Lonchidion derenzii sp. nov., a new lonchidiid shark (Chondrichthyes, Hybodontiforms) from the Late 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]Department of Geology, Universitat de València, C/Dr. Moliner 50, Burjassot, Valencia, Spain, E-46100, Hector.Botella@uv.es; [2]School of Earth Sciences, University of Bristol, Bristol, BS8 1TQ, United Kingdom

*Corresponding author

Lonchidiidae Herman, 1977 represents one of the most diverse and controversial family 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*, *Parvodu*s, *Lissodus* and *Lonchidion*, although the content of the family is still under discussion (see by example 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). Contrarily, Rees (2008) consider *Lonchidion* and *Lissodus* not so closely related to each other, excluding genus *Lissodus* from Lonchidiidae.

The majority of *Lonchidion* species has been described on the basis of disarticulated teeth, and complete or partial articulated skeletons has 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 genus ranges from the Middle-Upper Triassic (Fischer et al., 2011; Johns et al., 2014) to the Late 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 Late Triassic

(Carnian) of Spain, representing the earliest well-documented occurrence of the genus in Europe.

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 (36º 44' 49" N 5º 25' 12" O, see Martín-Algarra et al., 1995 for more detailed the geographical and geological setting). The Boyar Section is subdivided in 4 main units comprising strata belonging to the upper Muschelkalk and Keuper facies (Fig. 1B), which has been dated as Carnian (Upper Triassic) in age one 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 sieves meshes of 2, 0.125 and 0.063 mm respectively. Apart of the teeth of *Lonchidion*, conodonts and teeth and scales of other chondrichthyans and actinopterigians were also recovered. This middle part is characterised by platy limestone interbedded with grey marls and some sporadic dolomitic levels. The presence of pollen in the marly levels has been interpreted as evidence in favour of 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 (Botella et al., 2009b; Gillis and Donoghue, 2007; Manzanares et al., 2014) several specimens were embedded in a transparent polyester resin and subsequently sectioned along transverse or longitudinal planes, polish and then etched using 0.1m HCl for 5–10 s. Each sample was repolished and etched as many times as necessary to elucidate the enameloid microstructure. The material is housed in the Museum of Geology at the University of Valencia (MGUV).

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, Maastritchian, Lance Formation, Eastern Wyoming, U.S.A.

LONCHIDION DERENZII sp. nov.

(Figure 2A–L)

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

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

Holotype—MGUV–27.744 (Fig. 2A–C).

Additional Material—10 teeth; figured specimens (Fig. 2D–F, G–I, J–L MGUV–27.745, 27.746 and 27.747 respectively, Fig. 3A–C MGUV–29994). Rest of the specimens (MGUV–27.748).

Ocurrence—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 0.5 to 0.4 mm mesiodistally, 0.3 to 0.2 mm apicobasally, and 0.3 to 0.2 mm labiolingually, with a low coronal profile and the 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 centre of the apex of the V, while others show a straighter shape (Fig, 2B). Main central cusp small, rounded to triangular in shape, and labially inclined (Fig. 2E, F. H). Commonly 2–3 pairs of lateral cusplets, that 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.

Etched sections 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 labio-lingually 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 set *Lonchidion derenzii* sp. nov. apart from other contemporary Middle–Upper Triassic species of the genus. *Lonchidion derenzii* sp. nov. teeth differ from *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. have 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 paleontologist, 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 of the Iberian ranges (Botella et al., 2009a; Pla et al., 2013). The report now of *Lonchidion derenzii* sp. nov., 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. *L. derenzii* sp. nov. represents the earliest record of the genus in Spain, considering its Carnian age (Upper Triassic) according to the bivalve, conodonts 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 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 preferably in freshwater or brackish environments (Rees and Underwood, 2002; Heckert et al., 2007; Fischer et al., 2011; Johns et al., 2014). In this sense, although Boyar Section represents marine environments, and other Triassic marine sharks have been found in several levels through the whole section (pers. observation), 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).

