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A new Cretaceous dercetid fish (Neoteleostei: Aulopiformes) from the Turonian of Colombia

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The extinct neoteleost family Dercetidae includes elongate, long-jawed marine fishes that are known from the Late Cretaceous to Paleocene in deposits from the Levant, Europe, North Africa, England, Mexico and Brazil. The fossil record of the family in South America is very sparse and previously was restricted to outcrops in Brazil. Herein we describe a new dercetid fish from the Turonian of Colombia, †*Candelarhynchus padillai* gen. et sp. nov. A single articulated specimen is preserved in part and counterpart; the posterior part of the fish is missing. The specimen differs from other dercetid species by the following unique combination of morphological features: lack of scutes on the flanks of the body, presence of a single pair of transverse processes associated with the abdominal vertebrae, roofed posttemporal fossa, single row of small conical teeth on the dentary and maxilla, toothless premaxilla ornamented with pronounced longitudinal striations and protruding forward far beyond the anterior end of the dentary, and relatively large pectoral fins positioned high on the body. When included in a phylogenetic analysis of †Enchodontoidei, †*C. padillai* gen. et sp. nov. falls within a monophyletic family Dercetidae and is placed as sister taxon to the Late Cretaceous dercetid †*Hastichthys* from Israel, indicating faunal connections between the Eastern and Western Tethys. The new taxon provides novel insights into the distribution of dercetid fishes in the Western Tethys region during the early Late Cretaceous.

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Introduction

Dercetid fishes are extinct, elongate, long-jawed members of the order Aulopiformes that lived in marine waters from the Late Cretaceous (Cenomanian) through to the Paleocene (Danian) (Silva & Gallo 2011). Members of this family were widespread, and have been described from deposits representing the Eastern Tethys in the Levant, Europe and North Africa, as well as Western Tethys deposits of Mexico and Brazil (e.g. Silva & Gallo 2011; Alvarado-Ortega & Porras-Múzquiz 2012; Díaz-Cruz *et al.* 2016). Dercetids have long been known from deposits of the Eastern Tethys, with the genus †*Dercetis* named in the first half of the nineteenth century (Agassiz 1834). On the other hand, dercetid remains from the Western Tethys were only discovered during the last decade, and currently are restricted to a few genera known from the Turonian of Mexico and Brazil (Figueiredo & Gallo 2006; Blanco *et al.* 2008). Here we describe a third genus of Western Tethyan dercetids from Turonian deposits of Colombia, which represents only the second dercetid known from South America.

A number of new dercetid genera and species have been described in recent years, and their relationships with other aulopiforms have been the subject of a number of cladistic studies (e.g. Gallo *et al*. 2005; Blanco *et al*. 2008; Silva & Gallo 2011). The most recent phylogenetic analyses of fossil Aulopiformes by Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016) retained three families: †Enchodontidae, †Halecidae and †Dercetidae (albeit modified from their original composition), but left many other genera as *incertae sedis*. Here, we follow their classification. Silva & Gallo (2011) have also provided a comprehensive review of the taxa included in †Dercetidae and the history of the family that we do not repeat here.

Fossil fish from the Cretaceous of Colombia are principally known from well-preserved, three-dimensional specimens mostly of Barremian–Albian and Turonian age

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*Corresponding author. Email: vernygor@ualberta.ca (e.g. Santos 1994; Schultze & Stöhr 1996; Brito 1997), but records of well-preserved, articulated material compressed two-dimensionally are still under-reported. Although the occurrence of Turonian fish in Colombia has been known to geologists and palaeontologists since the mid-twentieth century from several localities, only a few publications have dealt with them in detail (e.g. Reinhart 1951; Páramo 1997a, 1997b, 2001; Brito & Janvier 2002). The Turonian of Colombia records a time of extensive inundation during a regional marine transgression (Etayo-Serna *et al*. 1976). Fish-rich levels have been recorded in publications and reports of geological explorations (Hubach 1931; Royo y Gómez 1943). Hubach (1931) highlighted the occurrence of a Turonian interval that is rich in vertebrates throughout the Colombian Eastern Cordillera, which he referred to as the 'nivel de peces' (fish level).

So far, the only described Turonian fishes in Colombia come from the Upper Magdalena Valley (UMV) (e.g. Reinhart 1951; Páramo 1997a, 1997b, 2001), and represent chondrichthyans of the groups Galeomorphii, †Ptychodontidae and †Sclerorhynchidae, and osteichthyans of the groups †Pachyrhyzodontidae, †Pycnodontiformes and †Tselfatioidei. Among the chondrichthyans, remains attributed to the galeomorphs comprise a series of 14 vertebrae (Páramo 1997a), while the ptychodontids are represented by teeth of several species of †*Ptychodus* Agassiz (i.e. †*P. chappelli* Reinhart, 1951, †*P. decurrens* Agassiz, 1839, †*Ptychodus* cf. *P. martini* Williston, 1900) and †*Ptychodus* sp. aff. *P. oweni* Dixon, 1850 (Reinhart 1951; Páramo 1997a). In addition, an isolated dentary plate of a ptychodontid fish of uncertain age and provenance was referred to †*Ptychodus* sp. by Brito & Janvier (2002), who suggested a possible Late Cretaceous age. The material of †Sclerorhynchidae is limited to the base of a rostral tooth from a large-sized individual assigned to †*Onchosaurus pharao* (Dames, 1887) (Páramo 1997a).

Among the osteichthyan fauna in the Turonian of Colombia, the †Pycnodontiformes are represented by a pair of splenials and a series of body plates, but unfortunately the morphological features seen in the material do not permit a more precise placement (Páramo 1997a). The †Pachyrhyzodontidae are represented by two species: †*Pachyrhizodus etayoi* Páramo, 2001, and †*Goulmimichthys gasparinii* Páramo, 2001, both so far only known from Colombia (Páramo 2001). The tselfatioids are represented by two specimens of †*Bachea huilensis* Páramo, 1997, which, with sizes estimated to be ~50 cm and ~1 m in length, represent one of the largest tselfatioids known (Páramo 1997b). Interestingly, despite the rich, diverse and well-known Turonian ichthyofauna from the UMV, Aulopiformes – to which †*Candelarhynchus padillai* gen. et sp. nov. belongs – have not previously been discovered in these assemblages. The new dercetid described here demonstrates the potential for Colombian deposits to produce fish fossils that are pivotal to understanding the evolution of ichthyofaunas in the southern portion of the Western Tethys during the Cretaceous.

Geological setting

The type material of †*Candelarhynchus padillai* gen. et sp. nov. was discovered *ex situ* in 2014 by a keen-eyed boy who visited the Monastery of La Candelaria near Ráquira, Boyacá, and noticed the fossil fish which was preserved as an impression in a flagstone on the path outside the monastery. Its occurrence was brought to our attention (MLP), prompting a visit to the monastery to confirm the find. During our examination, we discovered that both the part and counterpart were preserved in separate flagstones of the path; both were removed with the permission of the monastery and taken to the Centro de Investigaciones Palaeontológicas (CIP) for preparation and study. In February 2016, two of the authors (JL, MLP) located the people who had extracted the slabs and laid the path, and tracked down the provenance of the flagstones to the original quarry located 30 minutes' drive north-east of Ráquira, via the countryside of Tapias, Department of Boyacá, Colombian Eastern Cordillera. The quarry is at latitude 5.49916605, and longitude –73.57014252 (Fig. 1).

The outcrop in the quarry corresponds to fossiliferous, finely laminated, light to dark grey mudstones intercalated with beige to light grey, indurated mudstones of the lower-middle Turonian San Rafael Formation, with abundant globular planktonic foraminifera, ammonites such as the coilopoceratid †*Hoplitoides* von Koenen, 1998 (Fig. 2A, C, F), sporadic indeterminate acanthoceratids (Fig. 2D, E), occasional ?anomiid bivalves (Fig. 2B, F), and hundreds of articulated and disarticulated brachyuran crabs of the genus †*Cenomanocarcinus* Van Straelen, 1936, mostly on crab-rich surfaces (Fig. 2G, H), preserved as lateral (ammonites, bivalves) or dorsoventral (crabs) impressions parallel to the lamination. The association between abundant †*Hoplitoides* spp., acanthoceratid ammonites and the crab †*Cenomanocarcinus* sp. has been previously recognized for the lower to middle Turonian Stage of Colombia, particularly the middle and upper parts of the San Rafael Formation in Boyacá (Etayo-Serna 1968; Villamil & Arango 1998; Feldmann *et al.* 1999; Vega *et al.* 2007, 2010; Luque 2015; Luque *et al.* 2017), and the La Frontera Formation in Cundinamarca (Villamil & Arango 1998; Feldmann *et al.* 1999; Patarroyo 2016; Patarroyo & Bengtson 2017).

