

A new hybodontiform shark (*Strophodus Agassiz 1838*) from the Lower Cretaceous (Valanginian-Hauterivian) of Colombia

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ABSTRACT

The vertebrate marine faunas that inhabited northern South America during the Cretaceous are still poorly known. This study is a contribution to a growing wave of new studies on Lower Cretaceous vertebrates from Colombia. Here we report and describe a new species of a hybodontiform shark of the genus *Strophodus*, which we named *Strophodus rebecca* sp. nov., based on isolated teeth, that were collected in Valanginian-Hauterivian rocks of the Rosa Blanca Formation (Carrizal and El Sapo Members) near the town of Zapatoca, Santander Department, Andes of Colombia. In addition, we describe two other fragmented teeth assigned to *Strophodus* sp. from the Rosa Blanca Fm. The new species from Colombia represents the only Cretaceous record of *Strophodus* from Gondwana, offering new insights into the paleogeographic distribution of the genus, as well as increasing the knowledge about the scarce hybodontiform paleodiversity known from South America. The presence of *Strophodus* in the Rosa Blanca Formation suggests that these durophagous (shell-crushing) fishes played an important role as predators of the abundant and diverse invertebrate fauna present in these ancient tropical coastal ecosystems of Gondwana.

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INTRODUCTION

Hybodontiform sharks were one of the dominant and most successful freshwater and marine chondrichthyan lineages during the Triassic and Jurassic, but their abundance and diversity began to decline during the Middle Jurassic, to finally become extinct at the end of the Cretaceous (*Kriwet & Benton, 2004; Rees, 2008; Rees & Underwood, 2008; Cappetta, 2012; Cuny, 2013*). The fossil record of hybodontiform sharks mostly represents teeth, cephalic and fin spines, and dermal denticles (*e.g., Cappetta, 2012*); although some articulated and delicately preserved specimens have also been reported (*Stumpf et al., 2021*, and references therein). Many hybodontiform species were described using isolated teeth and spines only, one example is the genus *Asteracanthus* (*Agassiz, 1837*), considered to be one of the most common hybodontiforms, given that teeth and spines traditionally referred

to this genus have been reported worldwide from Middle Triassic to Upper Cretaceous strata (Rees & Underwood, 2008; Cappetta, 2012; Szabó & Főzy, 2020; Stumpf et al., 2021; Stumpf, Meng & Kriwet, 2022). Agassiz (1837) named the type species *Asteracanthus ornatissimus* using isolated fin spines characterized by prominent stellate tubercles from the Upper Jurassic of England. Using some ornamental variations as differential characters, Agassiz (1837) also erected the species *Asteracanthus acutus*, *Asteracanthus minor* and *Asteracanthus semisulcatus*. This laid the foundation for the subsequent naming of many new species based only on isolated fin spines, whose validity has been ambiguous in many cases, particularly due to the lack of discrete morphological characters for use in species differentiation (see Stumpf et al., 2021). Later, Agassiz (1838) created the genus *Strophodus*, based on distinctive crushing-type teeth from the Jurassic of Europe. The discovery of isolated fin spines of *Asteracanthus* associated with *Strophodus* teeth in Jurassic sediments of England led Woodward (1889) to consider the latter genus as a junior synonym of *Asteracanthus*, a taxonomic scheme that has remained unquestioned for more than one century. Recently, Stumpf et al. (2021) reported a well-preserved and articulated hybodontiform skeleton from the Late Jurassic of Germany with a characteristic combination of tuberculate dorsal fin spines, characteristic of *Asteracanthus*, and multicuspid teeth (with resemblance to *Hybodus* Agassiz, 1837 and *Egertonodus* Maisey, 1987) that markedly differ from crushing-type teeth referred previously to this genus. This evidence led Stumpf et al. (2021) to propose *Asteracanthus* and *Strophodus* as two valid genera, which can be readily distinguished from each other by differences in both teeth and dorsal fin spine morphology. For more details about historical and taxonomic background, fossil record and diversity of *Asteracanthus*, see Stumpf et al. (2021).

The present contribution focuses on the description of a new species of *Strophodus* based on isolated teeth from the Rosa Blanca Formation (Fm.) (Valanginian-Hauterivian), Andes of Colombia (Figs. 1A–1B). The new material described herein represents the first Cretaceous record of the genus *Strophodus* from Gondwana. The new data shed additional light onto the scarce hybodontiform paleodiversity known from South America, which is represented by few reports from the Triassic and Jurassic of Argentina (Cione et al., 2002; Johns, Albanesi & Voldman, 2014), Upper Jurassic and Lower Cretaceous of Brazil (Pinheiro et al., 2013, and references therein), Upper Jurassic–?Lower Cretaceous of Uruguay (Soto, Perea & Toriño, 2012), and Lower Cretaceous of Colombia (Carrillo-Briceño et al., 2016). Additionally, two fragmented teeth assigned to *Strophodus* sp. from the Rosa Blanca Fm. are also described here.

MATERIAL & METHODS

Fossil collection

Most of the fossils described here were found isolated on the surface of biomicrites (wackestone) layers (Figs. 1C–1D) and very few of them appeared *in situ* inside the rocks. Although hybodontiforms occur along the entire sequence of the Carrizal and El Sapo Members of the Rosa Blanca Formation, they are particularly more abundant between layers (P^I to Y) of the Carrizal Member and between layers (A to J) of El Sapo

