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ARTICLE

PSEUDODALATIAS HENAREJENSIS NOV. SP. A NEW PSEUDODALATIID (ELASMOBRANCHII) FROM THE MIDDLE TRIASSIC OF SPAIN

HÉCTOR BOTELLA,*[,1] PABLO PLASENCIA,[1,2] ANA MARQUEZ-ALIAGA,[1,2] GILLES CUNY,[3] and MARKUS DORKA[4]
[1]Departamento de Geología, Universidad de Valencia, Avda. Dr. Moliner, 50, 46100 Burjassot (Valencia), Spain, hecbose@postal.uv.es;
[2]Instituto Cavanilles de Biodiversidad Evolutiva;
[3]Natural History Museum of Denmark, Øster Voldgade 5-7, Copenhagen 1350 K, Denmark;
[4]Humboldt-Universität zu Berlin, Museum für Naturkunde, Invalidenstrasse 43, D-10115 Berlin, Germany

ABSTRACT—Pseudodalatiids, a chondrichthyan family of uncertain phylogenetic affinities, have been hitherto exclusively known from the tooth-based species *Pseudodalatias barnstonensis* (Sykes, 1971), which has a stratigraphic range restricted to the Upper Triassic of Europe. *Pseudodalatias* presents a characteristic dentition which allows it to hold and cut its prey, showing a neoselachian design, but lacking the triple-layered enameloid microstructure of neoselachian teeth. The discovery of *Pseudodalatias henarejensis* nov. sp. in the Ladinian of Spain extends the stratigraphical range and the palaeogeographical distribution of this family. This new species also demonstrates that a cutting-clutching dentition evolved progressively in the family Pseudodalatidiidae. Pseudodalatiids are likely to represent stem-batoids or stem-neoselachians rather than aberrant hybodonts.

INTRODUCTION

So far, pseudodalatiids have been exclusively known from the tooth-based species *Pseudodalatias barnstonensis* (Sykes, 1971), which is restricted to the Norian and the Rhaetian (Upper Triassic) of Europe. Isolated teeth of *P. barnstonensis* have been reported from the Rhaetian of several localities of Britain (Sykes, 1971, 1974; Duffin, 1980, 1999; Storrs, 1994), Belgium (Duffin et al., 1983; Duffin and Delsate, 1993) and France (Cuny et al., 1994; Cuny et al., 2000). Articulated lower jaw dentitions have been found in the Norian of Italy (Tintori, 1980).

Due to morphological similarities with the dentition of the extant neoselachian *Dalatias licha* (Bonnaterre, 1788), isolated teeth of *P. barnstonensis* were originally assigned to the genus *Dalatias* by Sykes (1971). However, Reif (1978a) demonstrated that the enameloid of *Pseudodalatias* lacks the complex triple-layered microstructure characteristic of the modern sharks (non-batoid neoselachians) and instead somewhat resembles that of hybodont sharks (but see below). Accordingly, he placed the Triassic species in the new genus *Pseudodalatias*, for which he erected the family Pseudodalatiidae. Reif (1978a) suggested that the genus *Pseudodalatias* was closer to the hybodonts than to the neoselachians, but he also noted it was probably not a hybodont. In fact, the histology of *Pseudodalatias* teeth is unique among sharks and, at present, relationships of Pseudodalatiids within the Elasmobranchii remain unclear (Reif, 1978a; Cappetta, 1987; Storrs, 1994; Cuny, 1995; Cuny and Benton, 1999; Duffin, 1999).

The present paper describes a new species of *Pseudodalatias* (*P. henarejensis* nov. sp.) from the Middle Triassic of Spain, which extends the stratigraphical range of pseudodalatiids and offers a novel phylogenetic interpretation of this family.

GEOLOGICAL SETTING

The Triassic sediments in the Iberian Ranges comprise three facies that broadly correspond to the classic tripartite subdivision Buntsandstein, Muschelkalk and Keuper. The Muschelkalk facies is represented by two dolomite units. The uppermost of these is the Cañete Dolomites and Limestones Formation (CDL). It is of Ladinian age based on ammonite, bivalve, foraminifera, and conodont assemblages (López-Gómez and Arche, 1992; López-Gómez *et al*., 2002). The studied section is located in the SE of the Iberian Ranges (Castilian branches) (Fig. 1) and was first studied from a palaeontological point of view by Márquez-Aliaga (1985) who demonstrated that it shows one of the richest faunas within otherwise rare Triassic sections available in Spain (López *et al*., 1987; Márquez-Aliaga and López, 1989). The material described below is composed of isolated teeth, retrieved from the dissolution of carbonate rocks with 10 per cent acetic acid, and comes from the uppermost member of the CDL Formation of Henarejos section (Henarejos, Cuenca, Spain). All specimens are housed in the Museo de Geología de la Universidad de Valencia (MGUV), Spain.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Family PSEUDODALATIIDAE Reif, 1978a