The part and counterpart of †*Candelarhynchus padillai* gen. et sp. nov. holotype are preserved compressed laterally in slabs of indurated and finely laminated light grey to beige mudstones, and associated with hoplitoid ammonites and scattered cenomanocarcinid crab

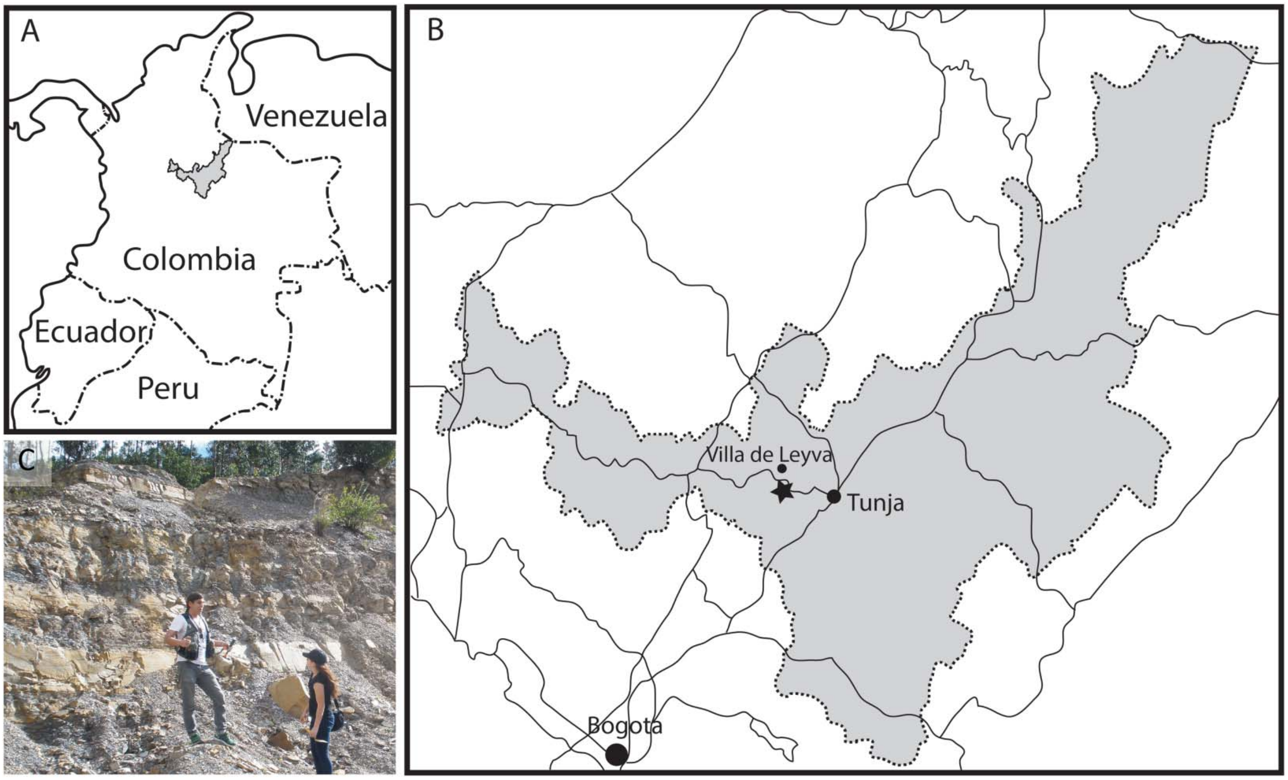

Figure 1. Location map for the fossil locality. **A,** map of Colombia with Boyacá Department shaded. **B,** Boyacá Department (shaded) with the fossil locality marked with a star, south of Villa de Leyva. **C,** photograph of the quarry with two of the authors (JL and OV) for scale.

remains. The identical facies and macrofossil content seen between the rocks cropping out in the quarry and the flagstones containing †*Candelarhynchus padillai* gen. et sp. nov. reveal not only the original source of the material and its lower to middle Turonian age, but also the affinities with other localities of the lower-middle Turonian San Rafael Formation nearby. This association confirms the lower to middle Turonian age of the new fossil fish specimen.

Material and methods

The part and counterpart of the referred specimen, CIP-00097 (MCR) A and B, are catalogued in the collections of the Centro de Investigaciones Paleontológicas, Villa de Leyva, Colombia. The description here is based on examination of the original specimen as well as latex peels of the specimen. Digital photographs were taken using both an Olympus OM-D E-M10II camera and a Dino-Lite Pro Digital Microscope AM-413ZTAS.

We here follow the classification for the families †Dercetidae, †Halecidae and †Enchodontidae within Aulopiformes given by Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016).

Phylogenetic analysis

The phylogenetic analysis is based on the data set of Silva & Gallo (2011) for the Enchodontoidei with the modifications of Díaz-Cruz *et al.* (2016) (Supplemental data 1). The character matrix includes 32 ingroup taxa and three outgroup taxa (†*Protostomias*, *Trachinocephalus* and †*Sardinioides*) as used by Díaz-Cruz *et al.* (2016). All characters were treated as unordered and of equal weight. Non-applicable characters were coded with hyphens; missing data were coded with question marks. The complete data matrix used in the present analysis is presented in Supplemental data 2.

The analysis was performed using PAUP* v. 4.0a151 (Swofford 2002), employing a heuristic search method with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. The most parsimonious trees (MPTs) recovered by the analysis were used to construct the strict consensus tree. The consistency (CI) and retention (RI) indices were calculated in Mesquite v. 3.03 (Maddison & Maddison 2015). Bootstrap and Bremer support values for the phylogenetic trees were calculated in TNT v. 1.1 (Goloboff *et al.* 2008). Character optimization at the ancestral nodes was performed using Farris optimization (Farris 1970) as implemented in TNT v. 1.1.

