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First record of a hybodont shark (Chondrichthyes: Hybodontiformes) from the Lower Cretaceous of Colombia

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The Mesozoic chondrichthyan fossil record from northern South America is scarce and poorly known containing only a few reports of lamniform and ptychodont species from the Upper Cretaceous of Colombia and Venezuela. Here, we report the discovery of two associated (found together) dorsal fin spines of a hybodont shark from the Valanginian deposits of the Rosablanca Formation (Andes of Colombia). This hybodont along with the presence of ammonites and other mollusks, turtles, plesiosaurs and ichthyosaurs support a marine depositional environment for this geological unit. Although both spines described here are fragmentary and without diagnostic characters to allow identification to generic level, their finding represents the first record of this shark group from northernmost part of South America and north-western margin of Gondwana. This new record expands the known distribution of this group of sharks during Lower Cretaceous.

Keywords: Mesozoic; Valanginian; Elasmobranchii; South America; Zapatoca

Introduction

Hybodontiform sharks belong to an extinct chondrichthyan lineage with a fossil record that spanned from the Paleozoic to end of the Mesozoic.[1] Their remains are frequently found in Mesozoic rocks around the world [1,2] especially in Triassic and Jurassic rocks where hybodonts are the dominant selachian group in both marine and non-marine environments.[3] This dominant clade became restricted at the end of the Jurassic when neoselachians started displacing hybodonts.[3] However, after the neoselachians radiation, hybodonts survived in restricted marine and fluvial ecosystem until the end of the Cretaceous, when the group became extinct.[1] The Mesozoic hybodont paleodiversity has been estimated by Cappetta [1] to represent at least seven families and 27 genera. However, there are still gaps in our knowledge of hybodonts, whose interrelationships are mostly reconstructed on the basis of isolated teeth [2] and few articulated specimens.[4]

The fossil record of Mesozoic chondrichthyans from northern South America is poorly known with only few remains of lamniforms and ptychodonts from the Upper Cretaceous of Colombia and Venezuela.[5–11] The Mesozoic fossil record of hybodonts in South America includes the following occurrences: several articulated and semi-articulated specimens from the Lower Cretaceous of Brazil (e.g. *Tribodus limae* Brito and Ferreira 1989 [12]), isolated teeth, cephalic and dorsal fin spines,

and dermal denticles from different strata of the Triassic and Jurassic of Argentina [13,14]; Upper Jurassic–? Lower Cretaceous of Uruguay [15] and Upper Jurassic and Lower Cretaceous of Brazil.[16–21] Here, we describe two dorsal fin spines of a hybodontiform from the Lower Cretaceous of Colombia (Rosablanca Formation), representing the first record of this shark group from the northernmost part of South America and shedding additional lights to the chondrichthyan paleodiversity of the northwestern margin of Gondwana during Lower Cretaceous time.

Materials and methods

The dorsal fin spines described here were found in a limestone layer of the Lower Cretaceous Rosablanca Formation (Figure 1) (El Alto locality: 6° 49' 30.21" N, and 73° 15' 9.43" W), a geological unit widely exposed in Zapatoca Town area (Santander Department), northeastern Cordillera of Colombia (Figure 1). The Rosablanca Formation has been interpreted as shallow marine deposits [22] of late Valanginian age, based on ammonites.[23,24] The presence of others fossil vertebrate such as turtles, plesiosaurs, ichthyosaurs, bony fish teeth, invertebrates such as ammonites, bivalves, oysters and gastropods support that the deposition of the Rosablanca Formation occurred under marine conditions.[23,24] The specimens referred here (IGMp-880644; IGMp-880645) are housed in the

