigned to symphyseal positions of the same species. The crown, lightly projected to the lingual face, is smoothly cusped with a central cusp. They do not have ornamentation ridges in addition to the lack of the labial peg. Also, the lingual peg is prominent and the base overhangs mesiodistally from the crown (Fig. 3H).

The enameloid is SCE where two sublayers can be differentiated. There is an outer compact layer of 5–10 μ m thick (Fig. 4J) whose crystallites extend parallel to each other and mainly perpendicular to the surface. The inner layer is underneath the outer one. It is thicker than the outer layer, 20 μ m (Fig. 4J), and its crystallites are arranged in groups, or badly defined 'bundles,' with different orientation between the different groups. All single crystallites inside the bundle are oriented in the same direction. The thickness of the enameloid is always thicker at the main cusp than in the lateral edges (Fig. 4I).

Remarks—Within the material from the Iberian Range, the teeth of *Prolatodon contrarius*, comb. nov., appear only half as numerous as those of *Prolatodon bucheri*, comb. nov. Both species appear together in some levels but they can be clearly distinguished (as noted by Chen et al., 2007). The teeth of *Prolatodon bucheri*, comb. nov., lack lateral cusplets, whereas most of the teeth of *Prolatodon contrarius*, comb. nov., have a certain number of cusplets. The labial peg of *Prolatodon contrarius*, comb. nov., and the lingual peg is more prominent in *Prolatodon contrarius*, comb.

nov. There are two rows of foramina in the labial face of the base in *Prolatodon bucheri*, comb. nov. (Fig. 3D), but there is only a single row in *Prolatodon contrarius*, comb. nov. (Fig. 3K, L). The ornamentation is more marked in teeth of *Prolatodon contrarius*, comb. nov., which also display more asymmetry between mesial and distal edges. Finally, the teeth of *Prolatodon bucheri*, comb. nov., are in general larger than those of *Prolatodon contrarius*, comb. nov.

Prolatodon contrarius, comb. nov., has been reported previously from the Ladinian and Carnian of British Columbia (Johns et al., 1997) and from the Anisian–Carnian of south China (Chen et al., 2007). As mentioned with *Prolatodon bucheri*, comb. nov., the number of teeth found in the Iberian Range (75 teeth) is higher than the number reported from the other localities (18 in Canada and three in China).

Johns et al. (1997) distinguished three different morphologies (A, B, C) within the teeth of *Polyacrodus* from British Columbia, which were assigned to '*Polyacrodus*' contrarius (= *Prolatodon* contrarius comb. nov.). All the teeth found in the Iberian Range are included in the variability described as types 'A' and 'B' (Johns et al., 1997:pl. 2, 3, figs. 1–11). No teeth of type 'C' are present within our material. Teeth of type 'A' sensu Johns et al. (1997) correspond to those we assigned to symphyseal positions (compare Fig. 3H with Johns et al., 1997:pl. 2, figs. 1–6), and mesial teeth positions (compare Fig. 3I–L with Johns et al., 1997:pl. 2, figs. 7–15). The presumed lateradistal teeth from the Iberian Range correspond to those assigned to type 'B' from Johns et al., 1997 (compare Fig. 3M–P with Johns et al., 1997:pl. 3, figs. 1–11).

The material of *Prolatodon contrarius*, comb. nov., from China consists of two complete presumed mesial teeth (Chen et al., 2007:fig. 3a–i) and one possible distal tooth (Chen et al., 2007;fig. 3j–l). The two presumed anterior teeth are similar to mesial teeth of Spain. According to Chen et al. (2007), distal teeth are somewhat reminiscent of those teeth reported by Johns et al. (1997) as type 'C,' although the circumferential rim is less developed and the cusps are higher on the Chinese teeth. We can add to these differences the organization of foramina, which are linearly organized in specimens from Johns et al. (1997) type 'C,' whereas teeth from south China (Chen et al., 2007) have randomly distributed foramina.