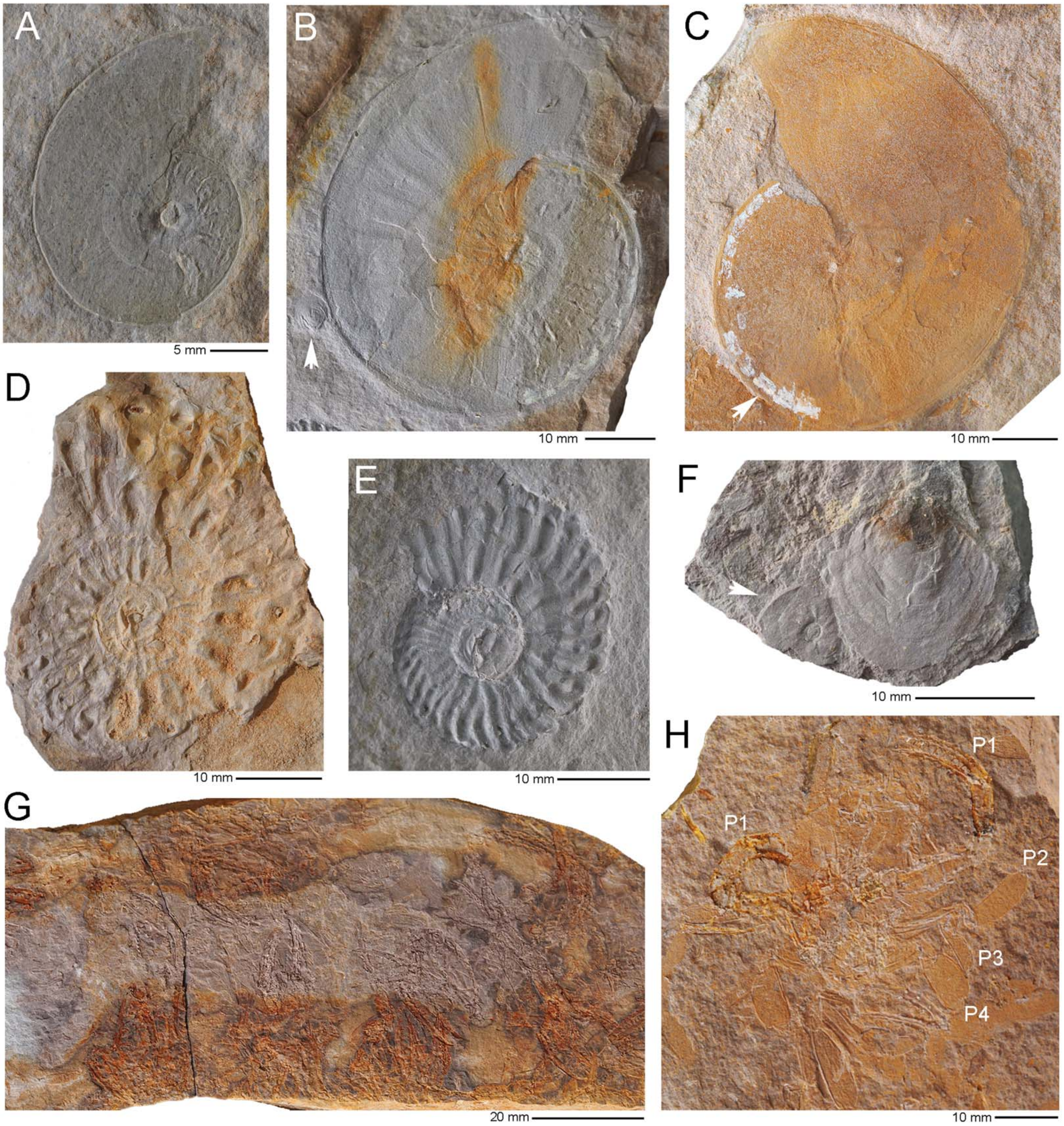

Figure 2. Invertebrates from the lower–middle Turonian San Rafael Formation near Ráquira, Boyacá, associated with †*Candelarhynchus padillai* gen. et sp. nov. **A–C,** †*Hoplitoides* spp.; **A,** CIP-TU-018; **B,** CIP-TU-012b, associated with a small bivalve (white arrow); **C,** CIP-TU-006c, showing some siphuncle (white arrows). **D, E,** †*Kamerunoceras*? sp.; **D,** CIP-TU-013; **E,** CIP-TU-012. **F,** anomiid? bivalve indet., CIP-TU-019, associated with small hoplitoid ammonite (white arrow). **G, H,** †*Cenomanocarcinus* sp.; **G,** crab-rich surface, showing a number of articulated and disarticulated overlapping carapaces and appendages; **H,** ventral view, showing the chelipeds (P1) and the ambulatory pereiopods 2 to 4 (P2–P4).

Anatomical abbreviations

Aa, anguloarticular; **ao**, antorbital; **brst**, branchiostegal rays; **cl**, cleithrum; **cor**, coracoid; **den**, dentary; **df**, dorsal fin; **dsph**, dermosphenotic; **ect**, ectopterygoid; **ent**, entopterygoid; **exs**, extrascapular; **fr(r)** and **fr(l)**, right and possible left frontals; **hyo**, hyomandibular; **io 1-4**, infraorbitals 1–4; **iop**, interopercle; **le**, lateral ethmoid; **md.c.**, mandibular sensory canal; **mes**, mesethmoid; **met**, metapterygoid; **mx**, maxilla; **op**, opercle; **or**, orbitosphenoid; **pa**, parietal; **pal**, palatine; **pmx (l)** and **pmx (r)**, left and right premaxillae; **pop**, preopercle; **ps**, parasphenoid; **pt**, pterosphenoid; **pto**, pterotic; **ptr**, pterygiophore; **ptt**, posttemporal; **pvb(l)** and **pvb(r)**, left and right pelvic bones; **pvfr**, pelvic fin rays; **q**, quadrate; **rar**, retroarticular; **sca**, scapula; **soc**, supraoccipital; **sop**, subopercle; **sorb.c.**, supraorbital sensory canal; **tr.pr.**, transverse process; **vc**, vertebral centrum.

Data archiving statement

The data for this study are available in Morphobank: http://www.morphobank.org/2663.

Systematic palaeontology

Division **Teleostei** Müller, 1845
Subdivision **Neoteleostei** Nelson, 1969
Order **Aulopiformes** Rosen, 1973
Family †**Dercetidae** Woodward, 1901

Included genera. †*Apuliadercetis* Taverne, 2006a; †*Benthesikyme* White & Moy-Thomas, 1940; †*Brazilodercetis* Figueiredo & Gallo, 2006; †*Caudadercetis* Taverne, 2006b; †*Cyranichthys* Taverne, 1987; †*Dercetis* Münster & Agassiz in Agassiz, 1834; †*Dercetoides* Chalifa, 1989; †*Hastichthys* Taverne, 1991; †*Leccedercetis* Taverne, 2008; †*Nardodercetis* Taverne, 2005b; †*Ophidercetis* Taverne, 2005a; †*Pelargorhynchus* von der Marck, 1858; †*Rhynchodercetis* Arambourg, 1943.

Genus †***Candelarhynchus*** gen. nov.

Type species. †*Candelarhynchus padillai* sp. nov.

Etymology. The generic name is derived from the combination of the Monasterio de la Candelaria, where the flagstones bearing the fossil fish were found, and 'rhynchus' – from the Greek word '*rhynchos*' (nose, snout). The generic name gender is masculine.

Diagnosis. A dercetid fish, based on the absence of a longitudinal opercular crest and reduced neural spines (synapomorphies of the family proposed by Gallo *et al.* 2005), with an elongate body as well as an elongate rostrum formed by the premaxillary bones protruding well beyond the dentary. The edentulous premaxilla is ornamented with longitudinal striations. The maxilla and dentary bear very small conical teeth. Dorsal fin short, with at least eight fin rays, positioned above the pelvic fins. The interopercular bone is triangular. No scutes are present on the flanks of the body.

†*Candelarhynchus* gen. nov. differs from all other dercetids by the following combination of characters: a single pair of well-developed transverse processes on the anterior abdominal vertebral centra (two pairs of transverse processes in †*Rhyncodercetis*, †*Dercetoides*, †*Brazilodercetis*, †*Hastichthys*, †*Apuliadercetis* and †*Caudadercetis*); posttemporal fossa roofed (unroofed in †*Brazilodercetis*, †*Dercetoides* and †*Pelargorhyncus*); pterotic not extending to or beyond the posterior extent of the occipital crest (extends to or past the posterior end of the occipital crest in †*Apuliadercetis*, †*Brazilodercetis*, †*Rhynchodercetis* and †*Cyranichthys*); no teeth on the premaxilla (premaxilla is toothed in †*Cyranichthys*, †*Dercetoides*, †*Dercetis*, †*Pelargorhynchus* and †*Caudadercetis*), a single row of teeth on the mandible (no teeth on dentary in †*Leccedercetis*); dorsal fin positioned over centra 29–31 (over centra 24–26 in †*Rhynchodercetis*, 23–25 in †*Dercetoides*, and begins over centrum 25 in †*Caudadercetis*); no enlarged scutes completely covering the body (large scutes cover the body in †*Cyranichthys*, †*Ophidercetis* and †*Pelargorhynchus*); no teeth on the dermopalatine (two or more dermopalatine teeth in †*Benthesikyme* and †*Nardodercetis*); and premaxillary bones ornamented with prominent striations (premaxillary bones are not ornamented in †*Benthesikyme* and †*Nardodercetis*).

†***Candelarhynchus padillai*** sp. nov.
(Figs 3–8)

Material. Holotype: CIP-00097 (MCR), part (A) and counterpart (B) of an incomplete fish; both parts preserve the anterior part of the fish (Fig. 3).