Diagnosis—(modified from Reif, 1978a). A shark family only known from teeth. A strong dignathic heterodonty is present, reflecting a cutting-clutching dentition. One tooth type, probably belonging to the upper jaws, presents crowns with a conical main cusp, circular to oval in cross section, usually flanked by small lateral cusplets. The base is anaulacorhize with a large external medial foramen and a large internal medial foramen. The base is U-shaped with two lobes. The other tooth type, probably belonging to the lower jaws, has a triangular, linguo-labially compressed crown with coarsely serrated edges. Both upper and

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*Corresponding author. hecbose@slumni.uv.es

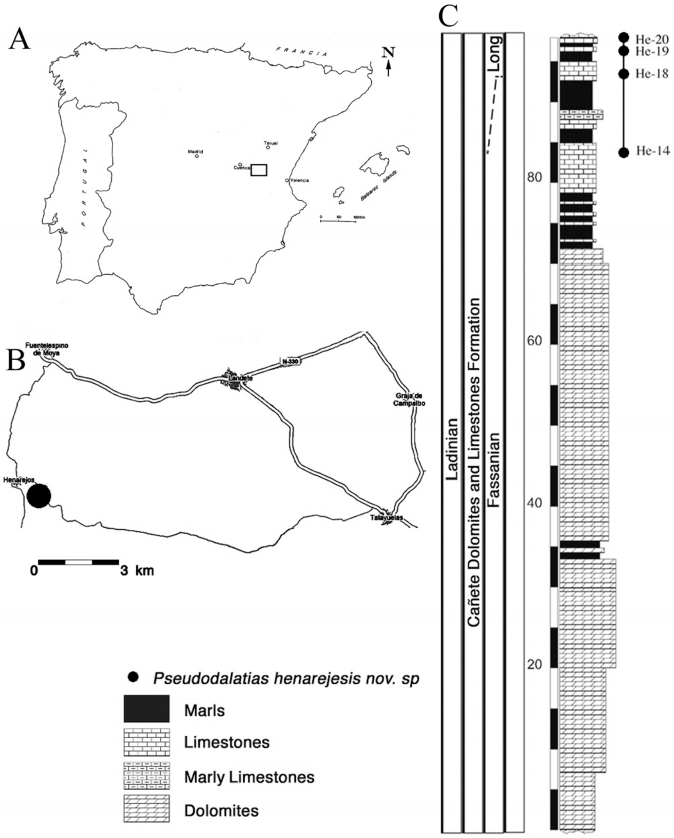

FIGURE 1. **A**, geographical situation of Henarejos, indicated by rectangle, in the Iberian Peninsula; **B**, detail of A, showing the exact location of the studied section; **C**, stratigraphic column of Henarejos section with indication of levels that yielded the material described in this work.

lower teeth have a thin, single crystallite enameloid capping layer. The crystallites of the enameloid have an orientation perpendicular to the tooth surface within the tissue and an orientation parallel to the surface in the outermost part of the layer. Underneath the enameloid is a layer of orthodentine. The pulp cavity may be invaded by atubular dentine forming the base of the teeth (see Reif, 1978b).

Remarks—Reif (1978a) provided a diagnosis for the Pseudodalatiidae based on the unique histological characters of the only known species at that time *P. barnstonensis* (Sykes, 1971). He stated that apart from the enameloid and the orthodentine layer, the rest of the crown and the whole root (base) are formed by trabecular, acellular bone (atubular dentine, Reif, 1978b). This character is observed in *P. barnstonensis* (Sykes, 1971), but not in *P. henarejensis* nov. sp., which preserves a central pulp cavity. Thus, we remove this character from the family diagnosis and consider it as a specific, probably derived, character of *P. barnstonensis* (Sykes, 1971) (see emended diagnosis of *P. barnstonensis* and comparisons). In the absence of a full set of teeth found in connection, it is impossible to ascertain which kind of teeth is the lower one and which kind is the upper one, hence the use of "probably" in the diagnosis. However, to keep the text concise, lower and upper will be used as a convention in the rest of the text.