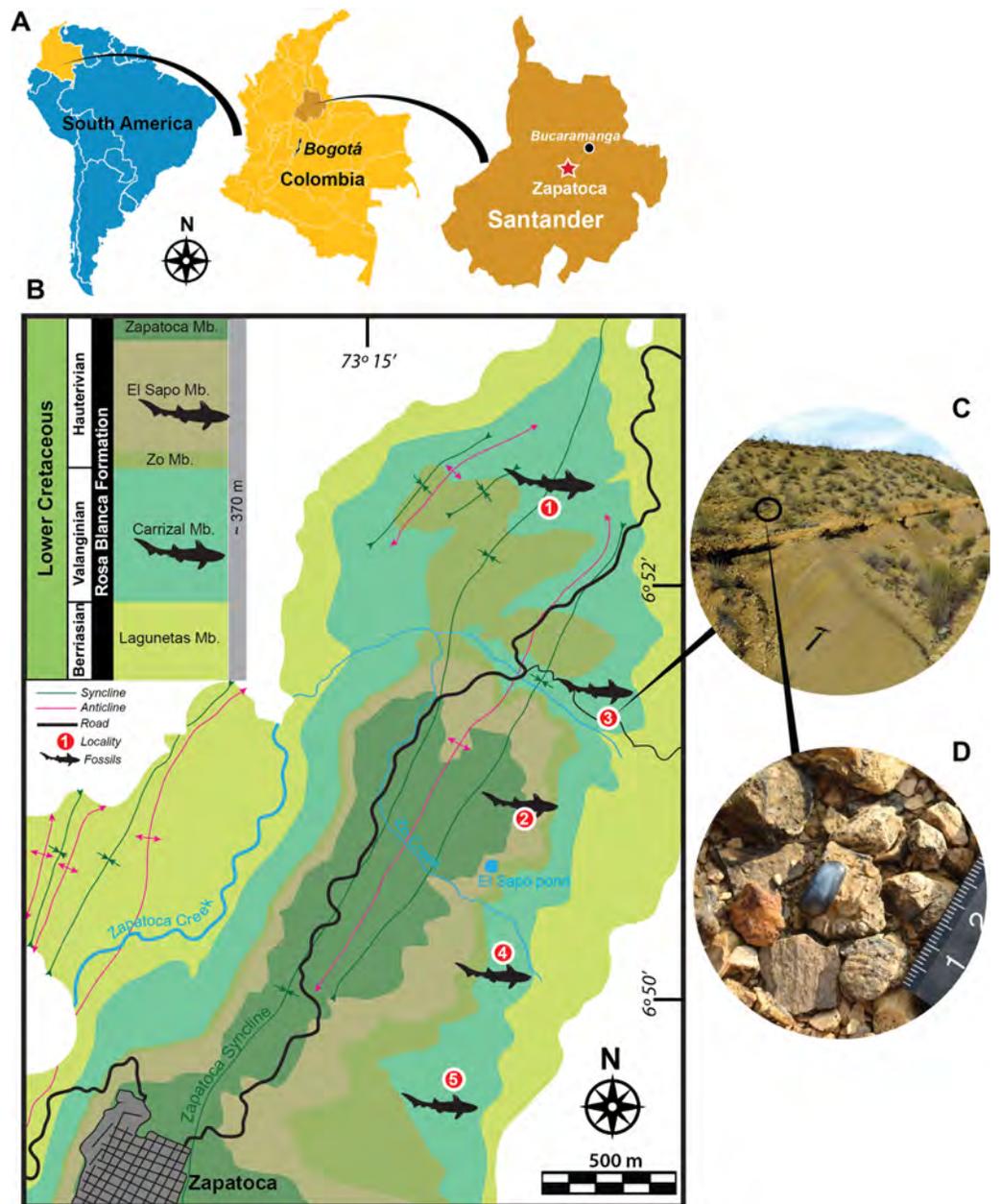


Figure 1 Geographical location, geological map and localities. (A) Geographical location. (B) Geological map of fossiliferous localities studies here of the Rosa Blanca Formation modified after *Etayo-Serna & Guzmán-Ospitia (2019)*. (C–D) Outcrop from Pico de la Vieja South locality, showing some isolated dental pycnodontiform fish remains. Fossiliferous localities: (1) La Virgen West, (2) El Sapo North, (3) Pico de la Vieja South, (4) El Sapo South, (5) El Caucho.

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Member, following the stratigraphic identification of *Etayo-Serna & Guzmán-Ospitia (2019)*. Field permits were obtained from the Servicio Geológico Colombiano, permit (No 20203800077871).

Fossil material

The fossil material described here belongs to the Paleontological Collection of the Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia. Most of the fossils were found relatively clean, for some of them rock matrix was carefully removed using a pneumatic air scribe. To preserve the fossils' integrity and original preservation we avoided applying any type of epoxy resins or consolidants.

Localities

Hybodontiform teeth were collected in five localities from two members of the Rosa Blanca Fm. (Fig. 1B). From the Carrizal Member, the following localities have been sampled: Pico de la Vieja South (6°51'19, 53"N, 73°13'57, 13"W), La Virgen West (6°52'24,61"N, 73°14'18,35"W), El Sapo South (6°24,61"N, 73°14'18,35"W), and the El Caucho (6°50'16,95"N, 73°14'56,82"W). The Carrizal Member corresponds to a shallow (~10 m depth) marine rock sequence, with abundant hardground *Thalassinoides* beds and decimetric wackestone beds alternating with calcareous mudstones; the total thickness is approximately 110 m; the age of this member, based on ammonoids (*Thurmanniceras pertransiens* and *Saynoceras verrucosum*), is Lower Valanginian-Upper Valanginian (*Etayo-Serna & Guzmán-Ospitia, 2019*). Only one specimen was sampled in the El Sapo North locality from the El Sapo member (6°50'43, 08"N, 73°14'29, 79"W). El Sapo Member is also a shallow marine sequence made of conspicuous *Thalassinoides* beds and decimetric wackestone alternating with terrigenous calcareous mudstone that indicate a major input of continental sediments in contrast to the Carrizal Member; the total thickness of the El Sapo member is approximately 80 m; the age for El Sapo Member based also on ammonoids (*Shasticrioceras anglicum*, *Bochianites kiliani*, *Oosterella colombiana* and *Olcostephanus boussingaultii*) is Lower Hauterivian (*Etayo-Serna & Guzmán-Ospitia, 2019*).

Comparisons

Taxonomic identification is based on an extensive bibliographical review and anatomical comparison with fossil specimens housed in the following Swiss collections: Natural History Museum of Basel (NMB); Palaeontological Institute and Museum at the University of Zurich (PIMUZ); JURASSICA Museum (MJSN) in Porrentruy, and René Kindlimann (RK) private collection with public access, Uster. Here we follow the proposal of *Stumpf et al. (2021)* to distinguish *Asteracanthus* and *Strophodus* as two valid genera. Systematic placement follows *Cappetta (2012)* and *Stumpf et al. (2021)*. Tooth descriptive terminology follows that of *Rees & Underwood (2008)*, *Leuzinger et al. (2017)*, *Szabó & Főzy (2020)*, and *Kumar et al. (2022)*.

Nomenclatural act

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature

(ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be accessed and the associated information viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The LSID for this publication is: urn:lsid:zoobank.org:pub:11ED37F2-6168-41CB-8DF3-AAE56976D9D6. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

RESULTS

Systematic paleontology

Class Chondrichthyes *Huxley, 1880*
 Subclass Elasmobranchii *Bonaparte, 1838*
 Order †Hybodontiformes *Patterson, 1966*
 Family †Acrodontidae *Casier, 1959*
 Genus †*Strophodus* *Agassiz, 1838*
 Type species †*Strophodus longidens* *Agassiz, 1838*

Strophodus recognized species.—Based on the list presented by *Stumpf, Meng & Kriwet (2022)* and the species recognized by *Szabó & Főzy (2020)*, *Kumar et al. (2022)*, and *Sharma & Singh (2021)*, *Strophodus* is represented by at least 12 species, which in stratigraphic order include: (1) *S. cf. reticulatus* *Agassiz, 1838* from the Middle Triassic of Switzerland (see *Rieppel, 1981*) and *S. reticulatus* from the Bathonian–Tithonian of England, France, Germany, Hungary and Switzerland (see *Stumpf, Meng & Kriwet, 2022* and references therein); (2) *S. smithwoodwardi* (*Peyer, 1946*) from the Toarcian of Switzerland; (3) *S. dunaii* (*Szabó & Főzy (2020)*), from the Aalenian of Hungary; (4) *S. tenuis* *Agassiz, 1838* from Aalenian–Bathonian strata of Germany and England (*Rees & Underwood, 2008*); (5) *S. longidens* (*Agassiz, 1838*) (type species) from the Bathonian of France; (6) *S. magnus* (*Agassiz, 1838*) from the Bathonian of England, France and India (*Rees & Underwood, 2008*; *Sharma & Singh, 2021*; *Rigal & Cuny, 2016*); (7) *S. indicus* (*Sharma & Singh, 2021*) from the Bathonian of India; (8) *S. jaisalmerensis* (*Kumar et al., 2022*) from the Bathonian of India; (9) *S. medius* (*Owen, 1869*) from the Bathonian–Callovian of France, England and India (*Rees & Underwood, 2008*; *Sharma & Singh, 2021*); (10) *S. subreticulatus* (*Agassiz, 1838*) from the Kimmeridgian of Switzerland; (11) *S. udulfensis* (*Leuzinger et al., 2017*) from the Kimmeridgian of Switzerland and possibly England (*Stumpf, Meng & Kriwet, 2022*); and (12) *S. tridentinus* (*Zittel, 1870*), from the Tithonian of Italy (considered as nomen dubium by *Szabó & Főzy, 2020*).

†*Strophodus rebecae* sp. nov.
(Figs. 2A1–2F4)

Etymology.—In honor of Rebeca Rueda, who charmingly has embraced different generations of geologists and paleontologists during fieldwork in Zapatoca.

Holotype.—UR-CP-0131 lateral tooth of indeterminate upper/lower jaw position (Figs. 2C1–2C5).

Type locality and horizon.—La Virgen West locality of the Carrizal Member, Rosa Blanca Fm. (Fig. 1B).

Referred material.—Five isolated teeth of indeterminate upper/lower jaw position. The sample includes two anterolateral teeth UR-CP-0129 (Figs. 2A1–2A4) and UR-CP-0130 (Figs. 2B1–2B4), and three lateral teeth UR-CP-0133 (Figs. 2F1–2F4); UR-CP-0135 (Figs. 2E1–2E4); UR-CP-0136 (Figs. 2D1–2D4). Differences between upper and lower dentition are poorly known in *Strophodus*, therefore distinguishing upper and lower teeth, especially using isolated elements, is a difficult task and is not supported.

Localities.—The specimens were collected from five localities (Fig. 1) of the Rosa Blanca Fm.: Carrizal Member (Pico de la Vieja South (UR-CP-0129), La Virgen West (UR-CP-0131), El Sapo South (UR-CP-0133), and El Caucho (UR-CP-0135, UR-CP-0136)), and the El Sapo Member (El Sapo North (UR-CP-0130)).

