

## The first Peruvian record of *Enchodus* (Actinopterygii, Aulopiformes, Enchodontidae) in the Upper Cretaceous Vivian Formation

\*Soledad Gouiric-Cavalli<sup>1,2</sup>, Alberto L. Cione<sup>1,2</sup>, David E. Tineo<sup>1,3</sup>, Leandro M. Pérez<sup>1,4</sup>,  
Martín Iribarne<sup>5</sup>, Miguel A. Allcca Torres<sup>6</sup>, Daniel G. Poiré<sup>1,3</sup>

<sup>1</sup> Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Godoy Cruz 2290 (C1425FQB), Ciudad Autónoma de Buenos Aires, Argentina.

<sup>2</sup> División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, UNLP, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina.  
sgouiric@fcnym.unlp.edu.ar; acione@fcnym.unlp.edu.ar

<sup>3</sup> Centro de Investigaciones Geológicas (CONICET-UNLP), Diagonal 113 No. 275, B1904DPK, La Plata, Buenos Aires, Argentina.  
dtineo@cig.museo.unlp.edu.ar; poire@cig.museo.unlp.edu.ar

<sup>4</sup> División Paleozoología Invertebrados, Museo de La Plata, FCNyM, Anexo I, B1900FWA, La Plata, Buenos Aires, Argentina.  
pilosaperez@gmail.com

<sup>5</sup> GeoPark, Florida 981, C1005, Ciudad Autónoma de Buenos Aires, Argentina.  
miribarne@geo-park.com

<sup>6</sup> Independent Consultant  
allccatorres@gmail.com

\* Corresponding author: sgouiric@fcnym.unlp.edu.ar; s.gouiriccavalli@gmail.com

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**ABSTRACT.** We describe isolated teleostean teeth found in no association with the jaw bone. The specimens have been recovered in Late Cretaceous marine deposits of the Vivian Formation in the Peruvian Sub-Andean Region. The deposition sequence from where the teeth come is interpreted as a shallowing-upward sequence of low salinity. The fish material is identified as *Enchodus* aff. *E. gladiolus* based on the presence of a small but well-developed post-apical barb, an anterior cutting edge, the crown is symmetrical in cross-section, have a sigmoidal profile, and bears strong ridges (=striations). The Peruvian material differs from the typical *E. gladiolus* teeth in having a faintly serrated anterior cutting edge which is absent in most specimens referred to *E. gladiolus*. We also highlight that taxonomic assignments made based on isolated teeth must be taken with care. Despite scarce, the material recovered denotes that the marine units of Peru can give valuable information about the Pacific fish fauna during the Late Cretaceous.

**Keywords:** Fishes, Actinopterygii, Peruvian Sub-Andean Region, South America.

**RESUMEN.** El primer registro peruano de *Enchodus* (Osteichthyes, Aulopiformes, Enchodontidae) en la Formación Vivian del Cretácico Superior. Se describen dientes aislados de peces teleosteos, los que no se encontraron asociados con huesos de las quijadas. Los especímenes han sido recuperados en depósitos marinos del Cretácico tardío de la Formación Vivian en la Región Subandina del Perú. La secuencia sedimentaria de donde provienen los dientes se interpreta como una secuencia somerizante de baja salinidad. El material de peces es referido como *Enchodus* aff. *E. gladiolus* con base en la presencia de una barba posapical pequeña, pero bien desarrollada, además de un borde cortante anterior; la corona es simétrica en sección transversal, con un perfil sigmoidal y fuertes crestas (=estrias). El material peruano se diferencia de los dientes típicos de *E. gladiolus* en tener un borde cortante anterior ligeramente aserrado que está ausente en la mayoría de los especímenes referidos a *E. gladiolus*. Se destaca también que las asignaciones taxonómicas realizadas a partir de dientes aislados se deben tomar con cuidado. A pesar de ser escaso, el material recuperado denota que las unidades marinas del Perú pueden brindar información valiosa sobre la fauna de peces del Pacífico durante el Cretácico Superior.

**Palabras clave:** Peces, Actinopterygii, *Región Subandina del Perú*, América del Sur.

## 1. Introduction

The Mesozoic fish record is extremely scarce in Peru, especially compared with coeval fossil bearing localities in neighboring countries of western South America such as Bolivia and Chile (e.g., Kriwet and Klug, 2012; Suárez *et al.*, 2003; Arratia, 2015).

Enchodontidae is a marine extinct fish clade of the teleostean neopterygian order Aulopiformes (Fielitz, 2004; Nelson *et al.*, 2016). Enchodontids were common in many marine environments during the Late Cretaceous of different continents (North America, South America, Africa, Asia, Europe, and Antarctica; e.g., Fielitz, 2004; Kriwet *et al.*, 2006; Silva and Gallo, 2011; Holloway *et al.*, 2017; Cione *et al.*, 2018; Díaz-Cruz *et al.*, 2019). The oldest record appears to be *Enchodus zimapanensis* from Albian-Cenomanian beds of Mexico (Fielitz and González-Rodríguez, 2010). To date, Enchodontidae consists of seven genera being *Enchodus* Agassiz, 1833 the most taxonomically diverse (Alvarado-Ortega *et al.*, 2020).