In summary, teeth from the Iberian Range (anterolateral and posterolateral), teeth of types 'A' and 'B' from Canada, and anterolateral teeth from China are very similar and all of them can be attributed to Prolatodon contrarius, comb. nov. However, despite the large number of teeth found in Spain (75), we have not found morphologies either as type 'C' sensu Johns et al. (1997) or as posterior sensu Chen et al. (2007), and, as discussed above, these two morphologies are also reasonably different. Therefore, it is a distinct possibility that the posterior tooth from China and the teeth of type 'C' from Canada do not belong to Prolatodon contrarius, comb. nov. In fact, Chen et al. (2007) point out that the assignment of the Chinese posterior teeth to Prolatodon contrarius, comb. nov., is dubious and Johns et al. (1997) note that the assignment of Canadian teeth of type 'C' to Prolatodon contrarius, comb. nov., is only based on similarities of the crown lingual ornamentation to the ornamentation of type 'A' specimens. A second possibility is that material from China, Canada, and Spain correspond to three different, but closely related, biological species, which share similar anterolateral teeth but differ in the morphology of posterior teeth.

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.

Order incertae sedis Family PSEUDODALATIIDAE Reif, 1978 Genus PSEUDODALATIAS Reif, 1978

Type Species—Pseudodalatias barnstonensis (Sykes, 1971).

PSEUDODALATIAS HENAREJENSIS Botella, Plasencia, Márquez-Aliaga, Cuny, and Dorka, 2009 (Figs. 3Q–U, 4K, L)

Material—One hundred and eighty-eight teeth and 76 fragments have been registered as MGUV 22839, 23242, and 25874–84 from the Bugarra section (levels Bu1-26, Bu1-13, Bu1-33, Bu-pl, CBU-10, and CBU-12); MGUV 18963–78, 25868–73, and 25885 from the Henarejos section (levels He-14, He-18, He-19, and He-20); MGUV 25626, 25637, 25638, 25642, 25643, 25684, and 25685 from the Macastre section (levels Mac-25, Mac-27, and Mac-33); and MGUV 25867 from the Moya section (level Moya II-8).

Description—Teeth of *P. henarejensis* can be clearly separated into two different morphologies assuming dignathic heterodonty. The crowns are well conserved, but tooth bases are scarce. The shape of the lower jaw teeth is characteristically spearhead-like, with up to five coarse denticles in the basal half of mesial and distal cutting edges (Fig. 3Q–S). Upper jaw teeth (Fig. 3T, U) present a unique conical main cusp, and are circular to oval in cross-section, often with a pair of small lateral cusplets.

Remarks—In general, there are no significant differences between the teeth described from the Iberian sections and those from the type locality (Botella et al., 2009). To consult a more detailed description of teeth of *P. henarejensis*, see Botella et al. (2009). The percentage of upper/lower teeth, 19% from the upper dentition and 81% from the lower dentition, is in agreement with the percentage reported from the type locality (Botella et al., 2009), 16% and 84%, respectively, showing that specimens of teeth from the upper jaw are less abundant.

Occurrence—Middle Triassic from the Iberian Range of Spain.

DISCUSSION

Age of the Fauna

All the chondrichthyan remains reported here have been recorded in CDL formation materials, which were considered by López-Gómez and Arche (1992) of Ladinian age. These findings were based on the fossil record of this unit, consisting primarily of bivalves, ammonoids, foraminifera, and conodonts. New studies and findings from different groups allow us to consider that the association of chondrichthyans studied corresponds to the upper Ladinian ('Longobardian'). Thus, in the Calanda, Henarejos, Moya, and Bugarra sections, the presence in the same levels of *Sephardiella mungoensis* and *Pseudofurnishius murcianus* Plasencia, Márquez-Aliaga, and Valenzuela-Ríos, 2004, permits us to date the studied assemblage as 'Longobardian.' Supporting this dating, bivalves recorded in all the studied sections belong to the 'Fauna de Teruel' assemblage of the upper Ladinian (Márquez-Aliaga and Martínez, 1996).