Diagnosis.—Species characterized by a typical crushing-type dentition with the following features: (1) Anterolateral teeth with a domed crown and a sub-rhomboidal shape in occlusal outline with vertical edges around their outline ornamented with irregular vertical ridges; (2) Relatively short lateral teeth (in comparison with other Jurassic species) with a parallelogram shape in occlusal outline, slightly domed in mesial section, with a pointed and lingually oriented mesial extremity, and labial and lingual vertical edges around their outline ornamented with irregular vertical ridges; (3) Anterolateral and lateral teeth with an occlusal ornamentation characterized by a reticulated pattern finely-pitted and without a crest.

Description.—The two anterolateral teeth UR-CP-0129 (13.84 mm length, 9.20 mm width) and UR-CP-0130 (12.06 mm length, 11.3 mm width) are elongated and have sub-rhomboidal shape in occlusal outline (Figs. 2A1–2B4). The crown is domed more towards its central part, and the occlusal ornamentation consist of a reticulated pattern finely-pitted, which is present from the top of dome to the upper limit of the edges. A weak crest in the mesial section of the crown and lingually displaced is visible only in UR-CP-0129 (Fig. 2A1), which may possibly reflect a sexual or positional variation between the lower and upper jaws, without ruling out that the absence of this character in UR-CP-0130 could also be due the result of functional wear. The crown is separated from the root by a shallow groove, overhanging it by vertical edges around the outline (edge angle approximately 90° with respect to the occlusal surface) which are ornamented with irregular vertical ridges. The root is preserved only in UR-CP-0129, part of this is still embedded in the matrix, and it seems to have double the height of the crown; some perforations (foramina) of varying size can be observed.

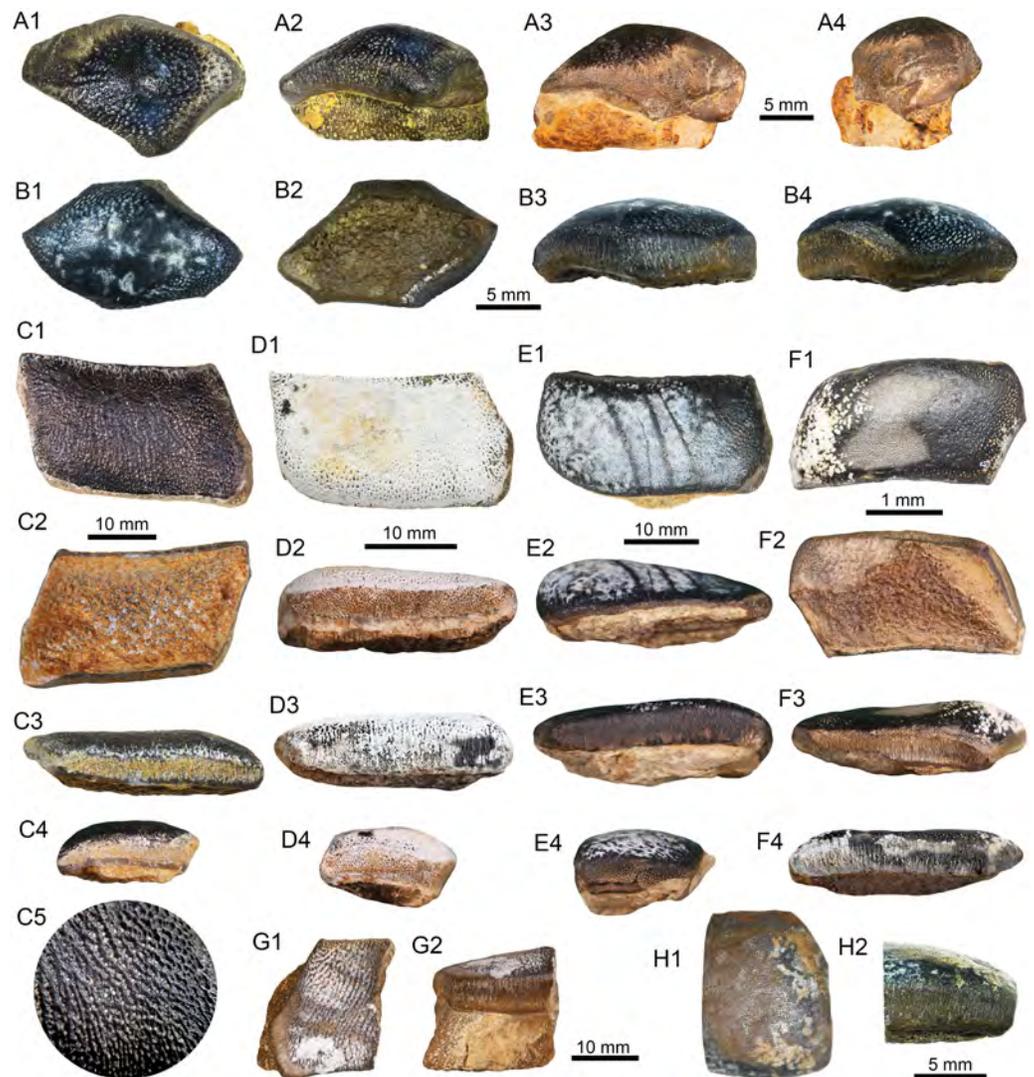


Figure 2 Teeth of *Strophodus rebecae* sp. nov. and *Strophodus* sp. from the Rosa Blanca Formation. (A1–B4) Anterolateral teeth (A1–A4): UR-CP-0129; (B1–B4): UR-CP-0130). (C1–F4). Lateral teeth (C1–C5): holotype UR-CP-0131; (D1–D4): UR-CP-0136; (E1–E4): UR-CP-0135; (F1–F4): UR-CP-0133). (C5). Close-up of the occlusal ornamentation in the holotype UR-CP-0131. (G1–H2). Fragmented lateral teeth of *Strophodus* sp. (G1–G2): UR-CP-0134; H1–H2: UR-CP-0132). View: basal (B2, C2, F2), distal (A4), labial (A3, D2, E2, F3, G2), lingual (C3, D3, E3, F4, H2), occlusal (A1, B1, C1, D1, E1, F1, C5, G1, H1), mesial (C4, D4, E4), mesio-labial (B4), mesio-lingual (A2, B3).

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Lateral teeth are represented by the holotype UR-CP-0131 (26.94 mm length, 16 mm width, Figs. 2C1–2C5), and UR-CP-0133 (31.82 mm length, 18.2 mm width), UR-CP-0135 (32.72 mm length, 15.13 mm width), and UR-CP-0136 (28.46 mm length, 16.02 mm width), all with well-preserved crowns but no roots (Figs. 2D1–2F4). All the lateral teeth are larger than the anterolateral ones described above, and a parallelogram shape in occlusal outline characterizes them. The crown has labial and lingual vertical edges (edge angle approximately 90° with respect to the occlusal surface) parallel to each other,

although the latter are slightly more concave. A sharp pointed and lingually oriented mesial extremity is present. The mesial part becomes slightly domed and no crest is visible. Although the root is not preserved in any of the lateral teeth, based on the preserved root of the anterolateral tooth UR-CP-0129 (Figs. 2A2–2A3) and the fragmented lateral tooth referred below as *Strophodus* sp. (Figs. 2G1–2G2), it is evident that the crown was overhanging the root by vertical edges which, in most cases, are ornamented with irregular vertical ridges. As in anterolateral teeth, the occlusal ornamentation consists of a reticulated pattern finely-pitted, and which is present from the top of the domed area to the upper limit of the edges (Fig. 2C5). In the holotype UR-CP-0131, the ornamentation is well preserved, while it shows signs of functional wear in other specimens.