Noticeably, other earliest (Middle–Late Triassic) records of the genus occur in freshwater facies from widely geographically separated localities (i.e., *L. paramillonensis* from South-America, *L. ferganensis*, *L. estesi*, *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 indicate a more ancient origin of *Lonchidion.*

Lonchidiidae Enameloid Microstructure

The enameloid of chondrichthyan teeth consist of elongated fluorapatite ($Ca_5(PO4)_3F$) 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). While in neoselachian sharks (Reif, 1973) and some batoids (Enault et al., 2015; Manzanares et al., 2016) crystallites appear organized in bundles (or fibers according Reif`s 1977 terminology), in all major stem-chondrichthyan groups crystallites are individualized (SCE), usually randomly oriented, lacking any degree of higher microstructural differentiation (Gillis and Donoghue, 2007; Botella et al., 2009b). 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*. Nevertheless, the supporting images show clearly a layer of randomly oriented individual crystallites without any superior microstructural differentiation -i.e., bundles or fibres- (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 Lonchidiidae 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. *L. lepagei* (Pla et al., 2013; Fig. 3D). Therefore, a single crystallite enameloid without any kind of arrangement into fibres (or bundles) is the widespread condition among Lonchidiidae.

ACKNOWLEDGMENTS

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

LITERATURE CITED

Błażejowski, B. 2004. Shark teeth from the Lower Triassic of Spitsbergen and their histology. Polar Research 25:153–167.

Bonaparte, C. L. J. 1838. Selachorum tabula analystica. Nuovi Annali delle Scienze naturali Bologna 2(1):195–214.

Botella, H., P. Plasencia, A. Marquez-Aliaga, G. Cuny, and M. Dorka. 2009a. *Pseudodalatias henarejensis* nov. sp. a new pseudodalatiid (Elasmobranchii) from the Middle Triassic of Spain. Journal of Vertebrate Paleontology 29:1006–1020.

Botella, H., P. C. J. Donoghue, and C. Martínez-Pérez. 2009b. Enameloid microstructure in the oldest known chondrichthyan teeth. Acta Zoologica 90(s1):103–108.

Cappetta, H. 2012. Handbook of paleoichthyology Vol. 3E. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. Verlag Dr. Friedrich Pfeil, München, 512 pp.

Chrzastek, A. 2008. Vertebrate remains from the Lower Muschelkalk of Raciborowice Górne (North-Sudetic Basin, SW Poland). Geological Quarterly 52:225–238.

Cuny, G., and S. Risnes. 2005. The enameloid microstucutre of the teeth of synechodontiform sharks (Chondrichtyes: Neoselachii). PalArch's Journal of Vertebrate Palaeontology 3(2):8–19.

Cuny, G., O. Rieppel, and P. M. Sander. 2001. The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada. Zoological Journal of the Linnean Society 133:285–301.

Cuny, G., P. Srisuk, S. Khamha, V. Suteethorn, and H. Tong. 2009. A new elasmobranch fauna from the Middle Jurassic of southern Thailand; pp. 97–113 in E. Buffetaut, G. Cuny, J. Le Loeuff, and V. Suteethorn (eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. The Geological Society, London, Special Publications 315.

Duffin, C. 1985. Revision of the Hybodont selachian genus *Lissodus* BROUGH (1935). Palaeontographica Abteilung a-Palaozoologie-Stratigraphie 188:105–152.

Duffin, C. 2001. Synopsis of the selachian genus *Lissodus* BROUGH, 1935. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 221(2):145–218.

Enault, S., G. Guinot, M. K. Boot, and G Cuny. 2015. Chondricthyan tooth enameloid: past, present and future. Zoological Journal of the Linnean Society 174:549–570.

Enax J., J. A. M. Janus, D. Raabe, M. Epple, and H.O. Fabritius. 2014. Ultrastructural organization and micromechanical properties of shark tooth enameloid. Acta biomateralia 10:3959–3968.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. University of California Publications, Geological Sciences 49:1–187.

Fischer, J. S. 2008. Brief synopsis of the hybodont form taxon *Lissodus* BROUGH, 1935, with remarks on the environment and associated fauna. Freiberger

Forschungshefte C 528:1–23.

Fischer, J., S. Voigt, J. W. Schneider, M. Buchwitz, and S. Voigt. 2011. A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries. Journal of Vertebrate Paleontology 31:937–953.

Gillis, J. A., and P. C. J. Donoghue. 2007. The homology and phylogeny of chondrichthyan tooth enameloid. Journal of Morphology 268:33–49.

Hay, O. 1902. Bibliography and catalogue of the fossil vertebrata of North America. Bulletin of United States Geological Survey 179:1–868.

