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: Esther Manzanares, Cristina Pla, Carlos Martínez-Pérez, Humberto Ferrón & Héctor Botella (2016): Lonchidion derenzii, sp. nov., a new lonchidiid shark (Chondrichthyes, Hybodontiforms) from the Upper Triassic of Spain, with remarks on lonchidiid enameloid, Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2017.1253585

To link to this article: http://dx.doi.org/10.1080/02724634.2017.1253585

Journal of Vertebrate Paleontology e1253585 (5 pages)

DOI: 10.1080/02724634.2017.1253585

SHORT COMMUNICATION

LONCHIDION DERENZII, SP. NOV., A NEW LONCHIDIID SHARK (CHONDRICHTHYES, HYBODONTIFORMS) FROM THE UPPER TRIASSIC OF SPAIN, WITH REMARKS ON LONCHIDIID ENAMELOID

ESTHER MANZANARES,[1] CRISTINA PLA,[1] CARLOS MARTÍNEZ-PÉREZ,[1,2] HUMBERTO FERRÓN,[1] and HÉCTOR BOTELLA,*,[1]; [1]Cavanilles Institute of Biodiversity and Evolutionary Biology and Department of Botany and Geology, Universitat de València, 46980, Valencia, Spain, Hector.Botella@uv.es; [2]School of Earth Sciences, University of Bristol, Bristol, BS8 1TQ, U.K.

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Citation for this article: Manzanares, E., C. Pla, C. Martínez-Pérez, H. Ferrón, and Héctor Botella. 2016. *Lonchidion derenzii*, sp. nov., a new lonchidiid shark (Chondrichthyes, Hybodontiforms) from the Upper Triassic of Spain, with remarks on lonchidiid enameloid. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2017.1253585.

Lonchidiidae Herman, 1977, represents one of the most diverse and controversial families of Hybodontiformes, the sister group of Neoselachii (i.e., modern sharks, skates, and rays). It was initially erected as a monogeneric family including only *Lonchidion* Estes, 1964, a genus of small euryhaline hybodonts from the Mesozoic. Recently, Cappetta (2012) recognized up to eight genera within the family: *Baharyodon, Diplolonchidion, Vectiselachos, Hylaeobatis, Isanodus, Parvodus, Lissodus*, and *Lonchidion*, although the content of the family is still under discussion (see, e.g., Rees, 2008; Khamha et al., 2016). Major discrepancies concern the phylogenetic relationships between *Lonchidion* and *Lissodus* and the taxonomic status of the latter. Thus, based on the general similarity of their teeth, Duffin (1985, 2001) considered *Lonchidion* as a junior synonym of *Lissodus*. Subsequently, Rees and Underwood (2002) restored *Lonchidion* as a valid genus, closely related to *Lissodus*, within the family Lonchidiidae (together with *Vectiselachos, Parvodus*, and *Hylaeobatis*). This interpretation has been followed by several authors (e.g., Fischer, 2008; Cappetta, 2012; Johns et al., 2014). In contrast, Rees (2008) considered *Lonchidion* and *Lissodus* not so closely related to each other, excluding *Lissodus* from Lonchidiidae.

The majority of *Lonchidion* species has been described on the basis of disarticulated teeth, and complete or partial articulated skeletons have been known only recently from juvenile specimens, assigned to *Lonchidion* sp., from the inland lacustrine Konservat-Lagerstätten outcrop of Las Hoyas (Lower Cretaceous, Spain) (Soler-Gijón et al., 2016). Currently, the stratigraphic distribution of the ranges from the Middle–Upper Triassic (Fischer et al., 2011; Johns et al., 2014) to the Upper Cretaceous (Estes, 1964).

In the present study, we describe a new species assigned to Lonchidiidae, *Lonchidion derenzii*, sp. nov., based on distinctive isolated teeth from the Upper Triassic (Carnian) of Spain, representing the earliest well-documented occurrence of the genus in Europe.

Institutional Abbreviation—**MGUV**, Museum of Geology at the University of Valencia, Valencia, Spain.