Differential diagnosis.—Following [Stumpf et al. \(2021\)](#), species based on teeth and previously assigned to the genus *Asteracanthus*, but possibly referable to *Strophodus* are considered here for comparisons. Assuming this, we compare our specimens from Colombia with the at least 12 recognized *Strophodus* species from the Jurassic of Europe and India ([Rees & Underwood, 2008](#); [Szabó & Főzy, 2020](#); [Kumar et al., 2022](#); [Sharma & Singh, 2021](#); [Stumpf, Meng & Kriwet, 2022](#)). In this regard, our new species from the Lower Cretaceous of Colombia can be distinguished from the following European and Asian species by the differences presented below. (1) *Strophodus rebecae* sp. nov. differs from *S. reticulatus* from the Middle Triassic and Middle Jurassic of Europe (regarded as invalid junior synonyms of *A. ornatissimus* by [Woodward \(1889\)](#), see [Stumpf et al. \(2021\)](#)), in having thinner and mesio-distally less elongate anterolateral and lateral teeth lacking an occlusal crest with a strong ornamentation characterized by radiating ridges ([Agassiz, 1838](#), plate 17; [Stumpf et al., 2021](#), figs. 7S–7U). The specimen referred by [Rieppel \(1981\)](#) to *S. cf. reticulatus* from the Middle Triassic of Switzerland appears to be readily differentiated from all other *Strophodus* species by possessing a higher number of anterior tooth files ([Stumpf, pers. comm., 2022](#)). (2) *Strophodus rebecae* sp. nov. differs from *S. dunaii* from the Aalenian of Hungary by having less rectangular lateral teeth in occlusal outline, lacking the strong ornamentation of branching ridges and the low and wide labially oriented transverse ridge that characterize *S. dunaii* (see [Szabó & Főzy, 2020](#), figs. 2–3). (3) *Strophodus rebecae* sp. nov. can be distinguished from *S. tenuis* from the Aalenian–Bathonian strata of England and southern Germany mainly by the presence, in the latter, of mesio-distally more elongate and more slender anterolateral and lateral teeth with a sigmoid curvature in occlusal outline and well developed and asymmetrically situated domed areas (see [Agassiz, 1838](#), plate 18, figs. 16–25). (4) *Strophodus rebecae* sp. nov. differs from *S. longidens* from the Bathonian of northern France, mainly for having mesio-distally less elongate anterolateral and lateral teeth; information on the teeth ornamentation was not described for the *S. longidens* holotype, which was destroyed during the Second World War (see [Szabó & Főzy, 2020](#)). (5) *Strophodus rebecae* sp. nov. differs from *S. magnus* from the Bathonian of England, France and India by having clearly lateral teeth that are mesio-distally less elongate (see [Agassiz, 1838](#), tab. 18, figs. 11–15; [Rees & Underwood, 2008](#), plate 5, figs. 1–11; [Rigal & Cuny, 2016](#), fig. 1; [Sharma & Singh, 2021](#), figs. 5–6). The reticulate and finely-pitted ornament pattern observed in the new species from Colombia resembles the ornamentation of *S. magnus*. (6) *Strophodus rebecae* sp. nov. differs from *S. indicus* from the Bathonian of

India by having mesio-distally less elongated lateral teeth and the lack of an ornamentation characterized by enameloid folds forming ridge and groove structure (see [Sharma & Singh, 2021](#)). (7) *Strophodus rebecae* sp. nov. can be distinguished from *S. jaisalmerensis* from the Bathonian of India by having mesio-distally less elongated anterolateral and lateral teeth, especially the lateral ones having a more concave lingual side and a sharper-pointed and lingually oriented mesial extremity. (8) *Strophodus rebecae* sp. nov. differs from *S. medius* from the Bathonian–Callovian of England, France, and India (see [Rees & Underwood, 2008](#); [Sharma & Singh, 2021](#)) by having less mesio-distally elongated anterolateral and lateral teeth, and a less convex and domed crown in lateral teeth that becomes flat in its most distal part. (9) If *Strophodus subreticulatus* from the Kimmeridgian of Switzerland is considered a valid species (because [Woodward \(1889\)](#) also regarded it erroneously as a junior synonym of *A. ornatissimus* (see [Stumpf et al., 2021](#))), it can be differentiated of *S. rebecae* sp. nov., by the mesio-distally less elongate lateral teeth with more rectilinear edges in occlusal outline (see [Agassiz, 1838](#), tab. 18, figs. 5–10). (10) *Strophodus rebecae* sp. nov. differs from *S. udulfensis* from the Kimmeridgian of Switzerland and possibly England ([Stumpf, Meng & Kriwet, 2022](#)), by having less mesio-distally elongated anterolateral and lateral teeth with less convex and domed crown and lacking the strong reticulated ornamentation that characterize *S. udulfensis*. (11) *Strophodus rebecae* sp. nov. can be differentiated from *S. tridentinus* from the Tithonian of Italy (considered as nomen dubium by [Szabó & Főzy, 2020](#)) by having lateral teeth with a less rectangular outline, a more projected and lingually oriented mesial extremity, and the lack of an occlusal crest rising a complex system of diverging folds (see [Szabó & Főzy, 2020](#)). (12) The closest tooth morphology to *Strophodus rebecae* sp. nov., was noticed in *S. smithwoodwardi* from the Toarcian of Switzerland. Anterolateral and lateral teeth in both species are relatively similar in occlusal outline and thickness of the crown. Nevertheless, lateral teeth in our specimens from Colombia lack the ornamentation pattern present in *S. smithwoodwardi* (see [Peyer, 1946](#), plate 2–3), for which it should not be ruled out that this condition could be the result of functional wear. In the new species from Colombia both labial and lingual marginal edges tend to be vertical and well developed around the tooth outline and ornamented with irregular vertical ridges, while in all the specimens of *S. smithwoodwardi* that we have compared, the labial edge of the crown tends to be angled (acute angle) in profile view with a characteristic smooth surface. Like in *Strophodus rebecae* sp. nov., lingual edges *S. smithwoodwardi* tend to be vertical, well developed and ornamented with irregular vertical ridges. Although the Colombian specimens and *S. smithwoodwardi* teeth seem to be very close in morphology they are most likely different taxa, as they are separated by at least ~50 million years; moreover, they were also separated by a great geographical distance.

DISCUSSION

The fossil record of Mesozoic chondrichthyans from the northernmost part of South America is scarce and mostly represented by lamniforms and ptychodonts remains from Colombia ([Reinhart, 1951](#); [Brito & Janvier, 2002](#); [Carrillo-Briceño et al., 2016](#); [Carrillo-Briceño, Parra & Luque, 2019](#); [Niño García, Parra-Mosquera & Macias-Villarraga, 2019](#))

and Venezuela (Moody & Maisey, 1994; Carrillo-Briceño et al., 2008; Carrillo-Briceño, 2009; Carrillo-Briceño, 2012; Carrillo-Briceño & Spencer, 2013; Guinot & Carrillo-Briceño, 2018), although a single report of a hybodontiform shark based on an isolated dorsal fin spine was also reported for the Rosa Blanca Fm. (Carrillo-Briceño et al., 2016). Hybodontiform reports in South America are also scarce, with some articulated and semi-articulated specimens of *Tribodus limae* (Brito & Ferreira, 1989), from the Lower Cretaceous of Brazil, and isolated teeth and cephalic and dorsal fin spines, from the Triassic and Jurassic of Argentina (Cione et al., 2002; Johns, Albanesi & Voldman, 2014), Upper Jurassic and Lower Cretaceous of Brazil (Woodward, 1888; Pinheiro et al., 2011; Pinheiro et al., 2013; Silva et al., 2011; Cupello et al., 2012), and Upper Jurassic-?Lower Cretaceous of Uruguay (Soto, Perea & Toriño, 2012). In this case, *Strophodus rebecca* sp. nov., from the Lower Cretaceous of Colombia represents the first report for the genus in the Americas. Previously, Bryant (1914) described *Strophodus shastensis* from the Upper Triassic of California in North America, which later was assigned to *Asteracanthus shastensis* by Jordan & Hannibal (1923); nevertheless, this species is currently recognized within the genus *Palaeobates* (Meyer, 1849) (Cuny, Rieppel & Sander, 2001; Cappetta, 2012; Pla, Márquez-Aliaga & Botella, 2013). Other reports of *Asteracanthus* from North America are restricted only to isolated fin and cephalic spines (e.g., Leidy, 1873; Miller, 1968; Baird & Horner, 1979).