Heckert, A. B., A. Ivanov, and S. G. Lucas. 2007. Dental morphology of the hybodontoid shark *Lonchidion humblei* Murry from the Upper Triassic Chinle Group, USA. New Mexico Museum of Natural History and Science Bulletin v. 41 (The Global Triassic), pp. 45–48.

Herman, J. 1977. Les Sélaciens des terrains néocrétacés and paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphic intercontinentale. Mémoires pour servir à l'explication des Cartes géologiques et Miniéres de la Belgique 15:1–401.

Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880:649–662.

Johns, M. J., G. L. Albanesi, and G. G. Voldman. 2014. Freshwater shark teeth (Family Lonchidiidae) from the Middle–Upper Triassic (Ladinian–Carnian) Paramillo Formation in the Mendoza Precordillera, Argentina. Journal of Vertebrate Paleontology 34:512–523.

Khamha, S., G. Cuny, and K. Lauprasert. 2015. Revision of *Isanodus paladeji* (Elasmobranchii, Hybodontiformes) from the Lower Cretaceous of Thailand.

Manzanares, E., D. Rasskin-Gutman, and H. Botella. 2016. New insights into the enameloid microstructure of batoid fishes (Chondrichthyes). Zoological Journal of the Linnean Society 177:621–632.

Manzanares, E., C. Pla, C. Martínez-Pérez, D. Rasskin, and H. Botella. 2014. The enameloid microsctucture of euselachian (Chondrichthyes) scales. Paleontological Journal 48:1060–1066.

Martín-Algarra, A., N. Solé de Porta, and A. Márquez-Aliaga. 1995. Nuevos datos sobre la estratigrafía, paleontología y procedencia paleoestratigráfica del Triásico de las escamas del Corredor del Boyar (Cordillera Bética Occidental). Cuadernos de Geología Ibérica 19:279–307.

Owen, R. 1846. Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals: Delivered at the Royal College of Surgeons of England in 1844 and 1846, Part 1: Fishes. Longman, Brown, Green and Longmans, London, 308 pp.

Patterson, C. 1966. British Wealden sharks. Bulletin of the British Museum of Natural History (Geology) 11(7):283–350.

Pla, C., A. Márquez-Aliaga, and H. Botella. 2013. The chondricthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). Journal of Vertebrate Paleontology 33:770–785.

Plasencia, P. 2009. Bioestratigrafía y paleobiología de conodontos del Triásico Medio del Sector Oriental de la Península Ibérica. Ph. D. dissertation, Universitat de València, Valencia, 420 pp.

Prasad, G. V. R., K. Singh, V. Parmar, A. Goswami, and C. S. Sudan. 2008. Hybodont shark teeth from the continental Upper Triassic deposits of India; pp. 413–432 in

G. Arratia, H.-P. Schultze, and M. V. H. Wilson (eds.), Fishes 4–Homology and

Phylogeny, Proceedings of the international meeting Miraflores de la Sierra, 2005, Verlag Dr. Friedrich Pfeil, Münichen, Germany.

Rees, J. 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology - preliminary results. Acta Geologica Polonica 58: 217–221.

Rees, J., and C. J. Underwood. 2002. The status of the shark genus *Lissodus* Brought, 1935, and the position of nominal *Lissodus* species within the hybodontoidea (Selachii). Journal of Vertebrate Paleontology 22:471–479.

Reif, W. E. 1973. Morphologie und Skulptur der Haifisch-zahnkronen. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 143:39–55.

Reif, W. E. 1977. Tooth enameloid as a taxonomic criterion: 1. A new euselachian shark from the Rhaetic-Liassic boundary. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1977:565–576.

Soler-Gijón R., F. J. Poyato-Ariza, J. G. Maisey, and J. Lane. A. 2016. Chondrichthyes. In: Poyato-Ariza, F.J., Buscalioni, A.D. & Fregenal-Martinez, M. (eds), Las Hoyas: A Cretaceous wetland. A multidisciplinary synthesis after 25 years of research on an exceptional fossil deposit from Spain.

Submitted May 23, 2016; accepted Month DD, YYYY.