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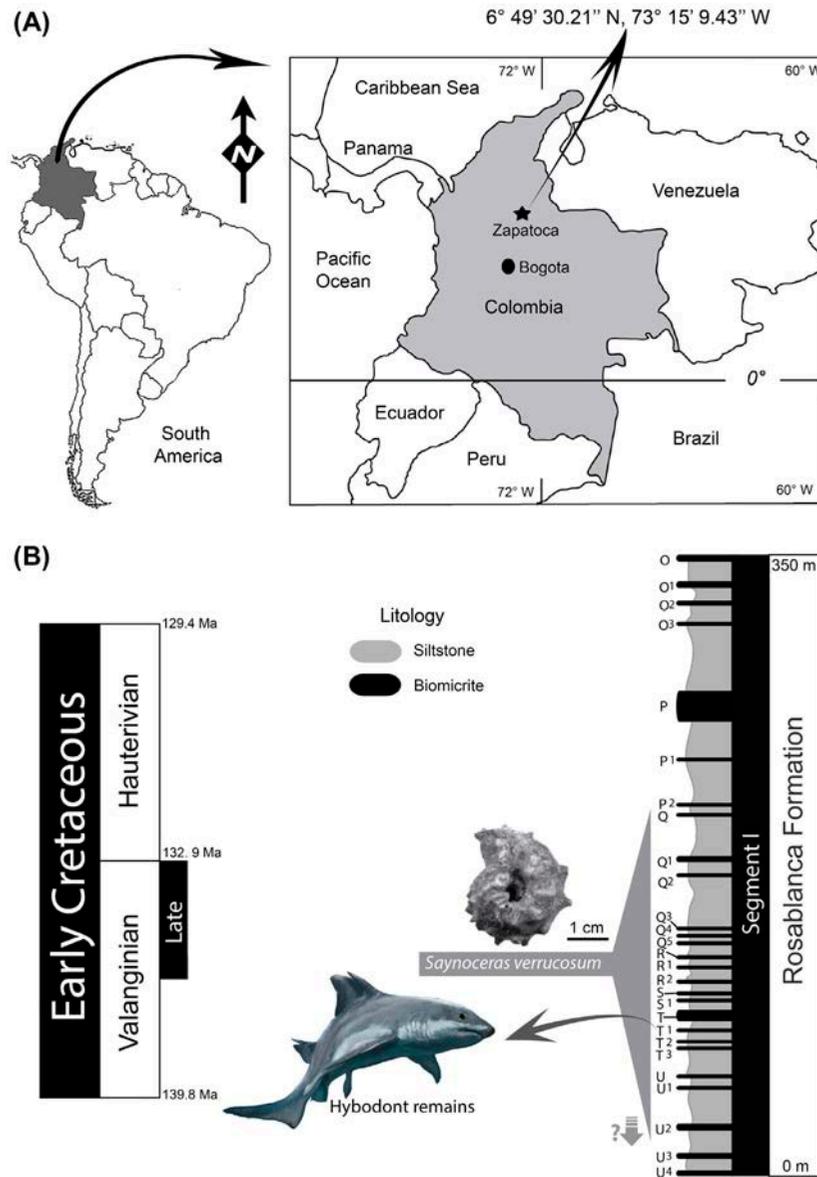


Figure 1. Geographical location map (A), and stratigraphic column of the Rosablanca Formation (B). South American map redrawn from Google Maps, Colombia map modified from [24], art illustration of the shark by Jorge Blanco.

paleontological collection of the Museo Geológico Nacional “José Royo y Gómez” of the Colombian Geological Survey (Servicio Geológico Colombiano, IGMp), in Bogotá, Colombia. The systematic classification follows Cappetta [1] and the hybodont fin spine terminology follows Maisey [25] and Rees and Underwood [3]. Taxonomic identification is based on an extensive bibliographical review and anatomical comparison studies with fossil specimens from the following collections: Natural History Museum of Basel, Switzerland; Palaeontological Institute and Museum at the University of Zurich Switzerland; René Kindlimann (RK) private collection with public access, Uster, Switzerland.

Systematic paleontology

Class Chondrichthyes Huxley, 1880 [26]
 Subclass Elasmobranchii Bonaparte, 1838 [27]
 Order Hybodontiformes Maisey, 1975 [28]
 Family Hybodontidae Owen, 1846 [29]
 Gen. et sp. indet. (Figure 2(A)–(I))

Referred material. Two incomplete and fragmented dorsal spines of indeterminate position. Both specimens were found in close proximity in the same horizon (less than 2 m of separation between each other), suggesting that both could belong to the same individual; however, the alternative hypothesis of different individuals is also plausible.