As previously referenced in the differential diagnosis section, anterolateral and lateral teeth of *Strophodus rebecca* sp. nov., can be differentiated from at least 12 *Strophodus* species recognized from the Jurassic of Asia and Europe (Agassiz, 1838; Peyer, 1946; Goto, Kuga & Hachiya, 1991; Michelis et al., 1996; Rees & Underwood, 2008; Citton et al., 2019; Szabó & Főzy, 2020; Kumar et al., 2022; Sharma & Singh, 2021; Stumpf, Meng & Kriwet, 2022, and references therein). In reference to ?*Asteracanthus biformatus* (Kriwet, 1995) from the Upper Jurassic of Portugal, this species was described based on cephalic and fin spines, though an isolated tooth was reported as ?*A. biformatus* (Kriwet, 1995, plate 1, fig 3). Stumpf et al. (2021) questions the validity of *A. biformatus*, like that of other described species that were identified based only on isolated fin spines due to the lack of discrete morphological characters for use in species differentiation. Szabó & Főzy (2020) also considered *A. biformatus* as a nomen dubium due to the poor preservational condition of the tooth assigned to this species. We share the opinion of Szabó & Főzy (2020) with respect to the bad preservational conditions of the isolated tooth of *A. biformatus*. However, the possibility that this tooth could belong to *Strophodus* should not be ruled out, and future work on that material or future findings could offer new insights on this. We also agree with the opinion of Szabó & Főzy (2020) regarding the validity of *Strophodus normanianus* (Dollfus, 1863), and the validity as comparative material of *Asteracanthus* (?*Strophodus*) *somaensis* Yabe, 1902, from Japan due to poor illustrations of the material. Although here we do not present a descriptive comparison with teeth referred to open nomenclature, our specimens from Colombia, especially lateral teeth, look different to those of indeterminate *Strophodus* species from the Jurassic of Madagascar (Priem, 1907), Europe (e.g., Peyer, 1946; Kriwet, Rauhut & Gloy, 1997; Vincent et al., 2013; Wills et al., 2019), and Asia (Goto, Kuga & Hachiya, 1991; Cuny, Suteethorn & Kamha, 2005; Cuny et al., 2009). Although the lateral tooth of *Strophodus* sp. illustrated by Cuny, Suteethorn & Kamha (2005, fig. 4),

from the Jurassic of Thailand could resemble in its occlusal outline the lateral teeth of *Strophodus rebecca* sp. nov. Additionally, there is an unnamed species of *Strophodus* from the Tithonian of Germany, a specimen represented possibly by the most complete associated set of jaws with teeth, which was described by [Pfeil \(2011\)](#) as *Asteracanthus* sp. The anterolateral and lateral teeth of this unnamed *Asteracanthus* species appear to be similar in shape (occlusal outline) to the teeth of *Strophodus rebecca* sp. nov. (see [Pfeil, 2011](#), figs. 7–8). However, it can be noticed that lateral teeth in *Strophodus rebecca* sp. nov. have more concave lingual edges, while in the specimen from the Tithonian of Germany the lingual edges in lateral teeth seem to be straight ([Pfeil, 2011](#), figs. 7–8). Better preparation and future detailed descriptions in the specimen from the Tithonian of Germany might be necessary to define the diagnostic characters of that unnamed species. It is important to note that [Pfeil \(2011\)](#) regarded the monospecific genus *Bdellodus* [Quenstedt, 1882](#), from the Toarcian of Germany, as a junior synonym of *Strophodus* (= *Asteracanthus*). In our opinion, this assumption suggested by [Pfeil \(2011\)](#) should be taken with caution, this is because the teeth of *Bdellodus bollensis* [Quenstedt, 1882](#), seem to have a morphology and a dental pattern (specially in lateral teeth) completely different from that observed in *Strophodus*.

In reference to Cretaceous reports of *Strophodus* (= *Asteracanthus* sp.), its record is relatively scarce in comparison to those from the Jurassic (e.g., [Yabe, 1902](#); [Priem, 1907](#); [Peyer, 1946](#); [Goto, Kuga & Hachiya, 1991](#); [Goto, Uyeno & Yabumoto, 1996](#); [Cuny, Suteethorn & Kamha, 2005](#); [Cuny et al., 2007](#); [Cuny et al., 2009](#); [Cuny et al., 2014](#); [Rees & Underwood, 2008](#); [Vincent et al., 2013](#); [Rigal & Cuny, 2016](#); [Romano et al., 2018](#); [Wills et al., 2019](#); [Szabó & Főzy, 2020](#); [Kumar et al., 2022](#); [Sharma & Singh, 2021](#)), and references therein). Most of the *Strophodus* records from the Cretaceous have been reported as indeterminate species from the Valanginian–Albian range of Europe, including England ([Batchelor & Ward, 1990](#)), France ([Priem, 1912](#); [Guinot, Cappetta & Adnet, 2014](#)), and Switzerland ([Pictet & Campiche, 1858](#); [Peyer, 1946](#)), and these teeth look different to those of *Strophodus rebecca* sp. nov. Recently [Sokolskyi & Guinot \(2021\)](#) suggest a pending taxonomic status for *Asteracanthus* (= *Sphaenonchus*) *compressus* [Rogovich, 1860](#), from Albian deposits of Ukrainian due to the disappearance of the holotype. The only existing evidence of *A. (= Sphaenonchus) compressus* is illustrated in [Rogovich \(1860, pl. 1, figs. 9–10\)](#), which shows what appear to be tooth fragments and the base of a cephalic spine. [Sokolskyi & Guinot \(2021\)](#) considered this species name as valid pending further sampling and/or information on the whereabouts of the missing specimen, which would be essential to clarify the taxonomy of this dubious species. *Asteracanthus aegyptiacus* [Stromer, 1927](#), from the Late Cretaceous of Africa, was described based on isolated dorsal and cephalic spines; but recently, [Michaut \(2017\)](#), using a great number of isolated fin and cephalic spines and teeth from the Maastrichtian of Niger, attempted to reconstruct the dentition of this species. However, the assignment of this material to *Asteracanthus*, or even *Strophodus* should be taken with caution, because the dental morphology of *A. aegyptiacus* seems to be very different from the two above mentioned taxa. [Batchelor & Ward \(1990\)](#) had already suggested that *A. aegyptiacus* has teeth that differ significantly from those of *Asteracanthus* and *Strophodus*. Recently [Stumpf et al. \(2021\)](#) noticed that *A. aegyptiacus*

exhibits a unique ornamentation pattern in its spines (see [Stromer, 1927](#); [Cappetta, 1972](#); [Werner, 1989](#)), that differs from that observed in stratigraphically older fin spines referred to *Asteracanthus*, thus making a positive referral to the later genus unlikely. According to [Stumpf et al. \(2021\)](#) *A. aegyptiacus* spines co-occur with those attributed to *Hybodus* as well as teeth of distobatid taxa. This could suggest that *A. aegyptiacus* could be congeneric with one of the co-occurring distobatid species of the Late Cretaceous of Africa, for example *Distobatus* [Werner, 1989](#), and *Aegyptobatus* [Werner, 1989](#). Taking into consideration all of this mentioned above, *Strophodus rebecae* sp. nov. could be tentatively considered the only valid Cretaceous species and the only record of the genus from Gondwana at the time. The known reports of *Strophodus* from the Cretaceous of Europe and South America suggest tentatively that the youngest record of the genus in both continents could be ?Albian in age (see [Pictet & Campiche, 1858](#); [Priem, 1912](#); [Peyer, 1946](#); [Batchelor & Ward, 1990](#); [Guinot, Cappetta & Adnet, 2014](#)).

Two fragmented and non-diagnostic lateral teeth from the Rosa Blanca Fm. are tentatively assigned here to *Strophodus* sp. (UR-CP-0132, [Figs. 2H1–2H4](#), and UR-CP-0134, [Figs. 2G1–2G2](#), from La Virgen West and El Sapo South localities, respectively). Although these specimens could belong to *Strophodus rebecae* sp. nov., their poor state of preservation does not allow us to diagnose these specimens. *Strophodus rebecae* sp. nov., corresponds to the second record of a hybodont shark from the Rosa Blanca Fm., since two large dorsal fin spines of an indeterminate species of ?*Asteracanthus* were reported by [Carrillo-Briceño et al. \(2016\)](#) from another locality (El Alto) different from where the specimens describe here come. An accurate taxonomical assignment for these two isolated dorsal fin spines is not possible due to their poor state of preservation. However, since *Strophodus* most likely had tuberculate fin spines ([Stumpf et al., 2021](#)), the material described by [Carrillo-Briceño et al. \(2016\)](#) combined with the *Strophodus* teeth described here, might indicate the presence of at least two distinct hybodontiforms in the Rosa Blanca Fm.