Type locality and age. Lower–middle Turonian (lower Upper Cretaceous Series), San Rafael Formation; Vereda Tapias, north-east of Ráquira, Department of Boyacá, Colombian Eastern Cordillera, latitude 5.49916605, longitude -73.57014252 (Fig. 1).

Etymology. The specific epithet is in honour of the late Dr Carlos Bernardo Padilla for his contribution to the salvage, protection and study of the fossils of Villa de Leyva, Colombia, and nearby areas.

Diagnosis. As for genus.

Description.

General characteristics. The holotype and only known specimen, CIP-00097 (MCR), is incomplete, missing the posterior part of the fish behind the dorsal fin; therefore, the standard length cannot be determined. The length of the preserved portion of the fish in the counterpart CIP-00097 (MCR) B, which preserves more of the posterior portion of the body, is 270 mm from the tip of the rostrum to the end of last preserved vertebra. The fish has a slender and elongate body, with a shallow head and prominent rostrum, similar to that of other dercetids but unlike that of the deeper bodied non-dercetid aulopiformes such as †*Ichthyotringa* Cope, 1878 and †*Aulopus* Cloquet, 1816 (see Pictet & Humbert 1866; Arambourg 1943; D'Erasmo 1946; Blanco-Piñón & Alvarado-Ortega

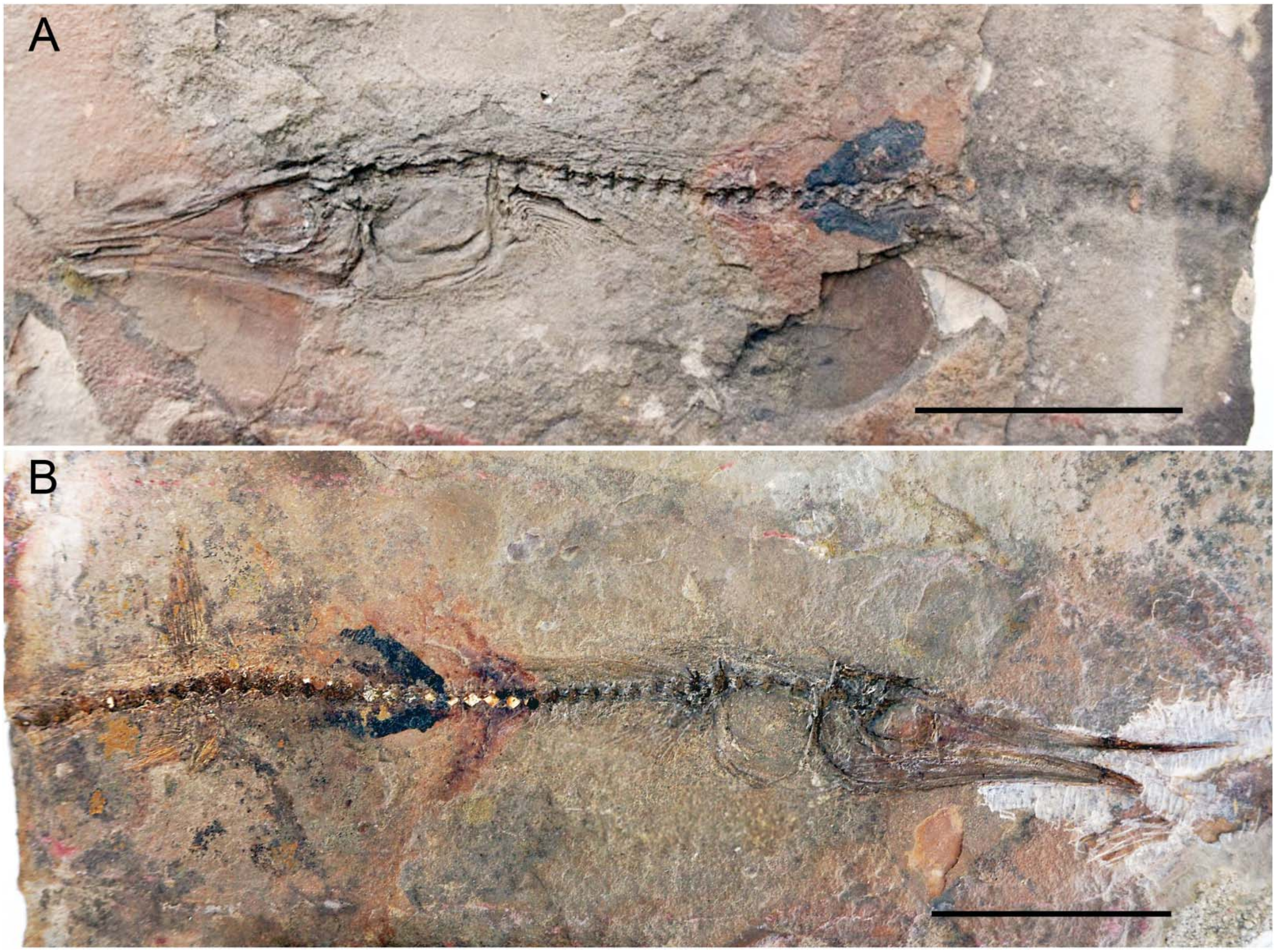

Figure 3. Photograph of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR), **A,** part and **B,** counterpart. Scale bars = 5 cm.

2005a, 2005b; Blanco & Alvarado-Ortega 2006; Chalifa 1989; Blanco *et al.* 2008; Figueiredo & Gallo 2006). The head of the fish, measured from the tip of the rostrum to the posterior margin of the operculum in CIP-00097 (MCR) B, is 110 mm. Head depth is approximately 24.5% of head length and the preorbital distance measured from the tip of the rostrum to the anterior margin of the orbit equals 62% of the head length. The body is of almost uniform depth with the greatest depth, just behind the head, being 28 mm. The short-based dorsal fin is located above the pelvic fins; the predorsal length is 210 mm. The pectoral fin is high on the side of the body, just behind the head. The anal and caudal fins are not preserved. There are no scutes preserved in the specimen.

Skull roof. The skull is preserved in lateral view. The head is very elongate and shallow; it is roughly triangular with the deepest part of the head just behind the orbit and gradually tapering towards the distal end of the slender and pointed rostrum (Figs 4, 5).

The frontals are the largest elements of the skull roof; they are narrow anteriorly and moderately expanded above the orbit and posteriorly where they contact the parietals. The suture between the frontals is most likely almost straight, but this cannot be clearly determined in the specimen. The frontal in CIP-00097 (MCR) A shows a sensory canal partially preserved above the orbit (Fig. 4). The visible portion of the supraorbital sensory canal appears to be open; it may have been fully enclosed at the posterior part of the orbit. The surface of the frontal bones is smooth and without ornamentation.

The parietals are much shorter than the frontals. The parietals are subrectangular and extended slightly anteriorly to fit the posterior end of the frontals. The parietals meet each other in the midline; posteriorly, they contact the supraoccipital and extrascapular bones. The supraoccipital is best preserved in CIP-00097 (MCR) A; it is a small