Genus PSEUDODALATIAS Reif, 1978a

Diagnosis—As for the family
Type Species—*Pseudodalatias barnstonensis* (Sykes, 1971)

PSEUDODALATIAS BARNSTONENSIS (Sykes, 1971)

Emended Diagnosis—A *Pseudodalatias* species with probable upper jaw teeth having a long, primary cusp circular in cross-section and one or two lateral cusplets on either side. Probable lower jaw teeth have a triangular and labio-lingually compressed crown. The lateral cutting edges of the crown show up to 10, but usually 6–8, denticles. The denticulation reaches the apex of the cusp. The base has a strong process which overlaps the neighbouring tooth on the posterolateral side. The orthodentine layer is thin and the pulp cavity is always invaded by the atubular dentine forming the base of the teeth.

PSEUDODALATIAS HENAREJENSIS, nov. sp.

Etymology—From the village of Henarejos, Province of Cuenca (Spain).

Type Locality—Henarejos Section, close to Henarejos village in the Iberian Ranges.

Holotype—Lower jaw tooth MGUV-18970, Figure 2, K-L. F2

Additional Material—More than 100 isolated teeth (MGUV-18963-18990), from the samples He-14, He-18, He-19, and He-20.

Occurrence—Uppermost member of CDL Formation at Type locality. Ladinian (Middle Triassic).

Diagnosis—A *Pseudodalatias* species based on isolated teeth. Probable upper jaw teeth have a low conical and symmetrical primary cusp, circular to oval in cross-section. One small lateral cusplet is usually present on each side, although they can be reduced or absent. The base shows two small, rounded lobes. Probable lower jaw teeth have a triangular and labio-lingually compressed crown. Coarse denticulation (up to 5, usually 2-4, denticles on each edge) on the mesial and distal cutting edges is limited to the basal half of the crown. The orthodentine layer is very thick. A well-developed central pulp cavity is present.

Description

Morphology—*Pseudodalatias henarejensis* shows dignathic heterodonty, with both the lower and upper jaw teeth having a smooth crown. The longitudinal striations which can be observed in some specimens (e.g. Fig. 2C, F, H, I, M; Fig. 3C) are due to F3 taphonomic alteration of the dentine and have also been observed in teeth of *P. barnstonensis* (Reif, 1978a).

Lower jaw teeth (Fig. 2): None of the teeth recovered so far have their base preserved. Their crown (less than 1 mm to 2, 5 mm high) shows a distinctive spearhead-like shape. The upper part of the crown is labio-lingually compressed. It has a triangular outline in labial or lingual view. In lateral view it is flattened and slightly curved in a lingual direction (Fig. 2D, G, M). Mesial and distal cutting edges are denticulated with up to five coarse denticles (Fig. 2H–L), although usually only two to four are present (Fig. 2A–G, M, N). The denticles are limited to the basal half of the crown, while its apical part always lacks denticulation (Fig. 2A–P). Below the most basal denticle the crown suddenly narrows and forms a round, moderately low 'neck' (e.g. Fig. 2A, B, H–O). Most of the teeth are curved in the distal direction (Fig. 2E, F, H, I, K, M, O).

The morphology of lower jaw teeth varies slightly, especially with reference to the symmetry of the crown and to the shape and number of the denticles. This is probably due to the tooth position in the jaw (see Discussion). Thus, only a few of the teeth found have a nearly symmetrical crown in labial or lingual view (Fig. 2A–C) and probably belong to symphyseal positions. In these teeth the mesial and the distal edges bear only two lobule-like denticles that are large and rounded (Fig. 2A–C). The lower denticle can show a weakly developed incision (Fig. 2C). Presumed lateral teeth (Fig. 2E–N) have denticles that are gently pointed in apical direction. Mesial denticles are more pointed than the distal ones. Notches between the denticles are deeper