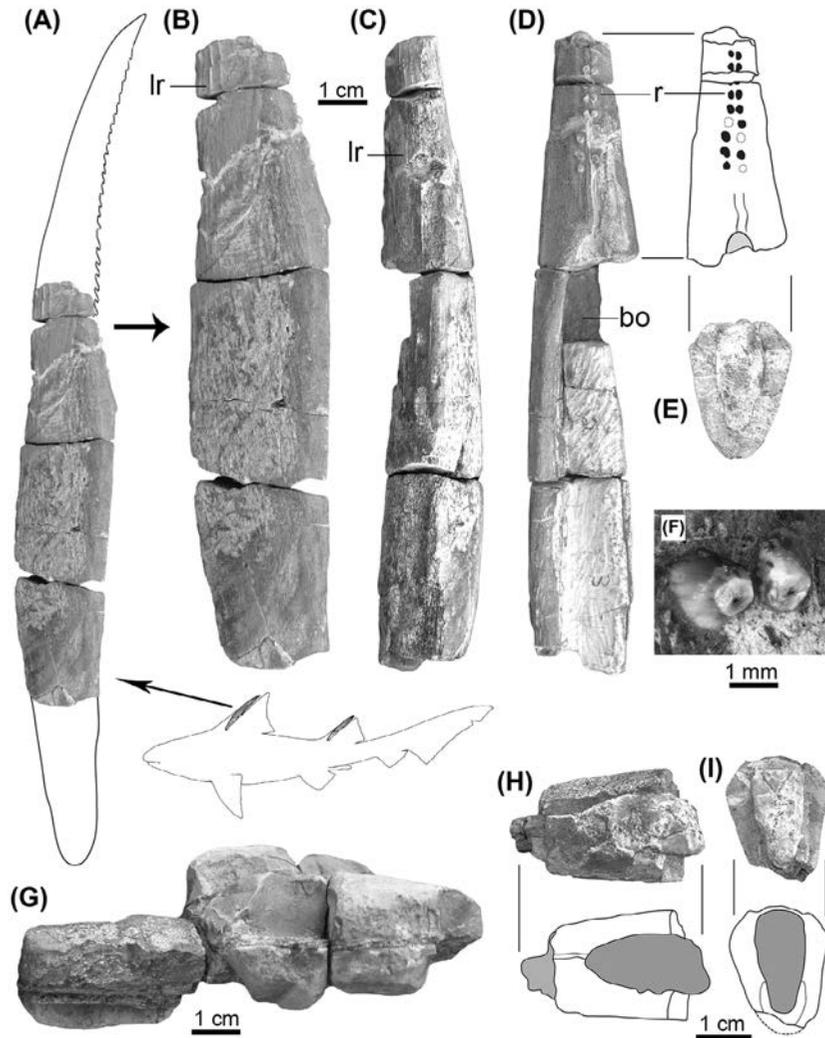


Figure 2. Hybodont fin spines from the Rosablanca Formation. (A–F) Specimen IGMp-880644; (G–I) Specimen IGMp-880645. Notes: Side view: right (A–B), anterior (C) posterior (D, H), cross section (E, I) and indet. (G). Couple of posterior hooks (F). Basal opening (bo), longitudinal ridges (lr) and hook rows (r). Hybodont shark body modified after Maisey [30].

Description. The most complete spine (IGMp-880644) has a robust shape with a length of 129 mm (Figure 2(A)–(F)). In cross section, the spine is approximately oval (Figure 2(E)), while the tip part of the right side below the basal opening and the unornamented base of this specimen are missing (Figure 2(A)–(D)); the anterior side of the spine is slightly straight. On the posterior side, there are two parallel rows of small hooks, without an evident groove between them (Figure 2(D)–(F)). The basal opening is long and wide, having an oval shape in its upper section. Complete longitudinal ribs are not well preserved due to potential erosional effects; however, some remains of these can be observed on the anterior part of both lateral surfaces (Figure 2(B) and (C)). Specimen IGMp-880645 corresponds to a small spine fragment that includes the upper section of the basal opening (Figure 2(H) and (I)) and an eroded and broken long

fragment (~120 mm) contained whitin in a calcareous matrix (Figure 2(G)). The inadequate preservation of those fragments does not permit the observation of longitudinal ribs or rows of small hooks. The insertion area of the spines cannot be observed in any of the two specimens describe here (IGMp-880644; IGMp-880645). For this reason, their assignation to an anterior or posterior position is not possible.

Discussion and conclusion

Hybodont fin spines are unique in several aspects, allowing us to distinguish them from fin spines of other xenacanthoid, ctenacanthoid, holocephalan, among others chondrichthyans.[25,28,30] Some of the most important hybodont fin spine characters can be found in Maisey [25,28] and Cione et al. [13], including (a) spines are

elongated and gently curved posteriorly showing a typical oval shape in cross section; (b) posterior face strongly convex with denticles always present and arranged in a pair of longitudinal rows; (c) spine deeply penetrating myotome with a wide and long basal opening representing approximately 60% of the spine total length; and (d) several longitudinal ridges on the anterior and lateral faces, but not present in *Asteracanthus* Agassiz, 1837.[31] Specimen IGMp-880644 although incomplete could represent at least 50% of the entire spine (Figure 2(A)). Its wide and long basal opening, the two rows with hooks on the posterior side and the presence of longitudinal ribs (Figure 2(A)–(F)), allow us to refer this to a hybodont shark. Although the other two eroded and broken spine fragments assigned to IGMp-880645 preserve no diagnostic characters, they were found associated with the specimen IGMp-880644, likely belonging both to the same individual. Usually the identification of hybodont genera based on isolated fin spines could be difficult, especially if these are not in association with teeth. Also, as mentioned Rees [2], diagnosis of some

Mesozoic hybodonts genera, on the basis of isolated teeth, could sometimes be difficult and entire dentitions are often needed.