GEOLOGIC SETTING AND AGE

The material studied here was collected from the Boyar Section near the cities of Ubrique and Grazalema, in the province of Cádiz, southern Spain (Fig. 1A). The section is located in the southwest part of the Betic Ranges (36°44′49″N, 5°25′12″W; see Martín-Algarra et al., 1995, for a more detailed geographic and geologic setting). The Boyar Section is subdivided into four main units comprising strata belonging to the upper Muschelkalk and Keuper facies (Fig. 1B), which has been dated as Carnian (Upper Triassic) in age on the basis of the contained bivalve, conodont, and pollen assemblages (Martín-Algarra et al., 1995). All teeth were recovered as isolated elements after dissolution in 5–10% formic acid of carbonate rocks (samples around 10 kg) from the middle part of the lower unit (Muschelkalk facies). After dissolution, the residues were screened with sieve meshes of 2, 0.125, and 0.063 mm, respectively. Apart from the teeth of *Lonchidion*, conodonts and teeth and scales of other chondrichthyans and actinopterigians were also recovered. This middle part is characterized by platy limestone interbedded with gray marls and some sporadic dolomitic levels. The presence of pollen in the marly levels has been interpreted as evidence in favor that the entire sequence being deposited in very shallow waters in close proximity to continental areas. The recovered teeth were photographed using a scanning electron microscope at the University of Valencia, Spain. In order to study tooth histology, and following the methodology described in the literature (Gillis and Donoghue, 2007; Botella et al., 2009a; Manzanares et al., 2014), several specimens were embedded in a transparent polyester resin and subsequently sectioned along transverse or longitudinal planes, polished, and then etched using 0.1 M HCl for 5–10 s. Each sample was repolished and etched as many times as necessary to elucidate the enameloid microstructure.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order EUSELACHII Hay, 1902
Superfamily HYBODONTOIDEA Owen, 1846
Family LONCHIDIIDAE Herman, 1977
LONCHIDION Estes, 1964

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

LONCHIDION DERENZII, sp. nov.
(Figs. 2, 3A–C)

Etymology—Named after Emeritus Professor Miquel de Renzi from the Universitat de València, Spain, for his contribution to the development of paleobiology in Spain.

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*Corresponding author.

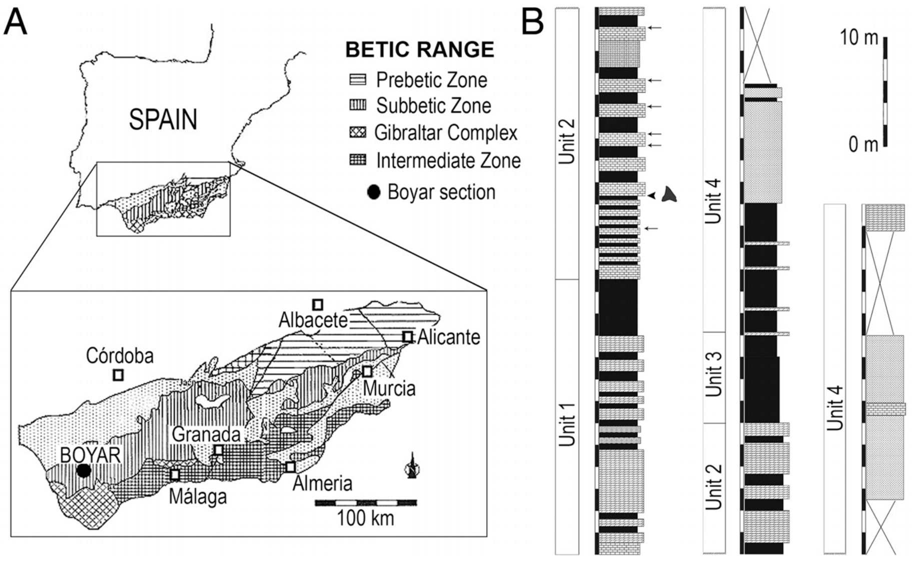

FIGURE 1. **A**, map of the Iberian Peninsula showing the location of the studied Boyar Section in the Betic Ranges. **B**, biostratigraphic column of the Boyar Section, with indication of levels sampled (thin arrows) and the level that yielded the material described in this work (black head arrow). Modified from Plasencia (2009).