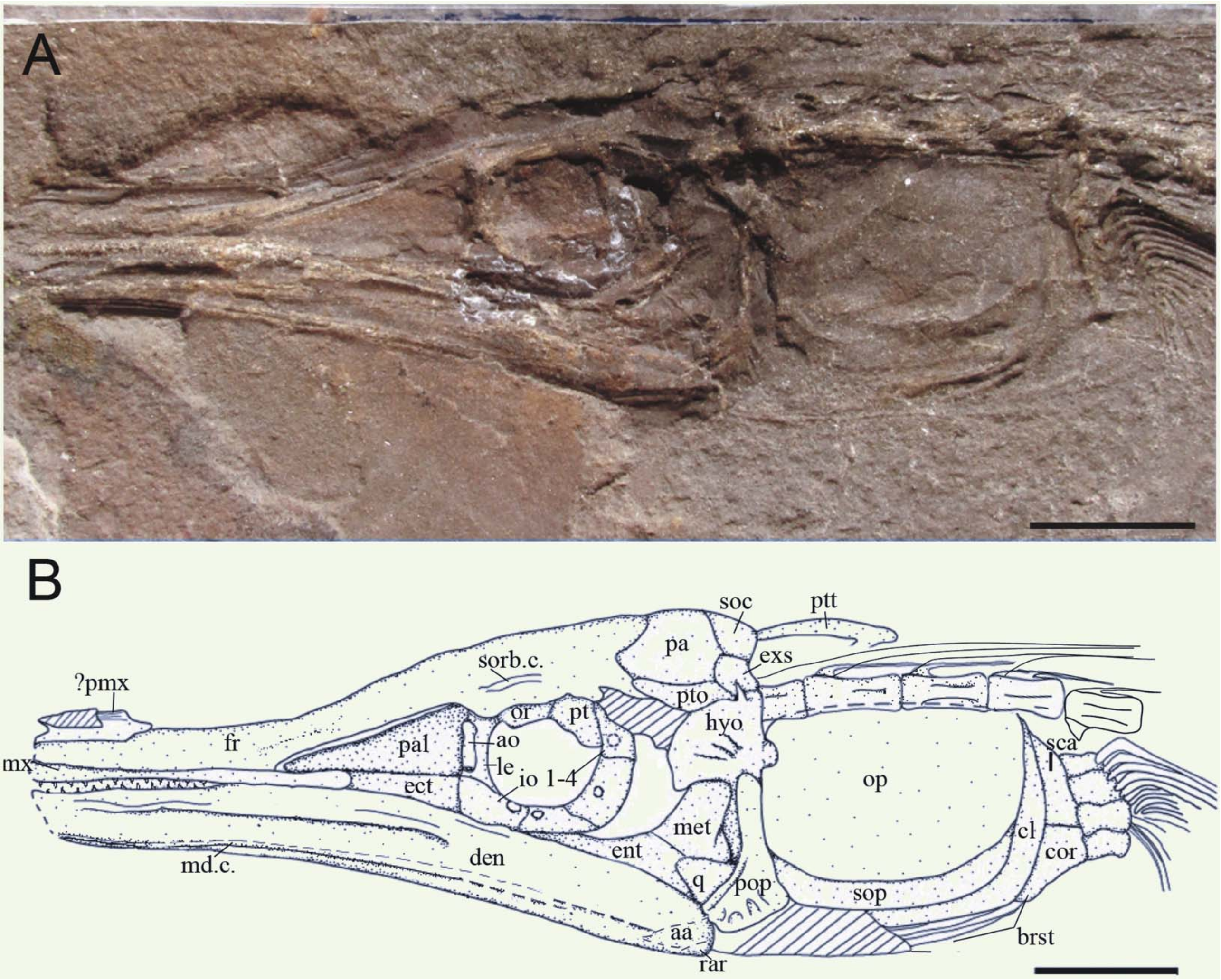

Figure 4. **A,** photograph and **B,** interpretive drawing of the head of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR) A. Scale bars = 1 cm.

subtriangular bone with a low median crest. The pterotic is an elongate and relatively narrow bone; it does not extend beyond the occiput region. There is no trace of a sensory canal in the pterotic, but this absence may be caused by poor preservation. The extrascapular is preserved in CIP-00097 (MCR) A; it is trapezoidal and contacts the pterotic, parietal and supraoccipital bones to form the posterolateral part of the skull roof (Fig. 4).

The ethmoid region is partially preserved. The mesethmoid is poorly preserved; only a partial impression of the posterior end of the bone can be identified in CIP-00097 (MCR) B. The posterior end of the mesethmoid is acute and fits between the left and right premaxillae and the anterior ends of the two frontals. The lateral ethmoid is a well-ossified element preserved in the anterior portion of the orbit; it is a rectangular bone contacting the frontal dorsally and the parasphenoid ventrally.

Jaws. The maxillary and premaxillary bones are best preserved in CIP-00097 (MCR) B. The premaxillae are extremely long, projecting forward well beyond the distal end of the mandible and forming a prominent rostrum (Fig. 5). The left and right premaxillae have become separated and displaced in the specimen, with the right premaxilla slightly angled ventrally to overlie the dentary at the anterior tip. The displacement of the right premaxilla indicates that the two were not sutured together as in some dercetids such as †*Cyranichthys* (Taverne & Goolaerts 2015). The premaxillary bones are ornamented with well-defined longitudinal striations. There are no teeth on the premaxillae.

The maxilla is only partially preserved in CIP-00097 (MCR) A. The preserved portion is long, shallow and bears minute pointed teeth. The total length of the maxilla cannot be determined.

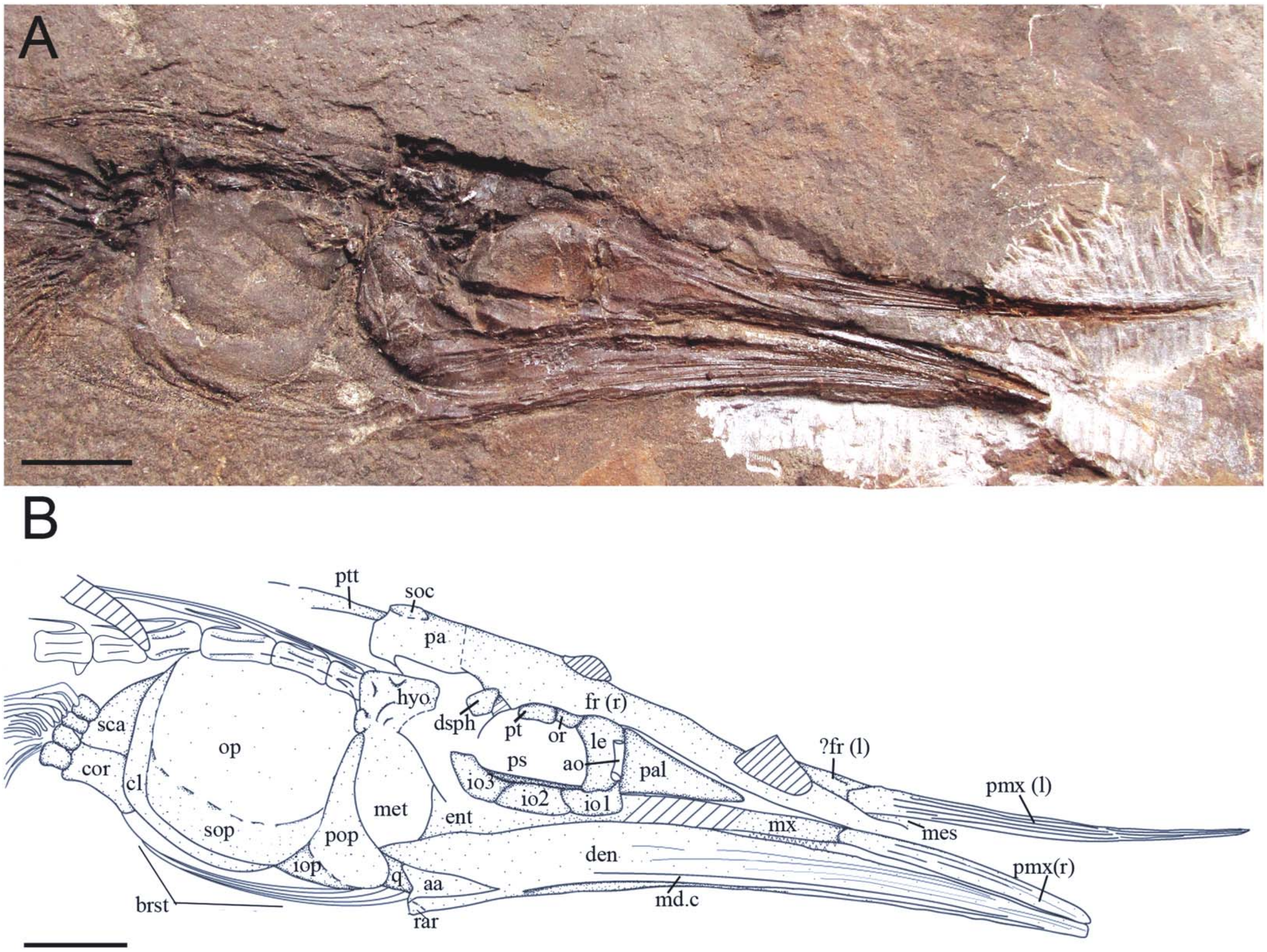

Figure 5. **A,** photograph and **B,** interpretive drawing of the head of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR) B. Scale bars = 1 cm.