The fossil record of *Enchodus* is abundant in rocks from the Albian-Cenomanian to Maastrichtian (e.g., Hay, 1903; Chalifa, 1996; Kriwet, 2003; Fielitz, 2004; Fielitz and González-Rodríguez, 2010; Cavin *et al.*, 2012; Newbrey and Konishi, 2015; Díaz-Cruz *et al.*, 2019). Despite there are a few reports of *Enchodus* (and Enchodontidae) from Cenozoic rocks; they have to be reviewed and confirmed (see Arambourg, 1952 and Rana *et al.*, 2005).

Over the years, several *Enchodus* nominal species were described, many of them based on isolated mandibular fragments and teeth (Goody, 1969, 1976; Chalifa, 1989, 1996; Holloway *et al.*, 2017). Thus, the tooth-based species and the phylogenetic relationships of *Enchodus* species are relatively weakly supported (Fielitz, 2004).

One of the most striking features of *Enchodus* species is the presence of long palatine bones with a single, large tooth (=fang), and a corresponding dentary tooth near the mandibular symphysis. These large teeth and others have very good potential of preservation and are relatively diagnostic (Grandstaff and Parris, 1990). Moreover, isolated palatine, lower and upper jaw teeth and isolated fragmentary bones have been used to identify material at species level (e.g., Carbot-Chanona and Than-Marchese, 2013) and considered type material (e.g., Holloway *et al.*, 2017). However, the definition of species based on

isolated teeth and isolated skeletal elements has been questioned (Goody, 1976; Chalifa, 1996).

The aim of this study is to describe and discuss the taxonomic assignment of isolated teeth recovered in Upper Cretaceous levels of Vivian Formation in Perú, South America. Additionally, we comment about the paleogeographic distribution of the genus *Enchodus*.

## 2. Material and methods

### 2.1. Material

Material consist of eight teeth -none of them associated with bone- housed at the INGEMMET (Instituto Geológico, Minero y Metalúrgico), Lima, Perú.

### 2.2. Methods

Teeth were studied and photographed under a binocular microscope. Also, a Scanning Electron Microscope FEI ESEM Quanta 200 with electron source from a tungsten filament, with accelerating voltage of 200 V- 30 kV of the SeMFi-LIMF (Servicio de Microscopía Electrónica de Barrido y Microanálisis del Laboratorio de Investigaciones de Metalurgia Física “Ing. Gregorio Cusminsky”, Facultad de Ingeniería, Universidad Nacional de La Plata) was used. The Energy Dispersive X-ray spectroscopy (EDAX) analysis was performed using an EDAX SDD Apollo 40 in the SEM. This equipment allows the detection of light elements of boron, with a resolution <135 eV, with a qualitative, semiquantitative and with the possibility of quantitative analysis on chemical elements in a microanalysis using a 1 mm<sup>3</sup> sample.

Descriptive terminology, follows mostly Ørvig (1951), Goody (1969, 1976), and Fielitz (2004). Open nomenclature is mostly according to Bengston (1988) and follows the International Code of Zoological Nomenclature.

## 3. Geological setting

The logged Río Apurucayali Section (Fig. 1 A, B) is composed by a sedimentary rocks sequence grouped in the Chonta Formation (Moran and Fyfe, 1933), Vivian Formation (Kummel, 1948), Cachiyacu Formation (Kummel, 1948), Huchpayacu Formation (Koch and Blissenbach, 1962),