Paleobiology

The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain) is composed exclusively of nonneoselachian sharks, supporting the idea that neoselachians were still rare in Europe by Ladinian times. Despite the absence of neoselachians, the chondrichthyan assemblage from Spain presents evidence of functional adaptation for a wide diversity of trophic strategies. In terms of diversity of species, the chondrichthyan paleocommunity was dominated by durophagous sharks (*Prolatodon bucheri*, comb. nov., *Prolatodon contrarius*, comb. nov., *Lissodus* aff. *L. lepagei*, and *Palaeobates angustissimus*). The grasping-crushing dentitions (with cusped anterior teeth and flat lateral teeth) of *Prolatodon bucheri*, comb. nov. (135 complete teeth), *Prolatodon contrarius*, comb. nov. (75), and *L. aff. L. lepagei* (24) constitute almost half of the total collected teeth. Dentitions of this mixed type are currently present only in heterodontids (Capetta, 1987), but their presence in Homalodontids and Lissodus (Rees and Underwood, 2002, noted that Lissodus dentitions are clearly of graspingcrushing type) show that this specialized dentition evolved independently in non-neoselachian sharks. This type of dentition implies clear durophagous feeding habits, which may include crustaceans, ostracods, or even shell animals such as gastropods and bivalves, all of them recovered from the studied sections (Fig. 1). In this sense, the teeth present in females of several living Rajiformes, which are morphologically very similar to the lateral teeth of Prolatodon bucheri, comb. nov., and Prolatodon contrarius, comb. nov. (and other homalodontids), also have a similar bilayered SCE (unpubl. data). We have studied the stomach contents of several captured specimens of Raja clavata, which consistently contain crustaceans, and, in lesser proportions, gastropods and small fishes. Interestingly, all of the teeth of the species L. aff. L. lepagei that have been found show strong evidence of functional wear. In the cusps of some specimens, the enameloid is completely worn, showing the dentine in the outer surface (Figs. 2T, V), lateral cusplets are highly eroded, and the smooth crowns present numerous micro-wear marks. This observation implies a diet with a large proportion of shelled animals. The other durophagous shark found in Spain is P. angustissimus (one complete tooth), although these teeth are of the grinding type adapted for feeding on hard prey with resistant shells (see Capetta, 1987). Dentitions adapted for a 'grasping and swallowing' strategy (clutching type sensu Cappetta, 1987) are represented in the present fauna by Hybodus bugarensis, sp. nov., and Hybodus plicatilis. The minute teeth of Hybodus bugarensis, sp. nov., which have slender and sharp cusps, indicate predation upon small soft-bodied animals, whereas the larger multicusped teeth of Hybodus plicatilis (Fig. 2M), which have large cusps ornamented with ridges (ornamentation with ridges has a mechanical reinforcement function for the tooth; see Cappetta, 1986), indicate a more general diet, preying on larger animals. The last type of dentition present among the identified chondrichthyan taxa from Spain is the cutting-clutching type (sensu Cappetta, 1987), characterized by a strong dignathic heterodonty where teeth of one jaw retain a high and narrow cusp, whereas the teeth of the other jaw are wider and flatter in the labiolingual direction forming an almost continuous cutting edge. This type is only represented by the taxon P. henarejensis, which, with 177 complete teeth, is the most abundantly collected species. Cutting teeth are very rare among non-neoselachian sharks (Duffin and Cuny, 2008) and Pseudodalatias is the only shark to have developed a cutting-clutching dentition lacking the triple-layered enameloid exclusive in neoselachians-although showing a special adaptation of their SCE microstructure (see Botella et al., 2009). Teeth of *Pseudodalatias* are extremely similar to those of some extant neoselachian of the family Dalatiidae Gray, 1851, not only in their morphology (note that isolated teeth of P. barnstonensis were originally assigned to the genus Dalatias by Sykes, 1971) but also in their particular tooth replacement pattern (shedding all the teeth of the same dental row at the same time; see Strasburg, 1963, and Tintori, 1980). These peculiar similarities in dentition indicate that pseudodalatids in Triassic seas may have exploited the unusual feeding habits exhibited by some extant dalatiids such as *Dalatias* and *Isistius*, which mainly consisted of 'parasitic' bites excising portions of flesh from large oceanic animals, including other sharks, marine mammals, and bony fishes (Gasparini and Sazima, 1996; Soto and Mincarone, 2001; Heithaus, 2004). Thus, P. henarejensis could have used its narrow upper teeth to anchor to larger animals (such us other sharks, osteichthyes, or marine reptiles, which are abundant in Middle Triassic shallow-water sediments of the Iberian Range), while teeth of the lower jaws slice into them. In summary, the numerous types of dentitions (grasping-crushing, grinding, clutching, and cutting-clutching) found among the Middle Triassic chondrichthyan fauna of the Iberian Range imply that these fauna dominated the predator community of the coastal ecosystems and yield evidence that the non-neoselachian sharks of the same paleocommunity could feed on a wide range of prey, including small soft-bodied animals, crustaceans, resistant-shelled animals, and even large vertebrates. This fact also influences the idea that the microstructural differentiation in a triple-layered enameloid is a necessary preadaptation facilitating the evolution of novel feeding strategies among neoselachians (Gillis and Donoghue, 2007) through a functional adaptation to increase the resistance to stresses and forces arising from new food processing strategies (Preuschoft et al., 1974; Reif, 1978, 1979; Thies and Reif, 1985). The fact that most of the feeding strategies present in neoselachians have been found in non-neoselachian sharks lacking a triple-layered enameloid does not support this suggestion (see also Lund and Mapes, 1984; Cappetta, 1987; Cappetta et al., 1990; Duffin, 2001; Duffin and Cuny, 2008).