Type Locality—Boyar Section, near the cities of Ubrique and Grazalema, in the province of Cádiz, Spain.

Holotype—MGUV-27744, a tooth (Fig. 2A–C).

Additional Material—MGUV-27745 (Fig. 2D–F), MGUV-27746 (Fig. 2G–I), MGUV-27747 (Fig. 2J–L), MGUV-29994 (Fig. 3A–C), and six additional teeth cataloged as MGUV-27748.

Occurrence—Middle part (level 92-A-40) of the lower unit (Muschelkalk facies) of the Boyar Section, dated as Carnian (Upper Triassic).

Diagnosis—A species based on isolated teeth. One parallel-sided to slightly triangular protruding labial peg at the crown shoulder; peg ornamented by a small cusplet and a well-developed labial crest that reaches the principal cusp; crown-root junction very constricted, representing half the width of the crown.

Description—Elongated and gracile teeth, measuring 0.4 to 0.5 mm mesiodistally, 0.2 to 0.3 mm apicobasally, and 0.2 to 0.3 mm labiolingually, with a low coronal profile and presence of very low lateral cusplets. In occlusal view, some teeth have a slight 'V' shape (Fig. 2E, H), with the main cusp situated in the center of the apex of the V, whereas others show a straighter shape (Fig. 2B). Main central cusp small, rounded to triangular in shape, and labially inclined (Fig. 2E, F, H). Commonly two to three pairs of lateral cusplets, which appear very abraded in our specimens (Fig. 2D–L), with the most distal cusplets of a height similar to the principal cusp, giving the crown a very distinctive 'whale tail' shape in labial view (Fig. 2A, G). Labial peg very prominent and narrow, developed above the crown-root junction, parallel-sided in occlusal view, with one small accessory cusplet on the labial crest (Fig. 2A–F, J–L). Occlusal crest well developed, mesiodistally expanded, reaching the last lateral cusplet and descending from the principal cusplet to the labial peg. Lingual face slightly convex below the principal cusp. Crown-root junction very constricted, half the width of the crown, with all the bases absent except in one partial specimen (Fig. 2A). The low number of specimens does not allow us to differentiate clearly between different morphotypes or position in the jaw.

Sections etched in 10% HCl for a few seconds revealed a layer of single crystallite enameloid (SCE), where individual crystallites are well discernible (Fig. 3A–C). Crystallites are around 2 μm in length and randomly arranged near the enameloid-dentine junction, whereas in the rest of the enameloid layer, they appear more compacted and preferentially oriented perpendicular to the crown surface.

Comparisons—The gracile and labiolingually narrow crown of our teeth, along with the well-developed peg, clearly identify them as *Lonchidion.* Apart from those features, the minimal coronal ornamentation characteristic of this morphologically very conservative genus makes the differentiation among *Lonchidion* species difficult (Rees and Underwood, 2002). Notwithstanding, the combination of a very prominent and narrow peg with an accessory cusplet and a ridge that reaches the principal cusp, along with the severe constriction of the crown-root junction, sets *Lonchidion derenzii*, sp. nov., apart from other contemporary Middle–Upper Triassic species of the genus. *Lonchidion derenzii*, sp. nov., teeth differ from those of *L. ferganensis* (Middle–Upper Triassic of Central Asia; Fischer et al., 2011) by the lack of the characteristic nodes at shoulder height labially. In addition, *Lonchidion derenzii*, sp. nov., does not show the vertical striation and crown shoulder nodes that commonly ornament *L. estesi* teeth from the Late Triassic of India (Prasad et al., 2008). On the other hand, notwithstanding that the simple crown of *L. derenzii*, sp. nov., resembles those of *L. paramillonensis* from the Middle–Upper Triassic of Argentina (Johns et al., 2014), the latter shows a more triangular shape in labial view and the number of accessory cusplets is higher than in *L. derenzii*, sp. nov. In addition, *L. derenzii*, sp. nov., has a strongly developed labial peg, and the constriction of the crown-root junction is more severe than in *L. paramillonensis*. A well-developed labial peg and the severe constriction of the crown-root junction also appear in *L. humblei* from the Upper Triassic of North America (Heckert et al., 2007), but this species lacks the accessory cusplet surmounting the labial peg as well as the lateral cusplets that are present in *L. derenzii*, sp. nov.