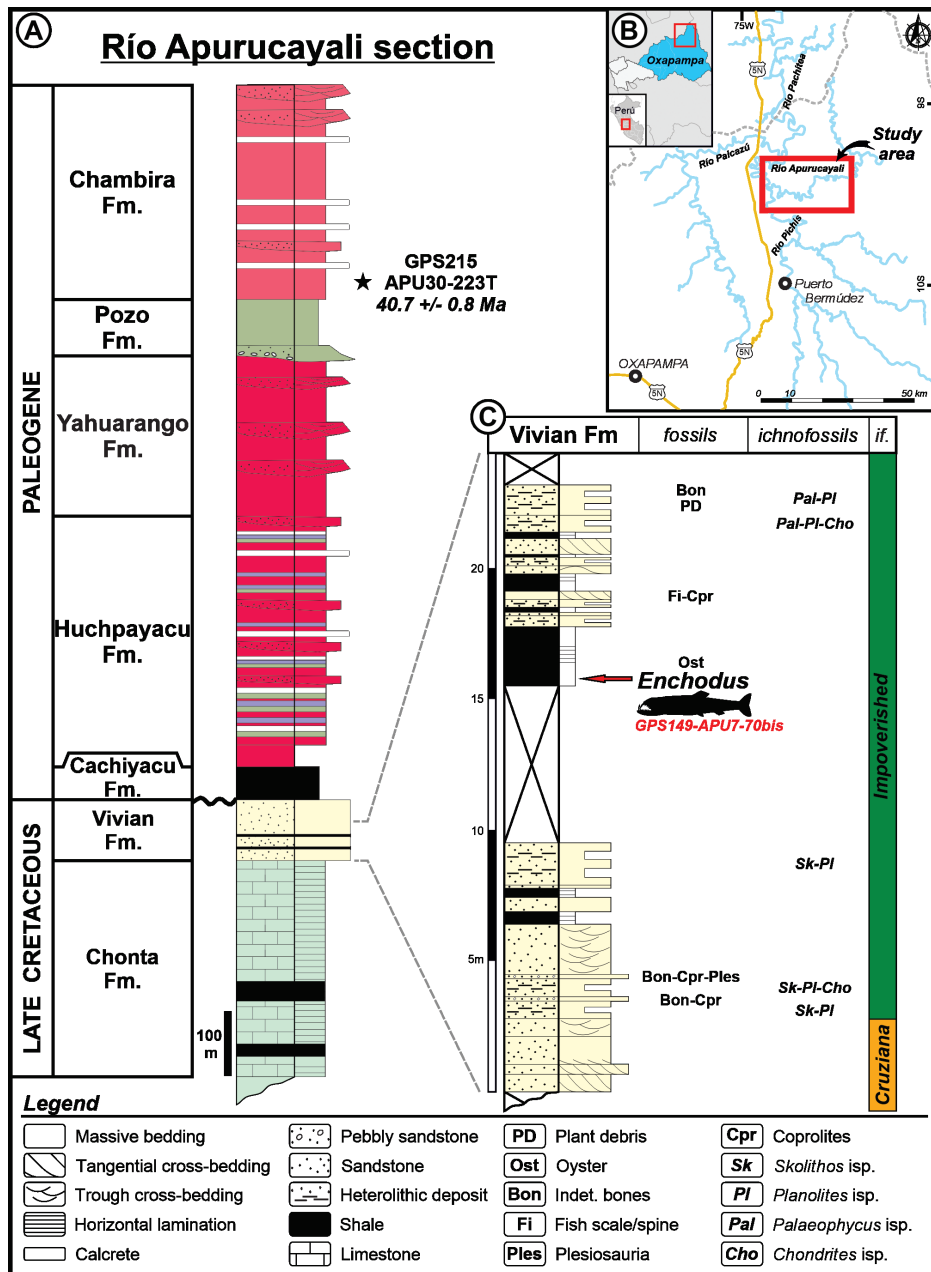


FIG. 1. A. Stratigraphic framework and general log of the Río Apurucayali Section. B. Map showing the location of Vivian Formation where *Enchodus* teeth were found. C. Sedimentary log of the lower part of the Vivian Formation showing the *Enchodus aff. gladiolus* bearing level, GPS149-APU7-70bis.

Yahuarango Formation (Kummel, 1948), Pozo Formation (Williams, 1949), and Chambira Formation (Kummel, 1946, 1948). Rocks of Chonta and Vivian formations are widely distributed in the Peruvian

sub-region. Both units were assigned to the Upper Cretaceous, while the other four units above are Paleogene in age (Jaillard et al., 1995; Poiré et al., 2017). Recently, Iribarne et al. (2018) have carried

out detrital zircon U-Pb analyses from a tuffite level of the lower Chambira Formation in the Río Apurucayali (Fig. 1B, GPS215-APU30-223T: S10°02'23"; W74°54'03") that gave a maximum depositional age of ~40.7±0.8 Ma. Palynological studies allowed to date the Vivian Formation from the Campanian to the Upper Maastrichtian (Elsik, 1964; Seminario and Guizado, 1973; Müller and Aliaga, 1981; Jaillard *et al.*, 1995). In southern Peru, in the Pongo de Mainique area, detrital zircons dating indicated a more precise age of 68.5 Ma (Kennan and Pindell, 2006), which are suggesting a younger deposition age of Middle-Late Maastrichtian.

In the jungle area of Ucayali, Junín, and Pasco departments, rocks of the Vivian Formation are outcropping in isolated sections of low thickness over the margins of large river courses, as occurs in the Río Apurucayali (Fig. 1B). In this area, the logged section of the Vivian Formation (Fig. 1C) is approximately 100 m thick. Its general strike direction is NNE-SSW dipping up to 10 degrees west. The lower part of the Vivian Formation is characterized by fine, very well-sorted, white, quartzose arenites named "White-sugar Vivian" that become red quartzites, with reddish pelitic levels, to their upper part named as "Red Vivian". In the lower part of the Vivian Formation in the Apurucayali River profile (Fig. 1C), eight sedimentary facies have been identified, which are represented by sandy, heterolithic, and shale facies (Fig. 1C). The main psammitic facies consist of whitish, pebbly-sandstones, massive (SGm) and tangential crossbedding (SGta), and whitish sandstone, with trough crossbedding (St) tangential crossbedding (Sta), hummocky cross-stratification (Shcs) and massive sandstone (Sm). The heterolithic deposits are composed of normal heterolithic facies (Ht) and very sand-rich heterolithic facies (Htvs). The fine, dark gray to black, shales, facies are laminated (Fl) or massive (Fm) (Poiré *et al.*, 2016).