FIGURE CAPTIONS

FIGURE 1. **A**, map of the Iberian Peninsula showing the location of studied Boyar section in the Betic Ranges and **B**, the biostratigraphic column of the 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). [planned for 2/3 of a whole page width]

FIGURE 2. *Lonchidion derenzii* sp. nov., **A–C**, holotype in labial, occlusal and lateral view respectively, MGUV–27744; **D–E**, paratype in labial, occlusal and lateral view respectively, MGUV–27745; **F–H**, paratype in labial, occlusal and lateral view respectively, MGUV–27746; **I–K**, paratype in labial, occlusal and lateral view respectively, MGUV–27747. Scale bar equals 100 µm. [planned for page width]

FIGURE 3. **A–C**, Scanning electron micrograph of *Lonchidion derenzii* nov. sp. enameloid, MGUV–29994, etched with 10% HCL for 5s. **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 enameloid layer, close 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). [planned for a whole page width]

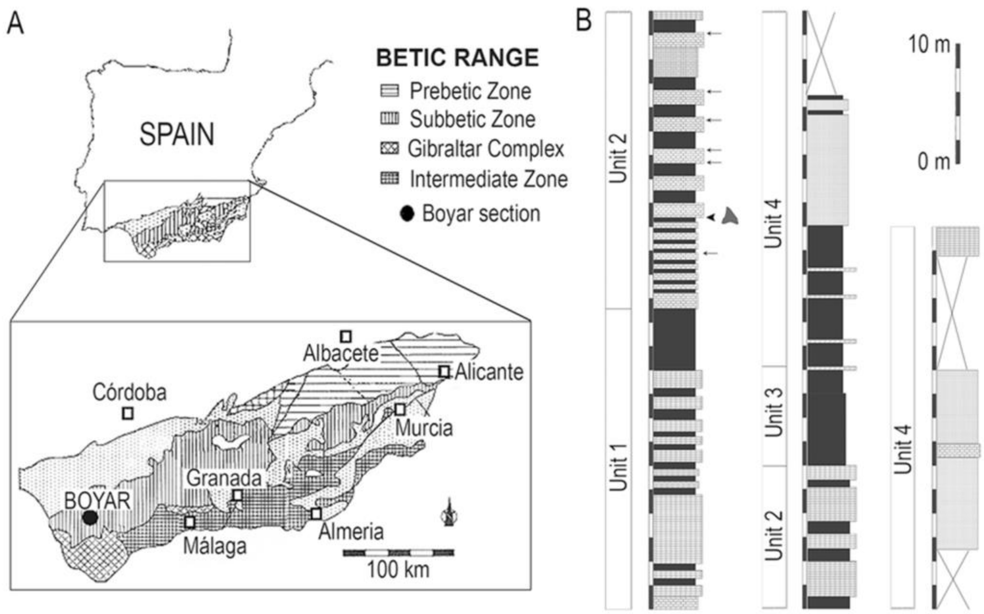

FIGURE 1. A, map of the Iberian Peninsula showing the location of studied Boyar section in the Betic Ranges and B, the biostratigraphic column of the section with indication of levels sampled (thin arrows) and the level that yielded the material described in this work (black head arrow). Modified from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

75x46mm (300 x 300 DPI)