The presence of *Strophodus rebecae* sp. nov. increases the paleodiversity known for this geological unit. Other vertebrates reported for the Rosa Blanca Fm., particularly from the surrounding areas of the Zapatoca town, include indeterminate fish remains ([Cadena, 2011a](#); [Benavides-Cabra & Páramo-Fonseca, 2020](#)), turtles ([Cadena & Gaffney, 2005](#); [Cadena, 2011a](#); [Cadena, 2011b](#); [Cadena, 2020](#); [Cadena, Jaramillo & Bloch, 2013](#)), pterosaurs ([Cadena, Unwin & Martill, 2020](#)), ichthyosaurs and elasmosaurid remains ([Cadena, 2011a](#); [Benavides-Cabra & Páramo-Fonseca, 2020](#)), and reported but not fully described material of a metriorhynchoid crocodylomorph ([Larsson, 2012](#)). Abundant dental and cranial remains of indeterminate pycnodont fishes (see [Fig. 1D](#)) were collected by one of the authors (E-AC) from the La Virgen West, Pico de la Vieja South, El Caucho, and El Sapo North and South localities of the Rosa Blanca Fm. and are currently under study. The Rosa Blanca Fm. ([Figure 3](#)) has been interpreted as shallow marine deposits ([Etayo-Serna & Guzmán-Ospitia, 2019](#); [Guzmán-Ospitia, 1985](#)). For this reason, it is not unreasonable to suggest that *Strophodus rebecae* sp. nov., was a species adapted to purely marine conditions, as has been reported for the other species of the genus, although freshwater-influenced isotopic composition was found in some *Strophodus* teeth of the Jurassic of Switzerland ([Leuzinger et al., 2015](#)). The trophic structure of the Central



Figure 3 Life reconstruction of *Strophodus rebecca* sp. nov. The marine paleoenvironment of the Rosa Blanca Formation during the Valanginian-Hauterivian. Art illustration of the shark by Jorge Blanco.

Full-size  DOI: [10.7717/peerj.13496/fig-3](https://doi.org/10.7717/peerj.13496/fig-3)

Atlantic Ocean at the northernmost portion of South America during the Valanginian and Hauterivian is still poorly known. Durophagous hybodontiform sharks, as well as other shell-crushing fishes like pycnodontiforms, must have played an important ecological role as predators in these ancient tropical coastal ecosystems, due to the abundant and diverse invertebrate fauna present at the Carrizal and El Sapo members, similar to proposals for other Cretaceous and Jurassic faunas (*Kriwet, 2001; Cawley et al., 2021; Cooper & Martill, 2020*).

CONCLUDING REMARKS

Strophodus rebecca sp. nov. from the Valanginian-Hauterivian of Colombia undoubtedly represents the only Cretaceous record of the genus from Gondwana, filling a gap in the knowledge of the paleodiversity and geographic distribution of this group of hybodontiforms outside of Europe during the Cretaceous. Additionally, this new record offers new insights into the scarce hybodontiforms paleodiversity known from South America. Paleoenvironmental inferences from the Rosa Blanca Fm. suggest that this species was adapted to marine environments, with a typical crushing-type dentition that may have allowed it to play an important role as a durophagous predator in this ancient tropical coastal ecosystem. The known fossil record of *Strophodus* from the Cretaceous of Europe and South America suggests that the youngest record of the genus could be ?Albian in age.

Institutional abbreviations

UR-CP Paleontological collection, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia

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Author Contributions

- Jorge D. Carrillo-Briceño conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Edwin-Alberto Cadena conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

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Data Availability

The following information was supplied regarding data availability:

All data is included in the article and figures.

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REFERENCES

- Agassiz LJR. 1837.** *Recherches sur les Poissons fossiles*. 2. Neuchâtel: Imprimerie de Petitpierre.
- Agassiz LJR. 1838.** *Recherches sur les Poissons fossiles*. 3. Neuchâtel: Imprimerie de Petitpierre.
- Baird D, Horner JR. 1979.** Cretaceous dinosaurs of North Carolina. *The Journal of the North Carolina State Museum of Natural History* **2**:1–28.
- Batchelor TJ, Ward DJ. 1990.** Fish remains from a temporary exposure of Hythe Beds (Aptian-Lower Cretaceous) near Godstone, Surrey. *Mesozoic Research* **2**:181–203.
- Benavides-Cabra CD, Páramo-Fonseca ME. 2020.** Primer reporte de plesiosauroides no elasmosauridos del Cretácico de Colombia, provenientes de la Formación Rosablanca en Zapatoca, Santander. I Congreso Colombiano de Paleontología.
- Bonaparte CL. 1838.** Selachorum tabula analytica. *Nuovi Annali della Science Naturali Bologna* **1**:195–214.
- Brito PMM, Ferreira PLN. 1989.** The first Hybodont shark, *Tribodus limae* n. gen. n. sp. from the Lower Cretaceous of Chapada do Araripe (North-East Brazil). *Anais da Academia Brasileira de Ciências* **61**(1):53–57.
- Brito PMM, Janvier P. 2002.** A ptychodontid (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of South America. *Geodiversitas* **24**(4):785–790.
- Bryant HC. 1914.** Teeth of a cestraciodont shark from the Upper Triassic of Northern California: University of California Publications. *Bulletin of the Department of Geology* **8**:27–30.
- Cadena E-A. 2011a.** Potential earliest record of podocnemidoid turtles, from the Early Cretaceous (Valanginian) of Colombia. *Journal of Paleontology* **85**:877–881 DOI [10.1666/10-097.1](https://doi.org/10.1666/10-097.1).
- Cadena E-A. 2011b.** First record of eucryptodiran turtles from the Early Cretaceous (Valanginian), at the northernmost part of South America. *South American Journal of Herpetology* **6**(1):49–53 DOI [10.2994/057.006.0107](https://doi.org/10.2994/057.006.0107).
- Cadena E-A. 2020.** Valanginian occurrence of Pelomedusoides turtles in northern South America: revision of this hypothesis based on a new fossil remain. *PeerJ* **8**:e9810 DOI [10.7717/peerj.9810](https://doi.org/10.7717/peerj.9810).

- Cadena E-A, Gaffney ES. 2005.** *Notoemys zapatoensis*, a new side-necked turtle (Pleurodira Platycheilyidae) from the Early Cretaceous of Colombia. *American Museum Novitates* **3470**:1–19 DOI [10.1206/0003-0082\(2005\)470<0001:NZANST>2.0.CO;2](https://doi.org/10.1206/0003-0082(2005)470<0001:NZANST>2.0.CO;2).
- Cadena E-A, Jaramillo CA, Bloch JI. 2013.** New material of the platycheilyid turtle *Notoemys zapatoensis* from the Early Cretaceous of Colombia; implications for understanding Pleurodira evolution. In: Brinkman DB, Holroyd PA, Gardner JD, eds. *Morphology and evolution of turtles*. Dordrecht: Springer, 105–120.
- Cadena E-A, Unwin D, Martill DM. 2020.** Early Cretaceous pterosaurs from Colombia. *Cretaceous Research* **114**:104526 DOI [10.1016/j.cretres.2020.104526](https://doi.org/10.1016/j.cretres.2020.104526).
- Cappetta H. 1972.** Les Poissons crétacés et tertiaires du bassin des Iullemmeden (République du Niger). *Palaeovertebrata* **5(5)**:179–251.
- Cappetta H. 2012.** Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: *Handbook of paleoichthyology*. Munich: Verlag Dr. Friedrich Pfeil.
- Carrillo-Briceño JD. 2009.** Presencia del genero *Ptychodus* (Elasmobranchii: Ptychodontiade) en el Cretácico superior de los Andes de Trujillo Venezuela. *Geominas* **37(50)**:207–210.
- Carrillo-Briceño JD. 2012.** Presencia de *Ptychodus mortoni* (Elasmobranchii: Ptychodontidae) en el Cretácico Superior de Venezuela. *Revista Geologica de América Central* **46**:145–150.
- Carrillo-Briceño JD, Ayala R, Chávez-Aponte EO, González-Barba G. 2008.** Registro de *Serratolamna serrata* (Elasmobranchii: Serratolamnidae) en el Cretácico Superior (Maestrichtiense) de los Andes Venezolanos. *Geominas* **36(47)**:160–163.
- Carrillo-Briceño JD, Cadena EA, Dececchi AT, Larson HCE, Du TY. 2016.** First record of a hybodont shark (Chondrichthyes: Hybodontiformes) from the Lower Cretaceous of Colombia. *Neotropical Biodiversity* **2(1)**:81–86 DOI [10.1080/23766808.2016.1191749](https://doi.org/10.1080/23766808.2016.1191749).
- Carrillo-Briceño JD, Parra JD, Luque J. 2019.** A new lamniform shark *Protolamna ricaurtei* sp. nov. from the Lower Cretaceous of Colombia. *Cretaceous Research* **95**:336–340 DOI [10.1016/j.cretres.2018.12.007](https://doi.org/10.1016/j.cretres.2018.12.007).
- Carrillo-Briceño JD, Spencer LG. 2013.** The first tooth set of *Ptychodus atcoensis* (Elasmobranchii: Ptychodontidae), from the Cretaceous of Venezuela. *Swiss Journal of Paleontology* **132**:69–75 DOI [10.1007/s13358-013-0053-3](https://doi.org/10.1007/s13358-013-0053-3).
- Casier E. 1959.** Contributions à l'étude des Poissons fossils de la Belgique, XII –Sélaciens et Holocéphales sinémuriens de la Province de Luxembourg. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **38(8)**:1–35.
- Cawley JJ, Marramà G, Carnevale G, Villafaña JA, López-Romero FA, Kriwet J. 2021.** Rise and fall of †Pycnodontiformes: diversity, competition and extinction of a successful fish clade. *Ecology and Evolution* **11**:1769–1796 DOI [10.1002/ece3.7168](https://doi.org/10.1002/ece3.7168).
- Cione AL, Acosta Hospitaleche C, Mennucci J, Cocca S. 2002.** The first shark from the Triassic-Jurassic of South America. *Neues Jahrbuch fur Geologie und Palaontologie Monatshefte* **1**:9–18.
- Citton P, Fabbi S, Cipriani A, Jansen M, Romano M. 2019.** Hybodont dentition from the Upper Jurassic of Monte Nerone Pelagic Carbonate Platform (Umbria Marche