Paleontological content in the lower part of the Vivian Formation at Río Apurucayali section (Fig. 1C) comprises some remains of isolated invertebrates (mollusks), vertebrate remains (fishes, reptiles: cf. Plesiosauria, coprolites) and some plant debris and carbonaceous material (Poiré *et al.*, 2016). Trace fossils are represented by the ichnogenera *Palaeophycus*, *Skolithos*, and *Chondrites*, which are distributed as ichnofacies of *Cruziana* in its lower part and *Cruziana-Skolithos* Impoverished

ichnofacies in its middle and upper part. The former is poorly developed, has centimeter-size diameter traces and a low bioturbation index (BI=1 to 2). On the other hand, these same ichnogenera in the Impoverished ichnofacies are well-developed but present smaller sizes (millimeters) and a high degree of bioturbation (BI=4 to 6) (Poiré *et al.*, 2016).

In general, the sedimentary rocks of the Vivian Formation have been considered as the product of a deposition in marine littoral (Jaillard *et al.*, 1995), distal fluvial (Rodríguez *et al.*, 2017), and fluvial-estuarine or fluvial-deltaic environments (Navarro, 2005). In this sense, although the presence of fossil traces of the *Cruziana-Skolithos* ichnofacies, very common in this unit, indicates a shallow marine environment, it is not present in the fossil level (lag), where the impoverished ichnofacies indicates deposition of sediments in brackish waters typical of an estuary (or a tide-dominated delta) (Poiré *et al.*, 2016). It should be noted that the former is from normal salinity marine waters and pass to the same fossil but tiny traces, typical of an impoverished brackish water ichnofacies (Howard and Frey, 1975).

#### 4. Systematic Paleontology

**Infraclass Teleostei *sensu* Arratia, 2013**  
**Order Aulopiformes Rosen, 1973**  
**Family Enchodontidae Woodward, 1901**  
**Genus *Enchodus* Agassiz, 1835**

**Type species:** *Esox lewesiensis* Mantell, 1822 pl., XIV, figs. 1-8; Sussex, UK, Turonian.

***Cimolichthys gladiolus*** Cope, 1872 p. 353.

***Enchodus gladiolus*** (Cope, 1872) in Goody 1976: 103-104 pl. 1, figs.11-12, pl.3, fig.3.

***Enchodus* aff. *Enchodus gladiolus***

Figure 2

**Referred Material:** A batch of eight teeth -none of them associated with bone- under the collection number CPI 7029 a-h (INGEMMET).

**Geographic and stratigraphic occurrence:** Site GPS GPS149-APU7-70bis (S09°58'44"; W74°49'19"), in the east or the Sub-Andean region in the Río Apurucayali, Pasco Department, Perú; shallowing-upward sequence with low salinity facies of Late Cretaceous Vivian Formation.