The mandible is deep posteriorly and tapers towards the dentary symphysis. The dentary is long, with an open mandibular sensory canal running close to the ventral margin of the bone. There is a single row of small conical teeth on the dentary. The surface of the bone is ornamented with longitudinal striations. Posteriorly, the dentary articulates with the much smaller wedge-shaped anguloarticular which bears a shallow articular facet for the quadrate. The retroarticular is small and oval in shape with no posterior process (Fig. 5).

Orbital region. The infraorbital bones are best preserved in CIP-00097 (MCR) A. Infraorbitals 1–3 are elongate, subrectangular bones; the fourth infraorbital bone is only partially preserved (Fig. 4). The third infraorbital is the largest bone in the series forming the posteroventral corner of the orbit. The infraorbital sensory canal opens through a small pore in each of the preserved infraorbitals. The narrow, curved antorbital bone bearing an enclosed sensory canal is preserved overlying the lateral ethmoid at the anterior edge of the orbit. A small poorly preserved element in the posterodorsal corner of the orbit in CIP-00097 (MCR) B is identified as the dermosphenotic but its details cannot be determined.

Only a small portion of the parasphenoid can be seen in CIP-00097 (MCR) A where it crosses the orbit below the midline and is partially covered by the infraorbital bones (Fig. 4). Both an orbitosphenoid and pterosphenoid bone are visible in the dorsal part of the orbit.

Hyopalatine bones and branchial arches. The suspensorium is oriented vertically in the specimen. The hyomandibular is partially preserved with a broad, robust, dorsal head and a rounded flange anteriorly. The hyomandibular has a single facet for articulation with the braincase, and a prominent opercular condyle. The quadrate is partially visible in CIP-00097 (MCR) B in which the posterior portion is covered by the preopercle. The quadrate is fan shaped and tapers ventrally into a condyle that articulates with the anguloarticular in a shallow facet (Fig. 5).

The anterior expansion of the hyomandibular head meets the metapterygoid ventrally. The metapterygoid is best preserved in CIP-00097 (MCR) A; it is broad and subrectangular in shape, contacting the entopterygoid anteroventrally.

The ectopterygoid is partially preserved anterior to the orbit. It is a long, slender bone underlying the posterior portion of the maxilla and extending posteriorly to contact the slightly broader entopterygoid. The presence of teeth on the ectopterygoid and entopterygoid cannot be confirmed because of the fragmentary preservation of these bones. A large triangular palatine is preserved anterior to the orbit; it is deep posteriorly and tapers into an acute anterior end.

The branchial skeleton is almost completely obscured by overlying bones, with only two branchiostegal rays visible. These are very long and thin, extending along the ventral margin of the opercular series.

Opercular series. The counterpart, CIP-00097 (MCR) B, preserves the opercle, subopercle, preopercle, and interopercle (Fig. 5). The opercle is the largest bone of the series; it is rectangular with rounded corners and is almost 1.2 times longer than it is deep. There is a single short and fine ridge directed posteroventrally from the anterodorsal corner of the bone, but no other ornamentation on the opercle. The subopercle is an elongate bone that extends the full length of the ventral margin of the opercle. The ventral margin of the subopercle is rounded and slightly convex, and the bone appears to expand anteriorly. The subopercle has a smooth surface without ornamentation.

The preopercle has a very slender dorsal limb that meets a short and greatly expanded ventral limb to form an obtuse angle. The preopercular sensory canal, partially preserved in CIP-00097 (MCR) B, has four branches in the ventral limb. The impression of a large triangular interopercle is visible behind the preopercle.

Vertebral column. The preserved portion of the vertebral column consists of 37 centra. All of the preserved vertebrae are abdominal, indicating that the fish had an extremely elongate body similar to that of other dercetids. The vertebral centra are all longer than they are high. The first four centra are the most elongate in the series, as in other dercetids; they are almost three times longer than they are high.

The neural arches are low and extend over the entire length of the associated centra; each neural arch bears a low, posteriorly directed neural spine. The neural spines are relatively short, their length being slightly greater than half the length of the vertebral centrum. Long epineurals extend posteriorly over the length of three vertebrae. There are no epicentral nor epipleural bones preserved, although the epipleural series might be expected as it is present in at least some dercetids (e.g. Goody 1969).

The vertebral centra bear a single pair of well-developed anterior transverse processes, beginning on the seventh centrum. The transverse processes are triangular in shape and are not fused to the centra (Fig. 6).

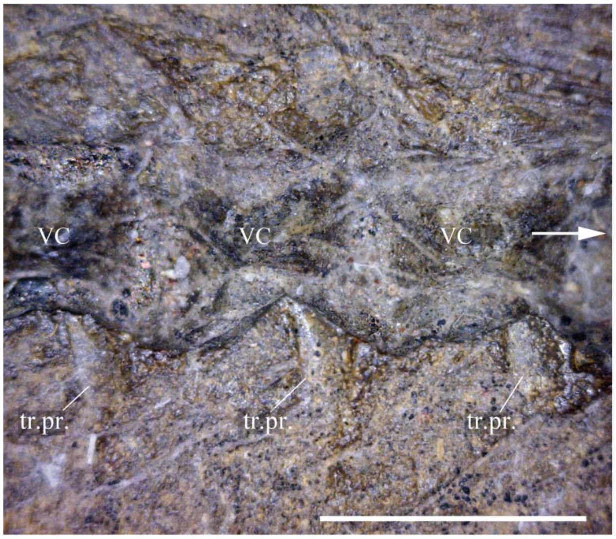

Figure 6. Photograph of the vertebral centra of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR) B. Arrow indicates anterior direction. Scale bar = 5 mm.

Very long, thin ribs are present and appear to be slightly arched; they are not well-preserved along the vertebral column. CIP-00097 (MCR) A preserves eight ribs associated with the abdominal vertebrae, while only six ribs can be distinguished in the counterpart, CIP-00097 (MCR) B. All ribs articulate on parapophyses. Presence of the supraneural bones cannot be determined in the specimen.

Paired fins and girdles. The pectoral girdle is only partially preserved in the specimen. The dorsal arm of the posttemporal, preserved as an impression, extends posteriorly from the occiput to approximately the midpoint of the opercle. Details of the ventral limb of the posttemporal cannot be determined. The supracleithrum is not preserved.

The posterior edge of the cleithrum is visible behind and below the opercle. It tapers dorsally to a point, which does not reach as far dorsally as the top of the opercle. The scapula and coracoid are preserved as impressions. The visible part of the scapula is triangular with a pointed dorsal end and an expanded ventral base where it contacts the coracoid. It is approximately twice as tall as the coracoid. The coracoid is trapezoidal in shape with an anteroventral projection. There is no trace of a coracoid fenestra. There are four large radials: two articulate with the scapula, the third radial is located at the articulation between the scapula and coracoid, and the fourth articulates with the coracoid. The pectoral fin is well developed and positioned high on the flank. There are 14 fin rays preserved in CIP-00097 (MCR) A.