Paleobiogeography

Paleobiogeographically, Middle Triassic Spanish sharks represent a diverse assemblage. Two of the species (Hybodus plicatilis and Palaeobates angustisimus) have been previously reported from several localities of northern Europe and seem to be common components of Middle Triassic shark faunas in the German Basin. In contrast, two of the other species found in Spain (Prolatodon bucheri, comb. nov., and Prolatodon contrarius, comb. nov.) have never been cited previously from the Triassic in Europe. Prolatodon contrarius, comb. nov., occurs in the Middle Triassic of British Columbia, Canada (Johns et al., 1997), and in the Middle–Late Triassic of Gualing, China (Chen et al., 2007), and Prolatodon bucheri, comb. nov., was undisputedly known only from the Middle Triassic of Nevada, U.S.A. (Rieppel et al., 1996; Cuny et al., 2001) (but see below). Finally, the rest of the fauna is composed of 'endemic' taxa that have never been recorded elsewhere (P. henarejensis, Hybodus bugarensis, sp. nov., and Lissodus aff. L. lepagei). This 'paleobiogeographical' heterogeneity of Spanish chondrichthyan fauna can be linked to Ladinian marine transgression (upper Muschelkalk facies, after the severe Anisian/Ladinian regression, 'Keupertype' facies), which allowed for the colonization of the shallow waters of the Iberian Peninsula by faunas coming from both Tethys provinces; the Germanic domain to the north and the Sephardic domain to the south (i.e., present-day Israel, North Africa, and Spain). This suggestion has been documented with other fossil faunas (Márquez-Aliaga, 2010). Thus, H. plicatilis and P. angustissimus, which are widespread across the entire shallow northern European basins (e.g., Germany, Poland, Luxemburg, northern France, and Switzerland), would have been able to migrate to the new Ladinian epicontinental seas of the Iberian Peninsula via the Alpine Basin (because both species occur in the Middle Triassic of Switzerland; Rieppel et al., 1981). Homalodontids, which were first documented in the Lower and Middle Triassic of western North America, could have reached the Iberian Peninsula via south China (Prolatodon contrarius, comb. nov., occurs in the Middle-Late Triassic of Guizhou Province, southwest China; Chen et al., 2007) through the Sephardic Province (i.e., the southern margin of the Tethys Ocean), using shallow neritic distribution paths that originated before the Cimerian terranes drifted away from Gondwana.

ACKNOWLEDGMENTS

We thank G. Cuny for his taxonomic training during the research stay of one of the authors (C.P.) in the Natural History Museum of Denmark and P. Plasencia for his help in the processing of the samples. This work has been partially supported by the program 458.10 of Direcció General de Patrimoni Cultural Valencià de la Conselleria de Cultura Educació i Esports (2007/0419–V and 2008/0432–V) and is a contribution to the IGCP 506–IUGS.

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Submitted July 4, 2012; revisions received October 25, 2012; accepted November 8, 2012.

Handling editor: Charlie Underwood.