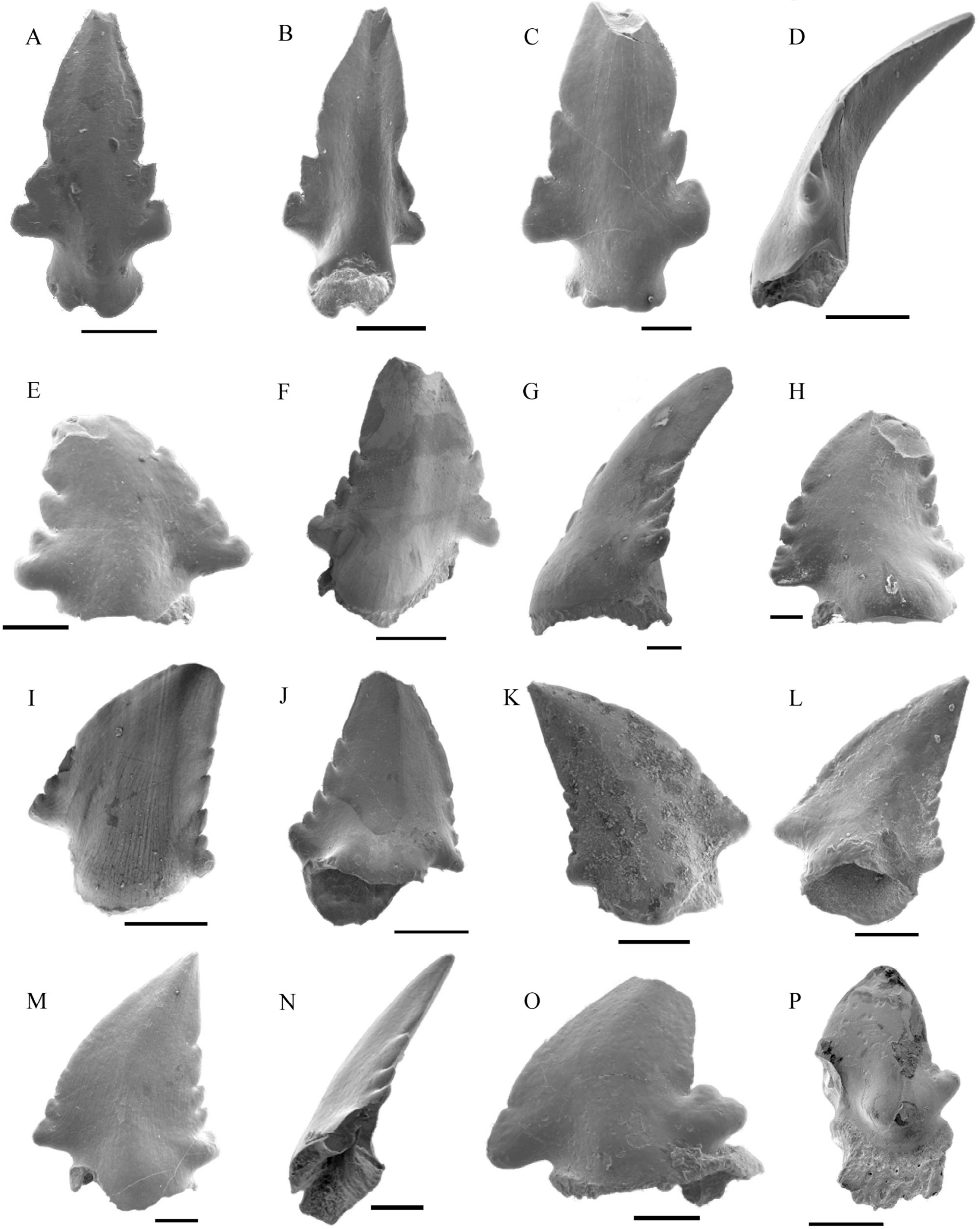

FIGURE 2. *Pseudodalatias henarejensis* nov. sp. lower jaw teeth. **A–D**, symphyseal teeth; **A**, **B**, MGUV-18963 (**A** in labial view, **B** in lingual view); **C**, MGUV-18964 in labial view; **D**, MGUV-18965 in lateral view. **E–N**, Lateral teeth; **E**, MGUV-18966 in labial view; **F**, **G**, MGUV-18967 (**F** in labial view, **G** in lateral view); **H**, MGUV-18968 in labial view; **I**, **J**, MGUV-18969 (**I** in labial view, **J** in lingual view); **K**, **L**, MGUV-18970 Holotype (**K** in labial view, **L** in lingual view); **M**, **N**, MGUV-18971 (M in labial view, N in lateral view). **O**, posterior tooth MGUV-18972. **P,** broken tooth with incomplete base MGUV- 18973. Scale bar equals 250 μm in **A**, **C** and **M**; 200 μm in **B**, **D**, **E**, **G**, **H**, **N** and **O**; 500 μm in **F**, **I**, **J**, **K**, **L** and **P**.