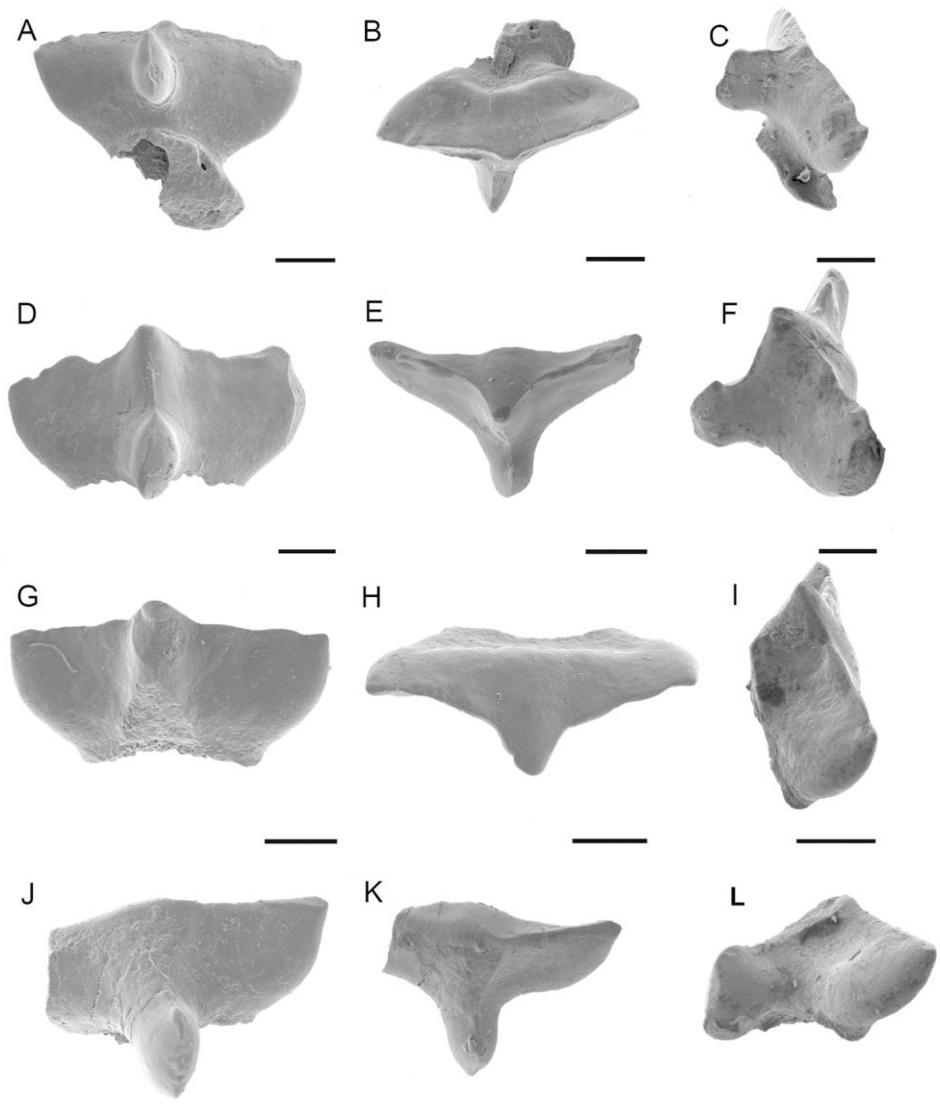

FIGURE 2. Lonchidion derenzii sp. nov., A–C, holotype in labial, occlusal and lateral view respectively, MGUV–27744; D–E, paratype in labial, occlusal and lateral view respectively, MGUV–27745; F–H, paratype in labial, occlusal and lateral view respectively, MGUV–27746; I–K, paratype in labial, occlusal and lateral view respectively, MGUV–27747. Scale bar equals 100 μm.

229x290mm (300 x 300 DPI)

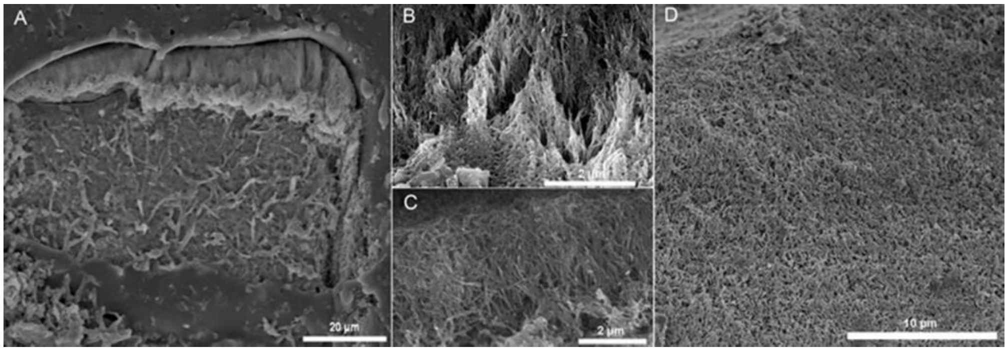

FIGURE 3. A–C, Scanning electron micrograph of Lonchidion derenzii nov. sp. enameloid, MGUV–29994, etched with 10% HCL for 5s. A, overview of tooth in longitudinal section showing a well-defined enameloid layer with an irregular enameloid-dentine junction; B, detail of the general aspect of the inner part enameloid layer, close 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).

62x21mm (300 x 300 DPI)