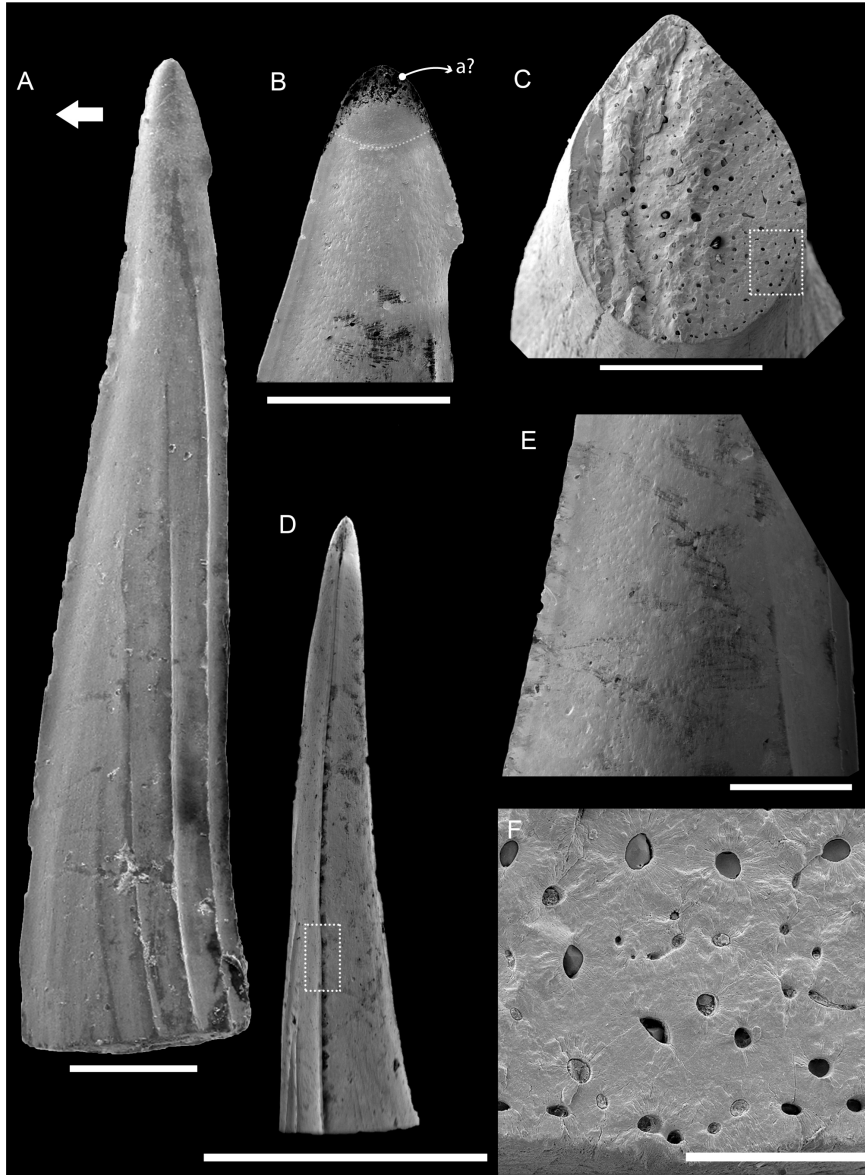


FIG. 2. *Enchodus* aff. *gladiolus* (CPI 7029a, b). **A.** CPI 7029a, photograph of the palatine tooth. **B.** CPI 7029a, detail of the apical barb, the dotted line shows the limit of the apical cap. **C.** CPI 7029b, cross section to show the pulp cavity and the profile. **D.** CPI 7029a, serration on the anterior margin of the tooth. **E.** CPI 7029a, anterior margin of the tooth to show the keel. **F.** CPI 7029b, pulp cavity showing the dentine trabeculae and denteons. Abbreviations: a?, acrodine. Scale bar: **A-C:** 1 mm; **D:** 3 mm; **E:** 500  $\mu\text{m}$ ; **F:** 200  $\mu\text{m}$ .

#### 4.1. Description

The material consists of eight fang-like, small teeth. Few teeth are complete but some are incompletely preserved. Despite no teeth were connected to bone, CPI 7029a (Fig. 2A) greatly agrees in morphology

with palatine fang-like teeth. CPI 7029a is about 8 mm long and 2 mm antero-posteriorly wide (measured at the tooth base). The tooth is distally compressed and slightly sigmoidal with an anterior cutting edge and a small posterior post-apical barb (Fig. 2A-B). The acrodine cap of the apical barb seems to be delimited

by a faint outline (Fig. 2B). Since the acrodine cap shows different gray tonalities, it could be possible that the enameloid was restricted to the tip of the cap (Fig. 2B). However, a detailed histological study is necessary to allow accurate identification of the tissues. The teeth shaft has several -at least twelve- very well-developed longitudinal and undivided ridges or folds (=striations; Fig. 2A). The anterior margin of the teeth bears a slightly wavy and well-developed keel (Fig. 2A, D). In cross section, teeth are compressed near the tip and symmetrical and drop-like more basally (Fig. 2C). The anterior margin has a faint irregular serration that is only observed under SEM (Fig. 2 D-E). A natural fracture in one tooth (CPI 7029b) shows that the pulp cavity at this height is filled with osteodentine (*sensu* Ørvig, 1951; Fig. 2F). The complex structure is interpreted as dentine trabeculae and denteons formed around vascular canals. Radiating tubules arise from these canals (Fig. 2F). The enameloid is not clearly distinguished in the natural section but it should be located distally to the parallel series of denteons (Fig. 2F).

#### 4.2. Taxonomic remarks

*Enchodus* is the genus of the family with more nominal species, longest stratigraphic range, and widest geographical distribution (see above). The teeth described herein resemble those of *Enchodus gladiolus* (Cope, 1872) in size and because they are symmetrical in cross section, have strong basoapical ridges or folds (=striations), a sigmoidal curvature of crown, an anterior cutting edge, and a small but well-developed post apical barb. Moreover, a phylogenetic analysis recently published (Díaz-Cruz *et al.*, 2019, fig. 7), shows that the sigmoid dermopalatine tooth is a synapomorphy of a clade gathering the species: *E. gladiolus*, *E. dirus*, the “*Enchodus*” from Gavdos (Cavin *et al.*, 2012), and *E. tineidae* (Holloway *et al.*, 2017). Noteworthy, “among these species the dermopalatine tooth of *E. gladiolus* shows a peculiar condition, a terminal wing or barb in the posterior end of its tip” (Alvarado-Ortega *et al.*, 2020, p. 12).

Teeth from Peru greatly resemble those identified as palatine teeth of *Enchodus* cf. *E. gladiolus* (Cenomanian from Nebraska; Jansen *et al.* 2012); *Enchodus gladiolus* (Turonian of Nebraska; Ouroumova *et al.*, 2016), *Enchodus gladiolus* (Maastrichtian of South Dakota; Becker *et al.*, 2010),

and *Enchodus* sp. (Campanian of Chiapas; Alvarado-Ortega *et al.*, 2020).