- Apennine, Italy) and its ecological implications. *Geological Journal* **54**(1):278–290 DOI [10.1002/gj.3174](https://doi.org/10.1002/gj.3174).
- Cooper SLA, Martill DM. 2020.** Pycnodont fishes (Actinopterygii, Pycnodontiformes) from the Upper Cretaceous (lower Turonian) Akrabou Formation of Asfla, Morocco. *Cretaceous Research* **116**:104607 DOI [10.1016/j.cretres.2020.104607](https://doi.org/10.1016/j.cretres.2020.104607).
- Cuny G. 2013.** *Requins -De la préhistoire à nos jours*. Paris: Belin.
- Cuny G, Liard R, Deesri U, Liard T, Khamha S, Suteethorn V. 2014.** Shark faunas from the Late Jurassic—Early Cretaceous of northeastern Thailand. *Paläontologische Zeitschrift* **88**(3):309–328 DOI [10.1007/s12542-013-0206-0](https://doi.org/10.1007/s12542-013-0206-0).
- Cuny G, Rieppel O, Sander PM. 2001.** The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada. *Zoological Journal of the Linnean Society* **133**(3):285–301 DOI [10.1111/j.1096-3642.2001.tb00627.x](https://doi.org/10.1111/j.1096-3642.2001.tb00627.x).
- Cuny G, Srisuk P, Khamha S, Suteethorn V, Tong H. 2009.** A new elasmobranch fauna from the Middle Jurassic of southern Thailand. *Geological Society of London, Special Publications* **315**:97–113 DOI [10.1144/SP315.8](https://doi.org/10.1144/SP315.8).
- Cuny G, Suteethorn V, Kamha S. 2005.** Review of the hybodont sharks from the Mesozoic of Thailand. In: Wannakao L, Srisuk K, Youngme W, Lertsirivorakul R, eds. *Proceedings of the international conference on geology, geotechnology and mineral resources of Indochina (GEOINDO 2005)*. Khon Kaen: Khon Kaen University 588–593.
- Cuny G, Suteethorn V, Khama S, Lauprasert K, Srisuk P, Buffetaut E. 2007.** The Mesozoic fossil record of sharks in Thailand. In: Tantiwanit W, ed. *Proceedings of the international conference on geology of Thailand: towards sustainable development and sufficiency economy*. Bangkok: Department of Mineral Resources, 349–354.
- Cupello CD, Bermúdez-Rochas DD, Martill DM, Brito PM. 2012.** The Hybodontiformes (Chondrichthyes: Elasmobranchii) from the Missão Velha Formation (?Lower Cretaceous) of the Araripe Basin, North-East Brazil. *Comptes Rendus Palevol* **11**(1):41–47 DOI [10.1016/j.crpv.2011.09.005](https://doi.org/10.1016/j.crpv.2011.09.005).
- Dollfus A. 1863.** La faune kimméridgienne du cap de la Hève; essai d'une révision paléontologique. *Protogea Gallica* **68**(2):102.
- Etayo-Serna F, Guzmán-Ospitia G. 2019.** Formación Rosa Blanca: subdivisión de la Formación y propuesta de Neoestratotipo. Sección laguna El Sapo, vereda El Carrizal, municipio de Zapatoca, departamento de Santander. In: Etayo-Serna F, ed. *Estudios geológicos y paleontológicos sobre el Cretácico en la región del embalse del Río Sogamoso, Valle Medio del Magdalena. Compilación de los Estudios Geológicos Oficiales en Colombia XXIII*. Bogotá: Servicio Geológico Colombiano, 3–54.
- Goto M, Kuga N, Hachiya K. 1991.** On the hybodont elasmobranch teeth of three genera from the Mesozoic of Japan. *Journal of the Geological Society of Japan* **97**(9):743–750.
- Goto M, Uyeno T, Yabumoto Y. 1996.** Summary of Mesozoic elasmobranch remains from Japan. In: Arratia G, Viohl GE, eds. *Mesozoic fishes 1—systematics and paleoecology*. Verlag Dr. Friedrich Pfeil, 73–82.

- Guinot G, Cappetta H, Adnet S. 2014.** A rare elasmobranch assemblage from the Valanginian (Lower Cretaceous) of southern France. *Cretaceous Research* **48**:54–84 DOI [10.1016/j.cretres.2013.11.014](https://doi.org/10.1016/j.cretres.2013.11.014).
- Guinot G, Carrillo-Briceño JD. 2018.** Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela. *Cretaceous Research* **82**:1–20 DOI [10.1016/j.cretres.2017.09.021](https://doi.org/10.1016/j.cretres.2017.09.021).
- Guzmán-Ospitia G. 1985.** Los Grifeidos infracretácicos *Aetostreon couloni* y *Cera-trostreon boussingaulti*, de la Formación Rosablanca, como indicadores de oscilaciones marinas. In: Etayo-Serna F, ed. *Proyecto Cretácico, Publicación especial del Ingeominas*. Ingeominas, 1–16.
- Huxley TH. 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* **43**:649–662.
- Johns MJ, Albanesi GL, Voldman GG. 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**(3):512–523 DOI [10.1080/02724634.2013.803976](https://doi.org/10.1080/02724634.2013.803976).
- Jordan DS, Hannibal H. 1923.** Fossil sharks and rays of the Pacific Slope of North America. *Bulletin of the Southern California Academy of Sciences* **22**:27–63.
- Kriwet J. 1995.** Beitrag zur Kenntniss der Fisch-fauna des Ober-Jura (unteres Kimmeridge) der Kohlengrube Guimarota bei Leiria, Mittel-Portugal. 1. *Asteracanthus biformatus* n. sp. (Chondrichthyes: Hybodontoida). *Berliner geowissenschaftliche Abhandlungen* **16**:683–691.
- Kriwet J. 2001.** A comprehensive study of pycnodont fishes (Neopterygii, Pycnodontiformes): morphology, taxonomy, functional morphology, phylogeny, and paleobiogeography. D. Phil. Thesis, Humboldt Universität.
- Kriwet J, Benton MJ. 2004.** Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214**:181–194 DOI [10.1016/S0031-0182\(04\)00420-1](https://doi.org/10.1016/S0031-0182(04)00420-1).
- Kriwet J, Rauhut OWM, Gloy U. 1997.** Microvertebrate remains (Pisces, Archosauria) from the Middle Jurassic (Bathonian) of southern France. *Neues Jahrbuch für Geologie und Paläontologie* **206**(1):1–28 DOI [10.1127/njgpa/206/1997/1](https://doi.org/10.1127/njgpa/206/1997/1).
- Kumar K, Bajpai S, Pandey P, Ghosh T, Bhattacharya D. 2022.** Hybodont sharks from the Jurassic of Jaisalmer, Western India. *Historical Biology* **34**(6):953–963 DOI [10.1080/08912963.2021.1954920](https://doi.org/10.1080/08912963.2021.1954920).
- Larsson H. 2012.** The Cretaceous Neotropics: Colombian vertebrates at the boundary of shifting environments and the Mesozoic marine interchange. In: *Society of vertebrate paleontology annual meeting, Raleigh, North Carolina, USA*.
- Leidy J. 1873.** Contributions to the extinct vertebrate fauna of the western territories. *Report of the United States Geological Survey of the Territories* **1**:14–358.
- Leuzinger L, Cuny G, Popov E, Billon-Bruyat JP, Johanson Z. 2017.** A new chondrichthyan fauna from the Late Jurassic of the Swiss Jura (Kimmeridgian) dominated