DISCUSSION

The lack of detailed studies on chondrichthyan faunas from the Triassic of the Iberian Peninsula has led paleontologists, for some time, to the mistaken perception that chondrichthyans were rare or absent in the region (e.g., Chrzastek, 2008). Nevertheless, during recent years, several works have indicated the presence of a rich and diverse chondrichthyan fauna from different localities in the Iberian ranges (Botella et al., 2009b; Pla et al., 2013). The present report of *Lonchidion derenzii*, sp. nov.,

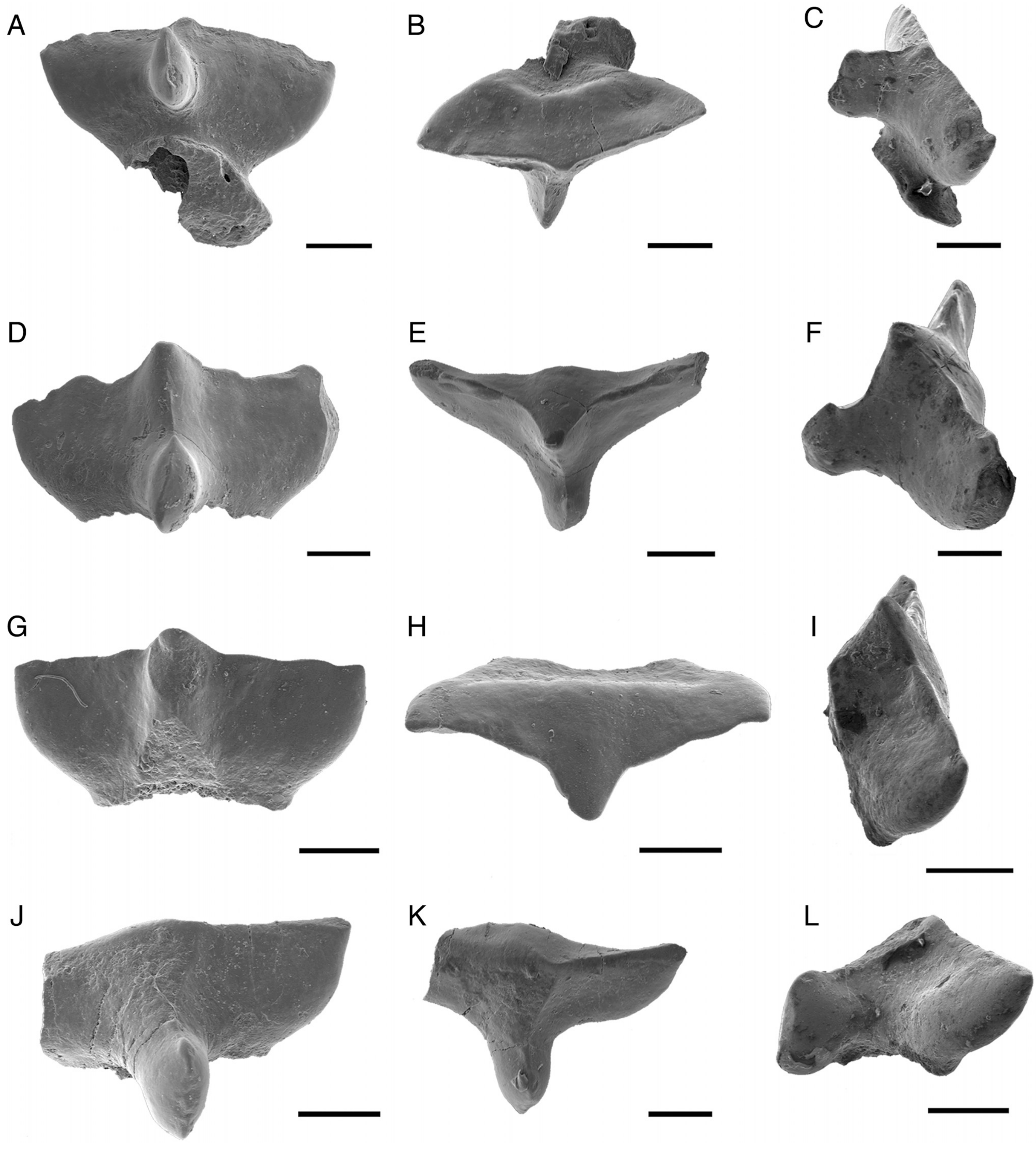

FIGURE 2. *Lonchidion derenzii*, sp. nov. **A**–**C**, MGUV-27744, holotype, in labial, occlusal, and lateral views. **D**–**F**, MGUV-27745, paratype, in labial, occlusal, and lateral views. **G**–**I**, MGUV-27746, paratype in labial, occlusal, and lateral views. **J**–**L**, MGUV-27747, paratype, in labial, occlusal, and lateral views. All scale bars equal 100 μm.

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shows that Triassic chondrichthyan remains are common not only in sediments of the Iberian ranges but also in other Triassic outcroups of the Iberian Peninsula. *Lonchidion derenzii*, sp. nov., represents the earliest record of the genus in Spain, considering its Carnian age (Upper Triassic) according to the bivalve, conodont, and pollen assemblages (Martín-Algarra et al., 1995).