Notwithstanding that Cope (1872, p. 353) mentioned that the barb was absent in the holotype (only specimen known to him and lost), Goody (1976, p.103), based on more complete materials, did a detailed review and assigned the species of Cope (1872) to the genus *Enchodus* mentioning the presence of a posterior apical barb. Since then the post-apical barb was described as commonly present in the species (*e.g.*, Becker *et al.*, 2010; Shimada *et al.*, 2006).

The Peruvian teeth differ from most of North American *E. gladiolus* in the presence of a faintly serrated anterior cutting edge. For this and because of the scarce material (isolated teeth) available for study we decided to refer them as *Enchodus* aff. *E. gladiolus*. Recently, Carbot-Chanona and Than-Marchese (2013, p.11, fig. 2Q-T), assigned an isolated palatine tooth from the Maastrichtian of the Ocozocoautla Formation (Mexico) to *Enchodus gladiolus*. Notably, the tooth illustrated has an even more heavily serrated anterior margin than the Peruvian teeth reported herein. We agree with previous authors (see above) in that taxonomic assignment of isolated teeth needs to be taken carefully, and more and better-preserved material is always desirable to allow an accurate assignment. Considering that some specimens, such as those described here, show characters that are not typical of one species, the specimens must be tentatively referred to specific level. We decided to refer the Peruvian specimens as *Enchodus* aff. *E. gladiolus* denoting that probably belongs to a new species but the available material does not allow a better assignment.

#### 4.3. Remarks on lifestyle

According to the morphology of the skull and due to the mouth gape, it has been postulated that *Enchodus* was a predator occupying a middle position in the food chain (Fielitz, 2004). Quite probably, *Enchodus* feeded on cephalopods and small fishes (Grandstaff and Parris, 1990) and was consumed by bigger teleosts (*e.g.*, Cavin, 1999), sharks, and even plesiosaurs (Cicimurri and Everhart, 2001).

The genus *Enchodus* clusters medium-sized, predatory fishes. The largest forms might be epipelagic but most of *Enchodus* species seem to have been shallow-dwelling fishes inhabiting marine shelf

or coastal waters (*i.e.*, above 200 m). Today, shelf and coastal waters have the greatest marine fish diversity and a high productivity; moreover, they are biogeographically distinct from the adjacent high seas and deep benthic environments (*e.g.*, Spalding *et al.*, 2007).

#### 4.4. Preservational remarks

The specimens here described were found in the shallowing-upward facies of psamites that pass to a mixed composition in the lower portion of the

Vivian Formation. This shallowing-upward sequence combines the features of the low salinity proximal environment.

The facies seem to have allowed the mineralogical preservation of the crystalline material that composes the teeth. This is confirmed by the analysis of major chemical elements carried out at the tooth crown surface (Fig. 3A) and tooth pulp cavity (Fig. 3B).

The EDX-spectrum of the tooth crown surface results in an almost negligible presence of C indicating the absence or poor representation of  $\text{CaCO}_3$ . We interpret that there was a little fossil-