Pelvic fins are preserved in CIP-00097 (MCR) B (Fig. 7). They are positioned well back on the body, below

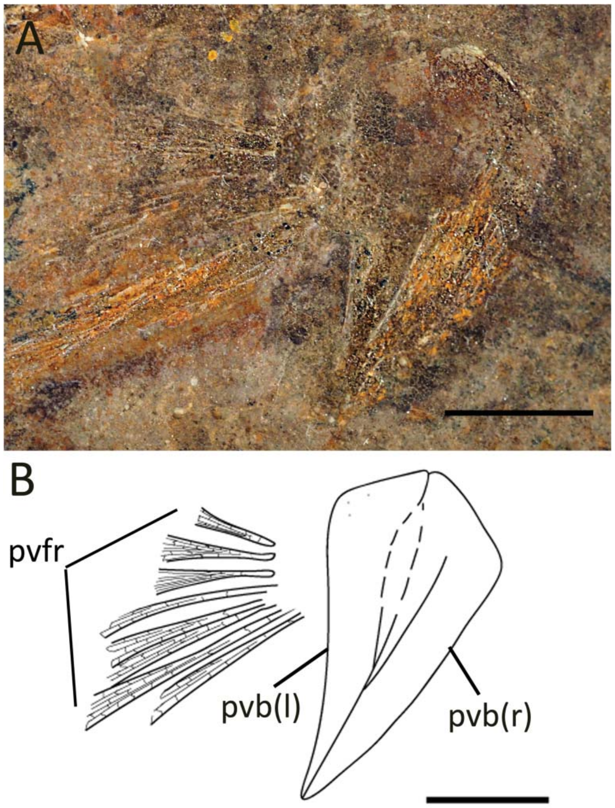

Figure 7. **A,** photograph and **B,** interpretive drawing of the pelvic fin of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR) B. Scale bars = 5 mm.

the midpoint of the dorsal fin base. The pelvic bones are displaced, with the anterior end tilted ventrally and posteriorly. There are at least eight fin rays preserved.

Median fins. Only the dorsal fin is preserved, visible in the counterpart, CIP-00097 (MCR) B (Fig. 8). The triangular dorsal fin is located above the 29th–31st abdominal vertebrae. It has a short base and at least eight dorsal fin rays. All of the fin rays are branched and segmented. The first two fin rays are the longest in the series, after which the rays are much shorter, causing the fin to slope sharply down posteriorly. The pterygiophores are poorly preserved and their number cannot be determined.

Phylogenetic results

The phylogenetic analysis retrieved 151 most parsimonious trees (MPTs) of 446 steps each. A strict consensus of the MPTs (Fig. 9) has a length of 473 steps and relatively low consistency index (CI) and retention index (RI) values of 0.222 and 0.459, respectively, indicating significant amounts of homoplasy. Bremer and bootstrap values indicate low support for most clades; only one clade (†*Saurorhamphus* + †*Eurypholis*) had a bootstrap support over 50% (Fig. 9).

The suborder †Enchodontoidei is recovered as a non-monophyletic group similar to the results of Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016). Two of the three outgroup taxa (†*Protostomias* and *Trachinocephalus*) fall within the ingroup and together with †*Apateopholis*, †*Yabrudichthys* and †*Atolvorator* form a polytomy with the monophyletic †Dercetidae. The new species, †*Candelarhynchus padillai*, is nested within the †Dercetidae and recovered as a sister taxon to †*Hastichthys*.

The †Ichthyotringoidea (†*Ichthyotringa* and †*Apateodus*) is monophyletic; the †Cimolichthyoidea and †Halecoidea appear as polyphyletic assemblages.

Discussion

Phylogeny

The overall results of our phylogenetic analysis agree with those of Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016), recovering a monophyletic †Dercetidae within a paraphyletic †Enchodontoidei. According to previous phylogenetic analyses (Gallo *et al.* 2005; Blanco *et al.* 2008; Silva & Gallo 2011; Díaz-Cruz *et al.* 2016), dercetids share a single non-ambiguous synapomorphy: reduced neural spines (character 71:1). The low and relatively short neural spines of †*Candelarhynchus padillai* support its placement as a dercetid in our analysis. Other characters supporting the family †Dercetidae include: shallow head (char. 2:1), long snout (char. 3:1), fused hypurals (char. 82:1), and presence of tripartite flank scutes (char. 85:3), although the new taxon cannot be coded for some of these characters. While the first three characteristics are homoplastic and also occur in non-dercetid taxa, the last feature (presence of tripartite flank scutes) is restricted to the †Dercetidae and appears in most members of the group. Variation in the flank scute morphology, however, exists within the dercetid group: flank scutes are cordiform in †*Pelargorhynchus*, triangular in †*Cyranichthys* and †*Ophidercetis*, and absent in †*Caudadercetis* and †*Candelarhynchus padillai*.

Addition of the new dercetid taxon resulted in the rearrangement of the groupings within the family. †*Candelarhynchus padillai* is recovered as the sister taxon to †*Hastichthys*, the two together forming a clade supported by three homoplastic characteristics: parietals not separated by the supraorbital (char. 18:0), vertically oriented mandibular suspensorium (char. 28:1), and ornamented premaxillary bones (char. 35:1). Together with †*Nardodercetis*, the above-mentioned taxa form a clade united by a single homoplastic character: opercle longer than deep (char. 59:1). A major dercetid clade comprising †*Hastichthys*, †*Candelarhynchus padillai*, †*Nardodercetis*,

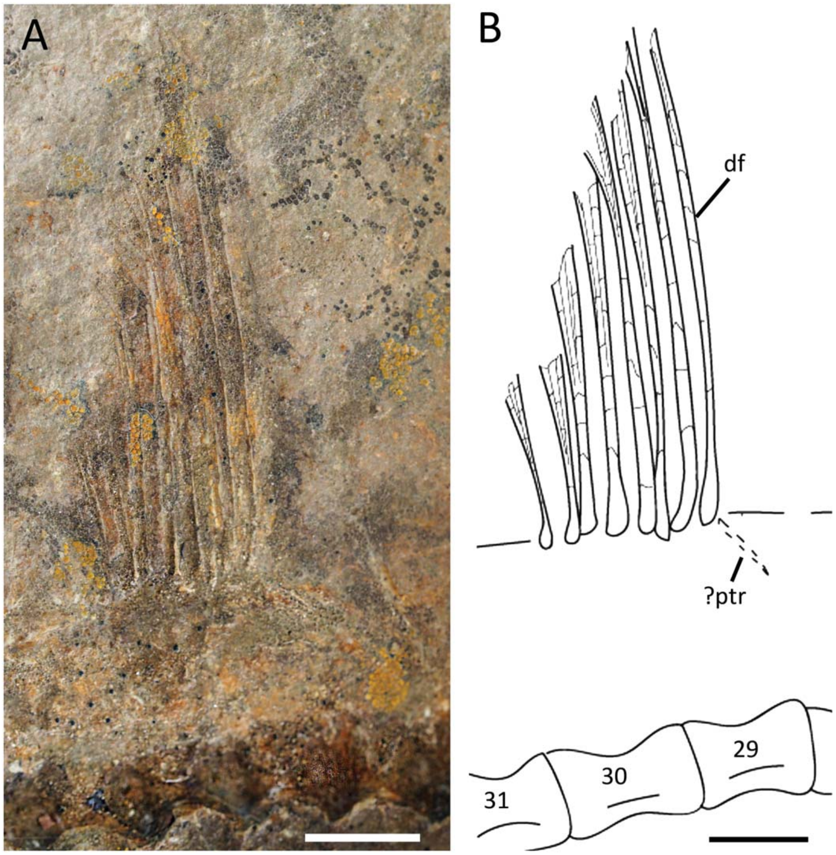

Figure 8. **A,** photograph and **B,** interpretive drawing of the dorsal fin of the holotype of †*Candelarhynchus padillai* gen. et sp. nov., CIP-00097 (MCR) B. Scale bars = 5 mm.

†*Rhyncodercetis*, †*Dercetoides*, †*Pelargorhynchus* and †*Caudadercetis* (Fig. 9) is supported by a unique synapomorphy: presence of a convoluted suture between hypurals 2 and 3 (char. 83:1). Overall, these results are in agreement with Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016). However, Silva & Gallo (2011) noted that the condition of the contact between the second and third hypurals is unknown in †*Pelargorhynchus* and similarly, †*Candelarhynchus padillai* is coded as "?" for character 81 since the specimen is missing the tail.