Moreover, although Patterson (1966) in his description of the Early Cretaceous taxon *Lonchidion breve breve* from England (United Kingdom) mentioned the presence of teeth from the Muschelkalk (Ladinian) of Craislheim in Germany "which are almost indistinguishable from *Lonchidion breve breve"* (1966:331), neither a description nor figures of these teeth were

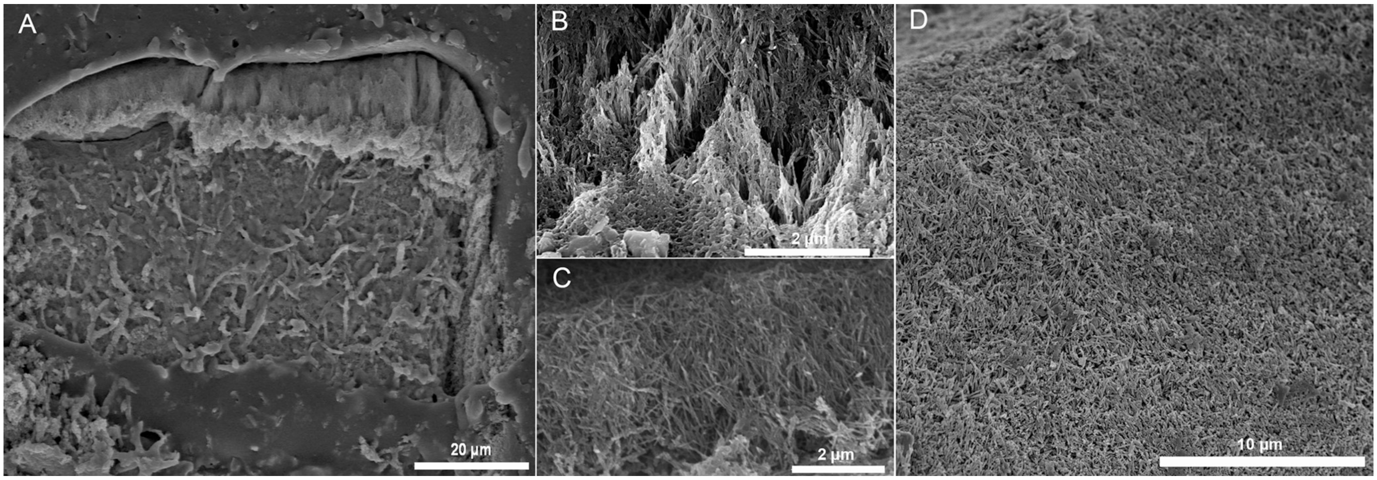

FIGURE 3. **A**–**C**, scanning electron micrograph of MGUV-29994, *Lonchidion derenzii*, nov. sp., enameloid, etched with 10% HCl for 5 s. **A**, overview of tooth in longitudinal section showing a well-defined enameloid layer with an irregular enameloid-dentine junction. **B**, detail of the general aspect of the inner part of the enameloid layer, close to the enameloid-dentine junction. **C**, detail of the individualized crystallites in the outer part of the enameloid layer. **D**, general aspect of the whole enameloid layer of *Lissodus* aff. *lepagei*, MGUV-25863 (from the Jaraf-3 Section in the Iberian Range, Spain).

provided. Therefore, *Lonchidion derenzii*, sp. nov., can also be considered as the oldest unequivocal record of the genus in Europe.