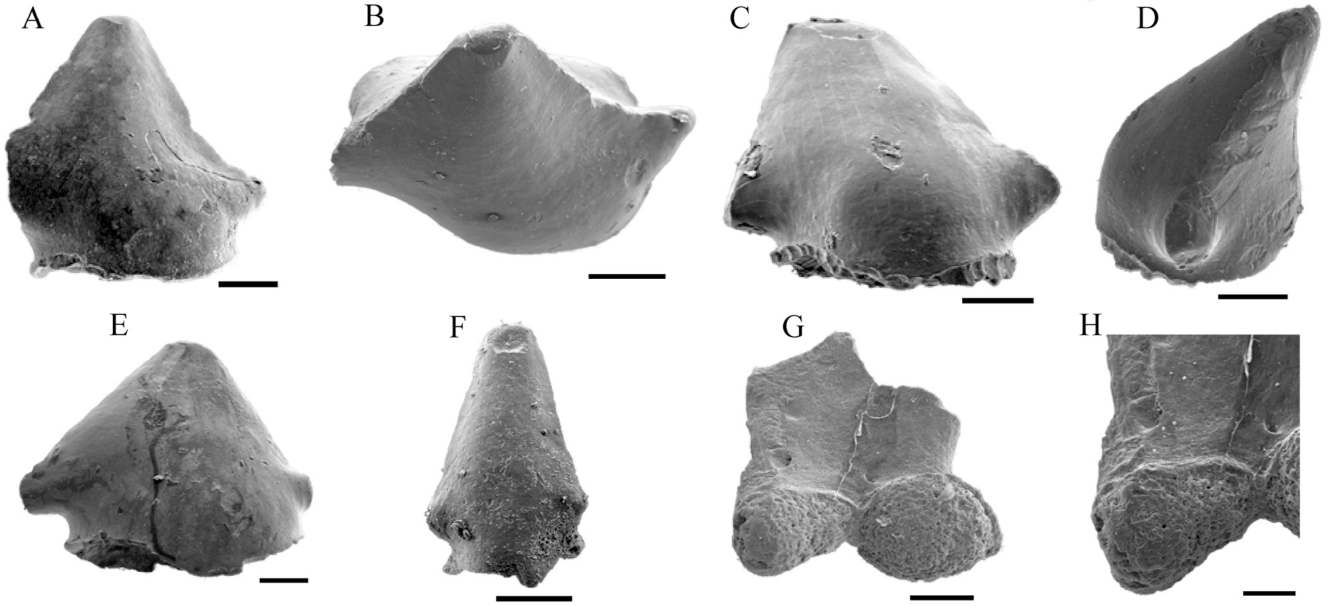

FIGURE 3. *Pseudodalatias henarejensis* nov. sp. upper jaw teeth. **A**, **B**, MGUV-18974 (**A** in labial view, **B** in apical view); **C**, **D**, MGUV-18975 (**C** in labial view, **D** in lateral view); **E**, MGUV-18976 in labial view; **F**, MGUV-18977 in labial view; **G**, **H**, MGUV-18978 broken base (**G** in lingual view, **H** detail of the same). Scale bar equals 250 µm in **A**, **D** and **E**; 200 µm in **B**, **C** and **F**; 150 µm in **G**; 100 µm in **H**.

on the distal side than on the mesial one. The distal side shows up to five, but more usually four denticles. The mesial side shows less denticles that the distal one (Fig. 2E, F, H, I-M). The most basal denticle can be slightly incised (Fig. 2E), as in symphyseal teeth, but this character is not developed so often in laterals. Some crowns are strongly curved in a distal direction and have a mesial edge that lacks serration or shows barely developed denticles. Their posterior cutting edge develops a single, slightly incised denticle in its basal part (Fig. 2O). These teeth are very small and could be associated with the most distal positions of the dental series.

Upper jaw teeth (Fig. 3A–F) have a crown that consists of a low conical, gently pointed primary cusp (0,5 to 1, 2 mm high), which is slightly arched in lingual direction (Fig. 3B, D). Most teeth develop a small, single cusplet on the basal part of each edge of the primary cusp (Fig. 3A–E). These cusplets are rounded and nearly perpendicular to the primary cusp (e.g. Fig. 3A, C, E). Some teeth lack cusplets (Fig. 3F). The cross-section of the primary cusp is circular in its basal part and becomes oval in its apical part. Cutting edges are poorly developed and restricted to the apical part of the primary cusp (Fig. 3B).

Tooth bases of *P. henarejensis* nov. sp. are rarely preserved. This fact has also been noted in *P. barnstonensis* (Sykes, 1971; Reif, 1978a). The best preserved bases are morphologically similar to those of upper jaw teeth of *P. barnstonensis* (compare Fig. 3G with Sykes, 1974, text-fig. 2; Reif, 1978a, fig. 3). Some specimens do show a small portion of the base attached to the crown (Fig. 2P), but their poor and fragmentary preservation does not allow for a definitive reconstruction. On the other hand, a few isolated bases that appear broken from their respective crowns are putatively assigned to the upper jaw teeth of *P. henarejensis* (see below). They are short and show a bifid, moderate U-shape (Fig. 3G). They are highly vascularized, and wholly covered with pores. Large labial and lingual foramina are found in a medial position between the lobes. A lateral foramen is also present at least on one side of the base, probably the mesial one (Fig. 3H).