Monophyly of †Enchodontidae has previously been proposed by Fielitz (2004), Silva & Gallo (2011) and Díaz-Cruz *et al.* (2016), and is also corroborated by our results. †Enchodontidae (Fig. 9) includes †*Unicachichthys*, †*Enchodus*, †*Parenchodus*, †*Palaeolycus*, †*Eurypholis* and †*Saurorhamphus*, and is supported by a single unique synapomorphy: presence of mid-dorsal scutes (char. 87:1). Members of this family also share a set of homoplastic characters: open supraorbital sensory canal (17:1), lack of the supraorbital bone (26:1), presence of the ascending process of the premaxilla (37:1), different size of teeth in the upper jaw (44:1), anteroventral prongs on the dentary (48:1) and presence of middorsal scutes (87:1).

Similar to the results of Díaz-Cruz *et al.* (2016), †*Unicachichthys* is recovered as the most basal member of †Enchodontidae and is distinguished from the other members of the family by the presence of multiple teeth on the dermopalatine (6:0) and a short anal fin (80:0; also observed in †*Eurypholis*). The type genus of the family, †*Enchodus*, is recovered in a polytomy with †*Parenchodus* and the clade (†*Palaeolycus* (†*Eurypholis*, †*Saurorhamphus*)); within this clade, †*Eurypholis* and †*Saurorhamphus* share two unambiguous synapomorphies: a hidden quadrate-mandibular articulation (char. 52:1) and presence of a spine on the posterior margin of the opercle (char. 61:1).

The other two enchodontoid groups included in the analysis, †Ichthyotringoidea and †Halecoidea, are recovered as non-monophyletic. †*Ichthyotringa* is a sister taxon to a clade comprising the *incertae sedis* taxon †*Nardorex* and the enchodontoid †*Rharbichthys*. Together these three taxa form a group (Fig. 9) supported by the absence of the antorbital (8:1) and the anguloarticular lacking a flange (51:1).

Of the included halecoid taxa, †*Hemisaurida* falls in the most basal polytomy within †'Enchodontoidei', and †*Halec* and †*Phylactocephalus* are recovered in a

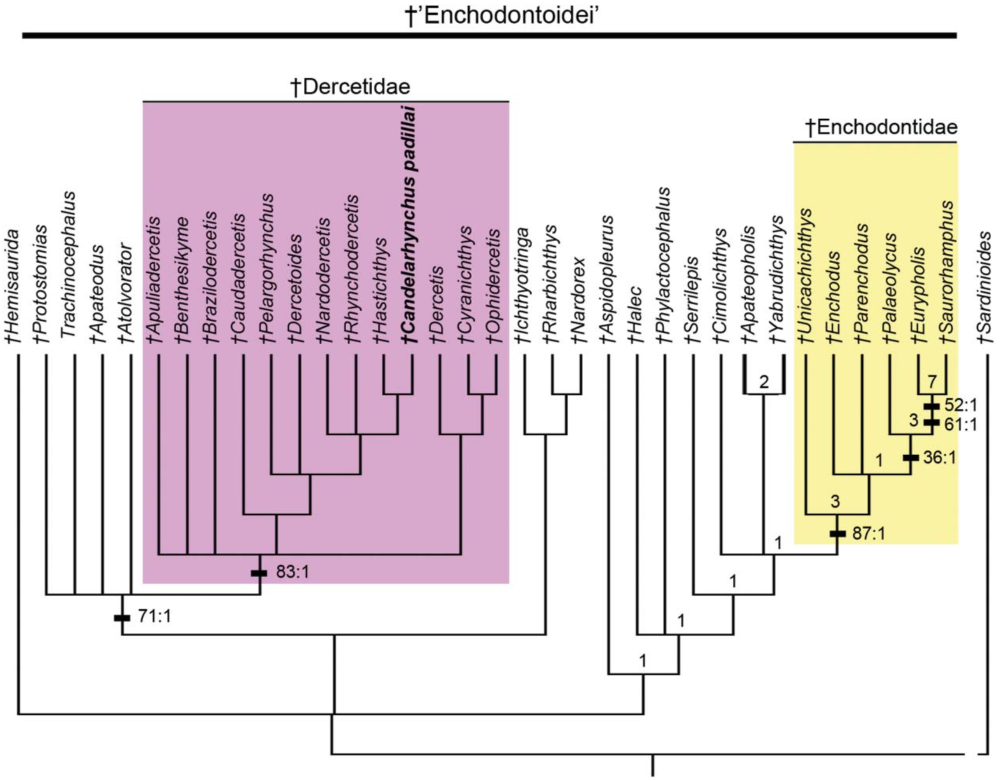

Figure 9. Strict consensus of 151 MPTs (CI = 0.234; RI = 0.483) obtained from the analysis of the †Enchodontoidei dataset. Values at the nodes indicate Bremer support/bootstrap (> 50%) values where present. Daggers (†) indicate extinct taxa. Synapomorphies supporting clades are indicated along the branches.

polytomy basal to †Enchodontidae (Fig. 9). A complete list of the features supporting clades recovered by the phylogenetic analysis is plotted over the strict consensus tree (Supplemental data 1, fig. 1).

Comments on dercetid distribution

Our phylogenetic results indicate the new dercetid †*Candelarhynchus padillai* is most closely related to †*Hastichthys gracilis*, from the early Cenomanian of the Levant (Chalifa 1989). †*Brazilodercetis longirostris*, from the Turonian of Brazil (Figueiredo & Gallo 2006), which is closer to †*C. padillai* in terms of age and geography than is †*H. gracilis*, was recovered as phylogenetically distant from the Colombian dercetid. Additionally, the Mexican and Brazilian dercetids were not recovered as close to one another, with both having a sister-group relationship with a fish found in younger (Campanian-Maastrichtian) Italian deposits. Silva & Gallo (2011, table 2) summarized the ages and geographical locations of known dercetids. The phylogenetic relationships recovered in our analysis reveal an overall disparity in geography and ages of the sister groups. Such a mosaic phylogenetic pattern might be explained at least in part by collection bias that exists between palaeontological excavations of the Eastern versus Western Tethys sites, with the latter being mostly underexplored. It is also possible that the seemingly unexpected sister-group relationships between temporally and geographically distant taxa is an artefact of the incomplete fossil record. Some of the dercetid taxa known from either a single occurrence or constricted area or time frame (e.g. †*Apuliadercetis*, †*Brazilodercetis*, †*Candelarhynchus*, †*Hastichthys*, †*Nardodercetis*) could in fact have a much wider distribution, as in the case of †*Rhynchodercetis*, a diverse genus of dercetid fishes described from across the Tethys and spanning the Cenomanian through Campanian. The example of the genus †*Rhynchodercetis*, however, highlights another concern regarding the existing phylogeny of †Dercetidae and †'Enchodontoidei' in general, that is, a lack of unambiguous synapomorphies supporting most of the groups. Multiple species described in the genus †*Rhynchodercetis* were placed in this genus based on the presence of homoplastic characters, so these characters do not preclude them from creating non-monophyletic groups. It is, therefore, essential to revise and update the existing list of characters used in the phylogenetic analyses to have a more robust support for the evolutionary relationships within the group.

Our current understanding of the phylogenetic relationships indicates that dercetids must have crossed back and forth between east and west and north and south multiple times; just within the genus †*Rhychodercetis* there are species found in the Cenomanian of the Levant, Komen and Morocco (Hay 1903; Arambourg 1954; Silva & Gallo 2011), and the Turonian of Mexico (Blanco & Alvarado-Ortega 2006). Silva & Gallo (2016) examined the Late Cretaceous distribution of dercetids and other enchodontoids (Ichthyotringidae, Halecidae and Enchodontidae). They determined several generalized tracks that could be associated with oceanic currents, eutrophication events or anoxic events. However, they did not analyse the individual species or genera, instead using occurrence data for †Dercetidae at the family level. When the phylogenetic relationships of the individual dercetid species are taken into consideration, the picture becomes quite confused. With the disparity in ages and locations among sister groups, there is little that can be determined in terms of biogeography of the group. It may be that with the increased focus on Mexico and South America providing new fossil discoveries, we may eventually be able to elucidate dercetid relationships and gain an increased understanding of the marine connections between different areas of the Tethys during the Late Cretaceous.

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Supplementary data

Supplemental material for this article can be accessed at: https://doi.org/10.1080/14772019.2017.1391884

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