Lonchidion has been proposed as an euryhaline genus living preferentially in freshwater or brackish environments (Rees and Underwood, 2002; Heckert et al., 2007; Fischer et al., 2011; Johns et al., 2014). Although the Boyar Section represents marine environments, and other Triassic marine sharks have been found in several levels through the whole section (pers. observ.), the record of *Lonchidion derenzii*, sp. nov., is limited to a particular level that represents a very shallow marine platform with close continental influence (Martín-Algarra et al., 1995).

Other earliest (Middle–Late Triassic) records of the genus occur in freshwater facies from geographically widely separated localities (i.e., *L. paramillonensis* from South America; *L. ferganensis, L. estesi*, and *L. incumbens* from Asia; and *L. humblei* from North America). As noted by Johns et al. (2014), this requires a dispersion based on a pattern of coastal migrations, but, in our opinion, it also necessarily indicates a more ancient origin of *Lonchidion*.

Lonchidiidae Enameloid Microstructure

The enameloid of chondrichthyan teeth consists of elongated fluorapatite ($Ca_5(PO_4)_3F$) crystallites embedded in an organic matrix, which contains mainly collagen and amelogenin-like proteins (see Gillis and Donoghue, 2007; Enax et al., 2014; Manzanares et al., 2016, and references therein). Although in neoselachian sharks (Reif, 1973) and some batoids (Enault et al., 2015; Manzanares et al., 2016) crystallites appear organized in bundles (or 'fibers' sensu Reif, 1977), in all major stem-chondrichthyan groups, crystallites are individualized (SCE), usually randomly oriented, and lack any degree of higher microstructural differentiation (Gillis and Donoghue, 2007; Botella et al., 2009a). However, in Hybodontiforms, although many species present a homogeneous layer of SCE (e.g., Reif, 1973; Gillis and Donoghue, 2007; Cuny et al., 2009; Pla et al., 2013; Enault et al., 2015), some Mesozoic taxa with crushing dentitions developed a distinct two-layered enameloid consisting of an outer compact single-crystallite layer and an inner layer with some crystallites organized into short, loosely defined bundles (Cuny et al., 2001; Pla et al., 2013; Enault et al., 2015).

Johns et al. (2014) described an enameloid showing fibrous structure in *Lonchidion paramillonensis*. The supporting images, however, clearly show a layer of randomly oriented individual crystallites without any superior microstructural differentiation, i.e., bundles or fibers (Johns et al., 2014:fig. 9). Our analysis of *Lonchidion derenzii*, sp. nov., enameloid demonstrates the presence of SCE (Fig. 3A–C). Individualized crystallites appear randomly arranged near the enameloid-dentine junction (Fig. 3B), whereas in the rest of the enameloid, the crystallites seem to be more preferably oriented perpendicular to the crown surface (Fig. 3C). Previous studies on the enameloid microstructure of other lonchidiid taxa also have reported the presence of a homogeneous SCE layer in *Lissodus angulatus* (Błażejowski, 2004), *Lissodus minimus* (Cuny and Risnes, 2005), and *Lissodus* aff. *Li. lepagei* (Pla et al., 2013; Fig. 3D). Therefore, a single crystallite enameloid without any kind of arrangement into fibers (or bundles) is the widespread condition among Lonchidiidae.

ACKNOWLEDGMENTS

We are thankful for the comments and suggestions of C. Duffin and G. Cuny that improved the quality of our work, and also to C. J. Underwood for editorial support. This work has been funded by the Spanish Government, Ministerio de Economía y Competitividad, Research Project CGL2014-52662-P.

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Submitted May 23, 2016; revisions received August 9, 2016;
accepted August 10, 2016.
Handling editor: Charlie Underwood.