Histology—Both the lower and upper teeth show the same enameloid microstructure, which is distinctive of Pseudodalatiids (Fig. 4). A very thin (5–a8 µm) single crystallite enameloid (SCE) layer is present, covering the whole crown. Underneath the enameloid, there is a thick orthodentine layer (see also Figs. 5A, B, E). The dentine tubules are numerous, slightly sinuous and run individually from a central pulp cavity towards the surface of the crown. Dentine tubules bifurcate distally close to the SCE. The central pulp cavity is high and linguo-labially flattened. In some of the specimens the most basal part of the pulp cavity is filled up with atubular dentine, which also makes up the base. F4 F5

SCE (Fig. 5) consists of very small, elongated crystallites (around 0,5 µm long). Individual crystallites are clearly discernable under high magnification. They are oriented perpendicular to the surface in the inner part of the layer (Fig. 5C, D), whereas in the outer part of the layer they are arranged parallel to the surface (Fig. 5D, F). A well-defined border separates the enameloid from the dentine core (Fig. 5A, B).

Comparisons

Teeth described here are assigned to *Pseudodalatias* based on their distinctive morphology and histological characters. The tooth morphology resembles that of *P. barnstonensis* in showing dignatic heterodonty with upper jaw teeth having a primary cusp and small lateral cusplets and lower jaw teeth having a triangular crown and coarsely serrated edges.

Teeth of *P. henarejensis* nov. sp. differ from *P. barnstonensis* teeth in the size (those of *P. barnstonensis* being up to three times larger) and in several other characters. Thus, in *P. barnstonensis* the orthodentine layer is very thin and most of the crown consists of atubular dentine (e.g. Reif, 1978a, fig. 5 c-d). In *P. henarejensis* nov. sp. the orthodentine layer is very thick and the pulp cavity is well-developed. In some specimens the orthodentine layer makes up almost the whole crown (Figs. 4, 5A). Upper jaw teeth of *P. barnstonensis* have a primary cusp which is longer and more arched in the lingual direction compared to that of *P. henarejensis* nov. sp. (compare e.g. Reif,1978a, fig. 3; Duffin, 1999, plate 26, fig. 10-11 with Fig. 3A-F). Upper jaw teeth of *P. barnstonensis* have one or two pairs of lateral cusplets (Sykes, 1971, text-fig. 2, pl. 2 fig. 1; Sykes, 1974, text-figs. 2, 3, pl. 2 figs. 7-9; Reif, 1978a, fig. 3) while in *P. henarejensis* nov. sp., upper jaw teeth show only