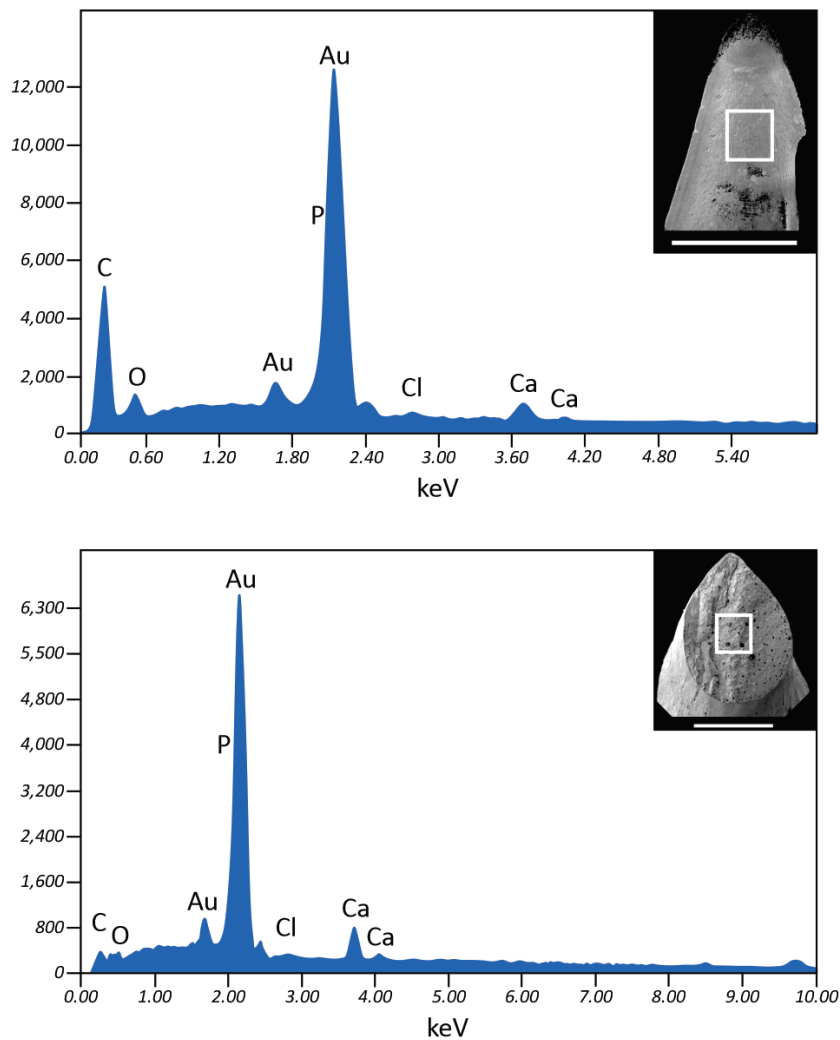


FIG. 3. *Enchodus* aff. *gladiolus* EDX-spectra. **A.** Chemical composition in the crown tooth surface, where a clear presence of C and O together with P, Cl and Ca is observed. **B.** Chemical composition of the pulp cavity, where the presence of C and O is negligible compared to A.

diagenetic alteration of the teeth with respect to the bearing sediments. Moreover, the EDX-spectrum of the tooth crown surface shows three main peaks -phosphorus, carbon, and oxygen- with minor peaks of calcium and chlorine. Those elements are the constituent of Calcite [ $\text{CaCO}_3$ ] and Hydroxyapatite [ $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$ ] being the hydroxyapatite the major mineral component of teeth and bones (Carter, 1990). Likewise, the spectrum of the external surface part of the tooth would be reflecting a higher content of C from the carrier rock (black massive mudstone), see figure 3A-B.

We conclude that the crystallinity of the dental material without an obvious alteration and the presence of Carbon in the apical surface of the tooth would indicate a fossil-diagenetic process that left an imprint on the phosphate material. Without an obvious replacement, the presence of elements that make up the carbonate fossil would be indicative of a protective nature of the fossil-bearing sedimentary level.

#### 4.5. Comments on the fossil record of *Enchodus gladiolus*

*Enchodus gladiolus* ranges from the Cenomanian to Maastrichtian. Most of the reports come from the Western Interior Seaway of North America. The lost type material (Cope, 1872) came from the Niobrara Formation (Coniacian-Santonian of Kansas; Goody, 1976). The oldest reports are Cenomanian (*e.g.*, Cumbaa *et al.*, 2010; Nagrodski *et al.*, 2012; Gallardo *et al.*, 2013; Jansen *et al.*, 2012). Other records are Turonian (Nebraska; Ouroumova *et al.*, 2016) and Maastrichtian (Dakota; Becker *et al.*, 2010). In the southern part of North America, the species was reported from the Maastrichtian of Chiapas, Mexico (Carbot-Chanona and Than-Marchese, 2013). In extracontinental areas, two fragmentary teeth assigned to *Enchodus cf. gladiolus* were found in Cenomanian beds of Nigeria (Vullo and Courville, 2014). However, the material is too fragmentary and should be compared with teeth of African species (see Arambourg, 1952). Teeth resembling *E. gladiolus* were also reported from the Campanian of Sweden (Bazzi *et al.*, 2015). However, those teeth do not have the postapical barb and the ridges are extremely faint (see Bazzi *et al.*, 2015, fig 5C). Bogan and Agnolin (2010, p. 185) identified one tooth from a marine Atlantic encroachment of Maastrichtian age

in northern Patagonia as “*Enchodus gladiolus* type” *sensu* Goody, 1976 aff. *E. gladiolus* Cope, 1872”. However, the tooth figured by Bogan and Agnolin (2010, fig. 6E-F) lacks typical characters such as well-developed ridges or folds (=striations), it is highly compressed, and it is not sigmoidal. Consequently, we consider that all the previous reports of *Enchodus gladiolus* outside North America are tenuous and must be reviewed when more and better-preserved material became available.

#### 5. Paleobiogeography

Due to the N-S development of the epicontinental sea during the Late Cretaceous, the latitudinal distribution of the *Enchodus* species was very extended -reaching Antarctica- (*e.g.*, Cione *et al.*, 2018; Fig. 4). This might be related with the higher average sea temperature and lower latitudinal gradient of temperature during the Late Cretaceous (Cavin *et al.*, 2012). Also, the widening of the Northern South Atlantic Ocean during the beginning of the Late Cretaceous improved the water circulation allowing the expansion of the enchodontids distribution (Silva and Gallo, 2016).