Among hybodonts from the Cretaceous of South America, only *Tribodus limae* is represented by articulated and semi-articulated specimens with fins specimens and teeth in association,[12,32] while its fine spines do not reach more than 125 mm in total length.[12,13] The size of the latter does not coincide with the large size of the specimens from Colombia. Other species as *Planohybodus marki* Pinheiro et al. [21], *Planohybodus* sp. and *Parvodus* sp., also reported from the Early Cretaceous of Brazil, are solely known by isolated teeth.[20,21]

One of the best preserved characters of the Colombian specimen IGMp-880644 is the two parallel rows of small hooks (without an evident groove between them) on the posterior side. The two hook rows of the Colombian specimens appear quite similar to those present on a fin spine of *Planohybodus peterboroughensis* Rees and Underwood [3], from the Middle Jurassic of England and deposited at the René Kindlimann private

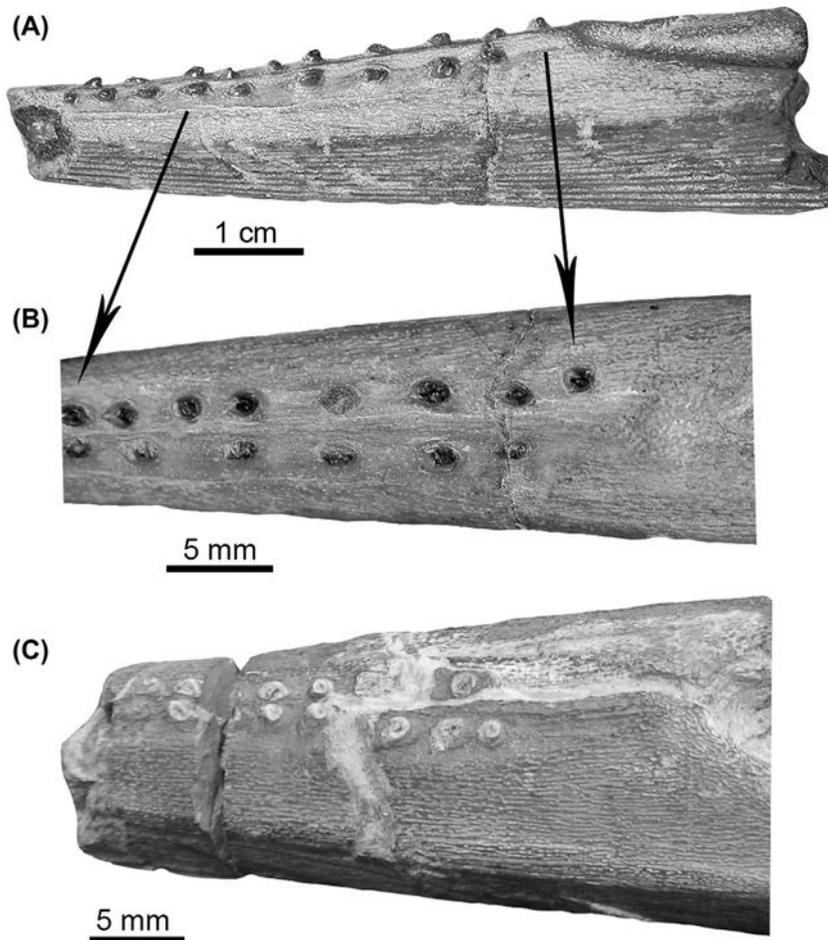


Figure 3. Parallel rows of hooks in Hybodont fin spines Middle Jurassic of England (A–B) and Lower Cretaceous of Colombia (C). Notes: (A–B) Specimen RK/5–255; (C) specimen IGMp-880644. Side view: right (A) and posterior (B–C).

collection (RK/5-255) (Figure 3(A) and (B)). The fin spines of the *P. peterboroughensis* (holotype P. 8386) illustrated by Rees and Underwood [3] exhibit two alternating rows of small hooks on their posterior side; however, they are missing the basal-most hook rows. Two parallel hook rows with also are present in the indeterminate hybodont fin spine illustrated by Cione et al. [13] from the Triassic–Jurassic of Argentina. This character has not been observed in fin spines of other hybodont genera that we have used for comparison. However, as has been suggested by Maisey [25], there is a considerable variation in the hook row distribution on the fin spines of hybodont sharks, whereas current knowledge about hybodont fin spine morphology and its importance in taxonomy remains scarce.

Due to the fragmentary condition and the absence of clearly diagnostic characters from the specimens described here from Rosablanca Formation, we refrain from any taxonomic identification to the generic level or below. We expect that future field expeditions and findings will offer more precise systematic information. Nevertheless, the presence of these hybodont remains in the Valanginian of Colombia expands the known, Lower Cretaceous, distribution of this shark group to cover the northwestern margin of Gondwana.

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