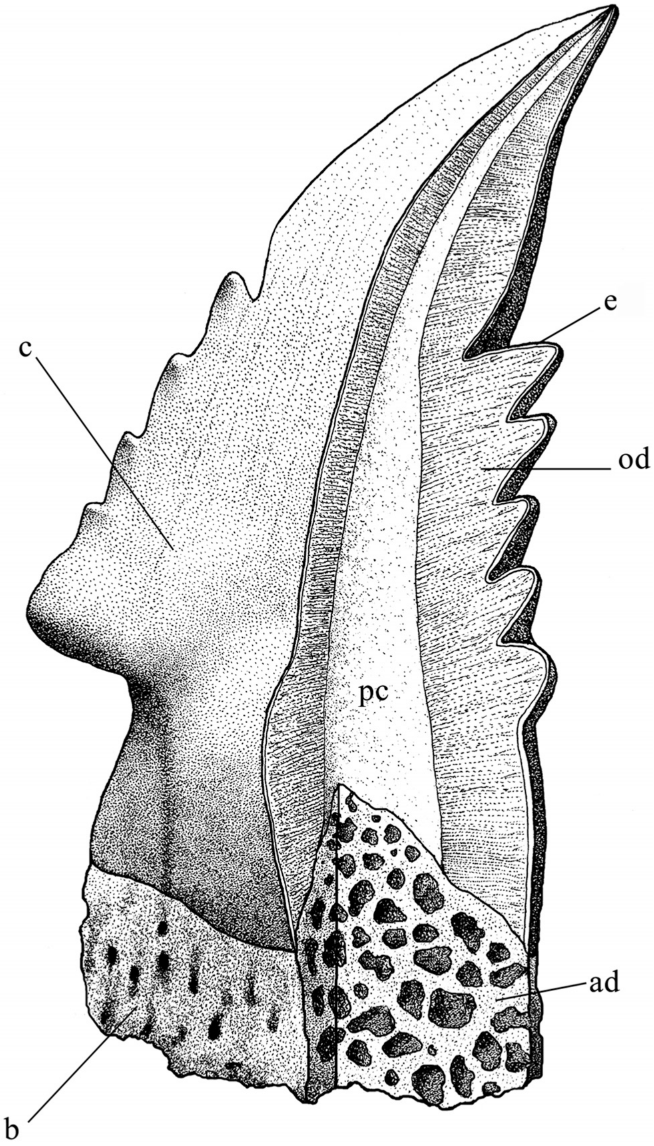

FIGURE 4. *P. henarejensis* nov. sp.; reconstruction of the tooth histology based on thin sections of specimens MGUV-18979 (lateral longitudinal section), MGUV-18980 and MGUV-18981 (longitudinal sections), MGUV-18982 MGUV-18983 (cross sections). **Abbreviations**: **ad,** atubular dentine; **b**, base; **c**, crown; **e**, enameloid layer; **od**, orthodentine; **pc**, pulpar cavity.

one pair of cusplets or lack lateral cusplets completely. Moreover, the lateral cusplets are almost perpendicular to the main cusp, while they are much more erect in the teeth of *P. barnstonensis*. Lower jaw teeth of *P. barnstonensis* have edges with up to 10, usually 6-8, denticles (e.g. Duffin and Delsate, 1993, Plate 1, fig 1a; Tintori, 1980; Reif, 1978a) and the denticulation reaches the apex of the cusp. In *P. henarejensis* nov. sp. there are at most 5, but usually 2–4, denticles on each edge, and they are restricted to the basal part of the edges (Fig. 2).

Lower jaw teeth of *P. henarejensis* nov. sp. are identified as symphyseals, laterals and posteriors based on comparisons with the description of articulated lower jaw tooth rows of *P. barnstonensis* (Tintori, 1980). As occur usually in *P. barnstonensis* (see Sykes, 1971, 1974; Tintori, 1980) upper jaw teeth of *P. henarejensis* nov. sp. are under-represented in the collection. Only 16 of more than 100 teeth belong to upper jaws. However, this could be due to an artefact related to their smaller size.

Discussion

Reif (1978a) stated that the enameloid microstructure of pseudodalatiids is unique among sharks. This idea is supported by a recent survey (Gillis and Donoghue, 2007) of enameloid microstructure of several chondrichthyan taxa spanning the phylogeny of the group. Non-batoid neoselachian teeth show a triple-layered enameloid, whereas the enameloid of non-neoselachian shark teeth is usually not differentiated, except in some hybodontiform species like *Hybodus* (Reif, 1978a), *Acrodus* and *Polyacrodus* (Cuny et al., 2001) that have a two-layered enameloid with an outer layer of compact SCE and an inner layer with crystallites organized into parallel bundles oriented perpendicular to the enameloid–dentine junction.

Gillis and Donoghue (2007) proposed that the triple-layered enameloid microstructure was a necessary preadaptation to the cutting teeth of many neoselachians. However, cutting dentition also evolved in some sharks possessing only single crystallite enameloid: *Carcharopsis* Agassiz, 1843, *Priohybodus* d'Erasmo, 1960*, Pororhiza* Casier, 1969 and *Thaiodus* Cappetta, Buffetaut and Suteethorn, 1990 (Lund and Mapes, 1984; Cappetta, 1987; Cappetta *et al*., 1990; Duffin, 2001; Cuny, 2006). Interestingly enough *Carcharopsis, Priohybodus* and *Thaiodus* share with *Pseudodalatias* a very compact single-layered, single-crystallite enameloid (Duffin and Cuny, 2008). However, *Pseudodalatias* is the only shark devoid of a triple layered enameloid to have developed a cutting-clutching dentition. The acquisition of this type of dentition was, however, gradual as demonstrated by the discovery of *P. henarejensis* nov. sp. in which the lower teeth show incomplete denticulation, and the upper teeth are not as pointed as in *P. barnstonensis,* and thus not as efficient for clutching prey. In addition, *P. henarejensis* nov. sp. and *P. barnstonensis* differ in an important histological character. As mentioned above, in *P. henarejensis* nov. sp. a well-developed central pulp cavity is present and the atubular dentine is restricted to the base and to the lower part of the crown (see Fig. 4). In *P. barnstonensis* the atubular dentine has invaded the whole pulp cavity. The reason why the development of a full cutting-clutching dentition in *Pseudodalatias* is linked to the development of atubular dentine in the tooth crown remains, however, to be explained.