In South America, materials referred to the genus *Enchodus* have been reported in the Turonian and Maastrichtian of Brazil (Cope, 1886; Woodward, 1907; Oliveira and Silva Santos, 1950; Rebouças and Silva Santos, 1956; Silva, 2007; Silva Santos and Salgado, 1969; Gallo *et al.*, 2006). The South American Maastrichtian record also comprises an isolated mention in Chile (Quiriquina Formation; Suárez, 2001; Suárez *et al.*, 2003), a figuration of a tooth (El Molino Formation of Bolivia; Gayet *et al.*, 1993), and a formal description in Argentina (Jagüel Formation in Río Negro; Bogan and Agnolin, 2010). However, as was pointed out above for *E. gladiolus*, many of these records need to be reviewed carefully and are in need of more and better-preserved specimens. Isolated teeth of *Enchodus* were recorded in the Campanian-Maastrichtian of Antarctica (Kriwet *et al.*, 2006; Cione *et al.*, 2018).

During the Late Cretaceous the radiation of *Enchodus* occurred in the United States -comprising part of the Western Interior Seaway and even New Jersey- from where four species have been reported (*i.e.*, *E. gladiolus*, *E. shumardi* Leidy, 1856, *E. petrosus* Cope 1874, and *E. dirus* Leidy, 1857, see Goody, 1976 and Cavin 2008). However, in relation to the recent



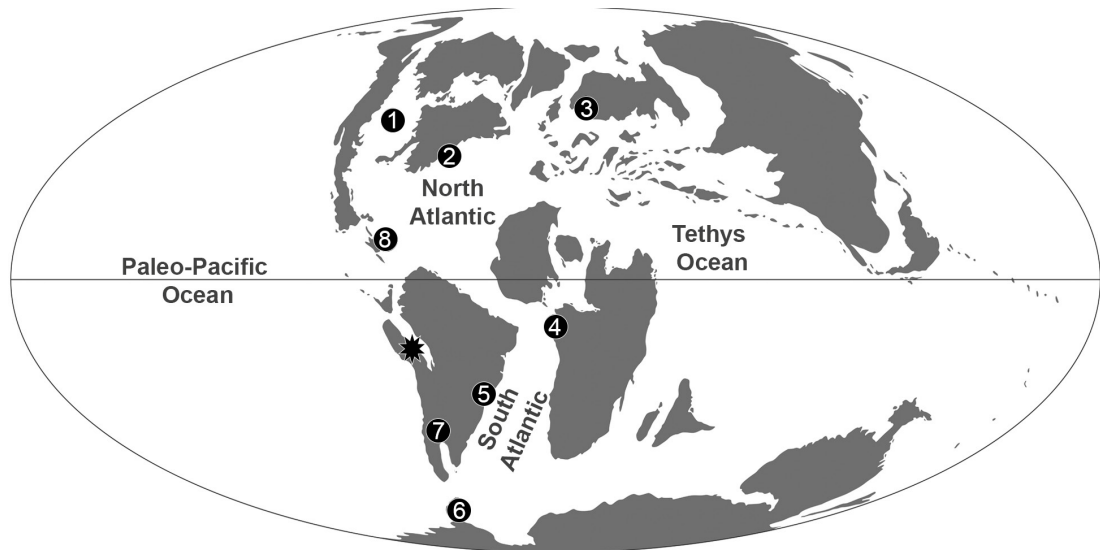


FIG. 4. Simplified paleobiogeographic distribution of the genus *Enchodus* during the Late Cretaceous (modified from Scotese, C.R. PaleoMap Project. <http://www.scotese.com/Default.htm>, accessed on May 2020). 1. Western Interior Seaway (Senonian- Maastrichtian). 2. New Jersey (Maastrichtian). 3. Sweden (Campanian). 4. Nigeria (Cenomanian). 5. Brazil (Turonian-Maastrichtian). 6. Antarctica (Campanian-Maastrichtian). 7. Argentina (Maastrichtian). 8. Mexico (Albian-Maastrichtian). The star points the (Campanian-Maastrichtian) record from Peru.

information (Alvarado-Ortega *et al.*, 2009; Fielitz and González-Rodríguez, 2010; Díaz-Cruz *et al.*, 2016, 2019), the radiation of *Enchodus* could have occurred outside the United States, including the present territory of Mexico. Although, as was mentioned by Díaz-Cruz *et al.* (2019), the biogeographical history of Enchodontidae is difficult to establish due to the short life span and wide inhabit region (the whole Tethyan Sea) of most of the genera.

The evidence highlights that -particularly- the Western portion of the Tethys Sea was crucial for the evolution of the Enchodontidae (see Díaz-Cruz *et al.*, 2019). Most of the *Enchodus* species are restricted to epicontinental seas of temperate to tropical waters.

The report from Peru might correspond to the connections of shelf areas of the western part of South America with those of North America during the Late Cretaceous. Finally, the few Cenozoic reports of enchodontids need to be confirmed (*e.g.*, Arambourg, 1952 mentioned but neither figured nor described rare and very small isolated teeth of *E. elegans* from Paleocene beds of Morocco; Rana *et al.*, 2005 identified a tooth from the Eocene of India as *Enchodus* sp. However, it does not show clear diagnostic features). Thus, enchodontids seems to became extinct at the K/Pg extinction event and

apparently, no other osteichthyan occupied immediately the ecospace in shelf areas.

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