The phylogenetic affinities of *Pseudodalatias* are difficult to determine. Its teeth show a neoselachian design with a U-shaped base firmly fused to the crown, but lack a triple-layered enameloid. However, the batoids, which are the sister-group of the rest of the neoselachians (Galea+Squalea) (Douady *et al*., 2003; Maisey *et al*., 2004; McEachran and Aschliman, 2004; Winchell *et al*., 2004) also possess teeth devoid of a triple-layered enameloid, and it has recently been proposed that some Triassic genera of uncertain affinities, like *Doratodus* and *Vallisia*, could in fact be primitive batoids (Rees and Cuny, 2007). This would suggest that, contrary to Underwood's (2006) assumption, the characteristic batoid tooth design appeared well after their divergence from the other neoselachians. It is therefore very tempting to consider *Pseudodalatias* as an experimental stem-batoid or perhaps stem-neoselachian, which would explain the lack of a triple-layered enameloid as well as the lack of any obvious batoid characteristic. Its tooth design is indeed more in accordance with this hypothesis rather than to include this genus among the Hybodontiformes.

With the report of *P. henarejensis* nov. sp. the stratigraphic range of the genus *Pseudodalatias* extends from the Ladinian (Middle Triassic) to Rhaetian (Upper Triassic).

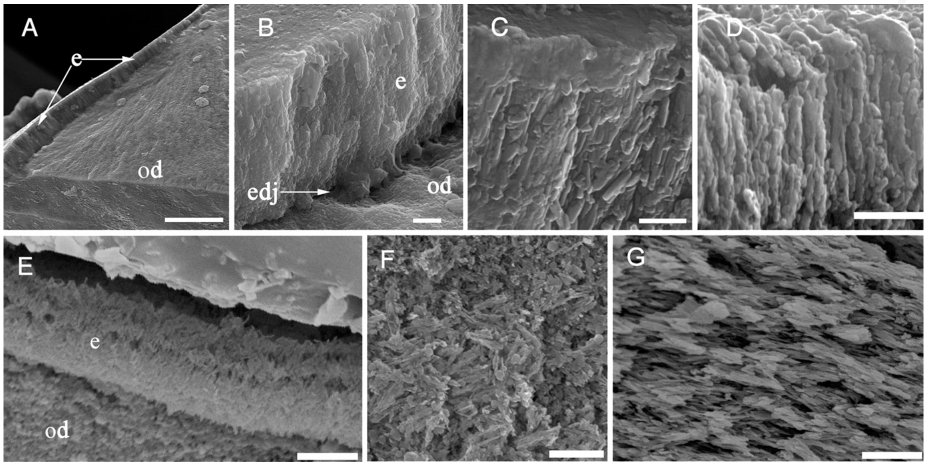

FIGURE 5. **A–F** tooth enameloid of *P. henarejensis* nov. sp. teeth. **A,** overview of vertical fresh fracture (not eched) of lower jaw tooth MGUV-18984 showing the thin enameloid layer capping the thick, massive orthodentine core; **B**, detail of A. Note the thinness of the enameloid layer (aprox. 10 µm) and the sharp enameloid-dentine junction; **C**, single crystallite enameloid ultrastructure of the same speciment; **D**, single crystallite enameloid ultrastructure of upper jaw tooth MGUV-18985 etched 5 seconds with 2n HCl. In both C and D, individual crystallites are clearly discernible within the layer and they have an orientation perpendicular to the surface except at the very outermost part of the layer where crystallites are oriented parallel to the tooth surface; **E**, single crystallite enameloid ultrastructure in cross section of lower jaw tooth MGUV-18986 etched 5 seconds in 2n HCl; **F**, surface of the lower jaw tooth MGUV- 18987 etched 2 seconds in 2n HCl showing individual crystallites oriented parallel to the surface in the outermost part of the layer and underneath these, the crystallites are aligned perpendicular to the surface; **G**, surface of a lower jaw tooth of *P. barnstonensis* (Sykes 1971) from the Upper Triassic of Lombardy for comparison, tooth GM-V-2008-3 (Natural History Museum of Denmark) etched 40 seconds in 10% HCl. **Abbreviations**: **e**, enameloid layer; **edj**, enameloid-dentine junction; **od**, orthodentine. Scale bar equals 25 µm for **A**; 4 µm for **G**; 2 µm for **E**; 1 µm for **B** and **F**; 0,5 µm for **C** and **D**.

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