- by hybodonts, chimaeroids and guitarfishes. *Papers in Palaeontology* 3(4):471–511 DOI 10.1002/spp2.1085.
- Leuzinger L, Kocsis L, Billon-Bruyat JP, Spezzaferri S, Vennemann T. 2015.** Stable isotope study of a new chondrichthyan fauna (Kimmeridgian, Porrentruy, Swiss Jura): an unusual freshwater-influenced isotopic composition for the hybodont shark *Asteracanthus*. *Biogeosciences* 12(23):6945–6954 DOI 10.5194/bg-12-6945-2015.
- Maisey JG. 1987.** Cranial anatomy of the lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. *American Museum Novitates* 2878:1–39.
- Meyer HV. 1849.** Fische, and Crustaceen, Echinodermen und andere Versteinerungen aus dem Muschelkalk Oberschlesiens. *Palaeontographica* 1:243–279.
- Michaut M. 2017.** Hybodontoides du Maastrichtien au sud du Niger. hal-01667933.
- Michelis I, Sander PM, Metzendorf R, Breikreutz H. 1996.** Die Vertebraten fauna des Calloviums (Mittlerer Jura) aus dem Steinbruch Störmer (Wallücke, Wiehengebirge). *Geologie und Paläontologie in Westfalen* 44:1–66.
- Miller HW. 1968.** Additions to the Upper Cretaceous vertebrate fauna of phoebus landing. *North Carolina Journal of the Elisha Mitchell Scientific Society* 84(4):467–471.
- Moody JM, Maisey JG. 1994.** New Cretaceous marine vertebrate assemblages from north-western Venezuela and their significance. *Journal of Vertebrate Paleontology* 14(1):1–8.
- Niño Garcia A, Parra-Mosquera JD, Macias-Villarraga PA. 2019.** Upper Cretaceous chondrichthyes teeth record in phosphorites of the Loma Gorda Formation. *Boletín de Ciencias de la Tierra* 46:27–32.
- Owen O. 1869.** Description of a Great Part of a jaw with the teeth of *Strophodus medius*, Ow. from the Oolite of Caen in Normandy. *Geological Magazine* 6(59):193–196 DOI 10.1017/S0016756800159035.
- Patterson NC. 1966.** British Wealden sharks. *Bulletin of the British Museum (Natural History) Geology* 11:283–350.
- Peyer B. 1946.** Die schweizerischen Funde von *Asteracanthus* (*Strophodus*). *Schweizerische Palaeontologische Abhandlungen* 64:1–103.
- Pfeil FH. 2011.** Ein neues *Asteracanthus*-Gebiss aus den Kieselplattenkalken (Oberjura, Tithonium, Malm Zeta 3, Mörnshelm-Formation) des Besuchersteinbruchs in Mühlheim. *Jahresbericht 2010 und Mitteilungen Der Freunde der Bayerischen Staatssammlung für Paläontologie und Historische Geologie München* 39:36–60.
- Pictet F-J, Campiche G. 1858.** Description des fossiles du terrain crétacé des environs de Sainte-Croix. *1ère partie Matériaux pour la Paléontologie Suisse* 2:1–380.
- Pinheiro FL, de Figueiredo AEQ, Dentzien-Dias PC, Fortier DC, Schultz CL, Viana MSS. 2013.** *Planohybodus marki* sp. nov. a new fresh-water hybodontid shark from the Early Cretaceous of northeastern Brazil. *Cretaceous Research* 41:210–216 DOI 10.1016/j.cretres.2012.12.005.
- Pinheiro FL, Figueiredo AEQ, Fortier DC, Viana MSS, Schultz CL. 2011.** Fauna de vertebrados eocretácicos de um afloramento da Bacia de Lima Campos, Ceará, Brasil. *Revista Brasileira de Paleontologia* 14(2):189–198 DOI 10.4072/rbp.2011.2.07.

- Pla C, Márquez-Aliaga A, Botella H. 2013.** The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). *Journal of Vertebrate Paleontology* **33**(4):770–785 DOI [10.1080/02724634.2013.748668](https://doi.org/10.1080/02724634.2013.748668).
- Priem MF. 1907.** Note sur les Poisson fossiles de Madagascar. *Bulletin de la Société géologique de France* **4**(7):462–465.
- Priem MF. 1912.** Sur des poissons des terrains secondaires du Sud de la France. *Bulletin de la Société géologique de France* **4**(12):250–271.
- Quenstedt FA. 1882.** *Bdelloodus bollensis* aus dem Posidonienschiefer bei Boll. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **38**:137–142.
- Rees J. 2008.** Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology-preliminary results. *Acta Geologica Polonica* **58**(2):217–221.
- Rees J, Underwood CJ. 2008.** Hybodont sharks of the English Bathonian and Callovian (middle Jurassic). *Palaeontology* **51**(1):117–147 DOI [10.1111/j.1475-4983.2007.00737.x](https://doi.org/10.1111/j.1475-4983.2007.00737.x).
- Reinhart RH. 1951.** A new shark of the family Ptychodontidae from South America. *University of California Publications in Geological Sciences* **28**:195–202.
- Rieppel O. 1981.** The hybodontiform sharks from the Middle Triassic of Mte, San Giorgio, Switzerland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **161**:324–353.
- Rigal S, Cuny G. 2016.** On the rarity of anterior teeth of *Asteracanthus magnus* (Euselachii: Hybodontiformes). *Neues Jahrbuch für Geologie und Paläontologie* **279**(1):35–41.
- Rogovich AS. 1860.** On fossil fishes of provinces of the Kiev Academic District. First issue. Placoid fishes. Placoidei Ag. and Ganoid fishes. Ganoidei Ag. [in Russian]. Natural History of the Provinces of the Kiev Academic District. *Paleontology. Systematic part. Kiev* 87.
- Romano M, Citton P, Cipriani A, Fabbi S. 2018.** First report of hybodont shark from the Toarcian Rosso Ammonitico Formation of Umbria-Marche Apennine (Polino area, Terni, Central Italy). *Italian Journal of Geosciences* **137**(1):151–159 DOI [10.3301/IJG.2018.01](https://doi.org/10.3301/IJG.2018.01).
- Sharma A, Singh S. 2021.** A small assemblage of marine hybodont sharks from the Bathonian of the Jaisalmer Basin, India. *Neues Jahrbuch für Geologie und Paläontologie* **301**(3):317–333 DOI [10.1127/njgpa/2021/1014](https://doi.org/10.1127/njgpa/2021/1014).
- Silva MC, MSSd Carvalho, Barreto AMF, Carvalho IS. 2011.** Paleoictiofauna da Formação Aliança (Jurássico Superior), Bacia de Jatobá, Nordeste do Brasil. In: Carvalho IS, Srivastava NK, Strohschoen OJ, Lana CC, eds. *Paleontologia: Cenários de Vida*. Volume 4. Rio de Janeiro: Editora Interciência, 595–608.
- Sokolskyi T, Guinot G. 2021.** Elasmobranch (Chondrichthyes) assemblages from the Albian (Lower Cretaceous) of Ukraine. *Cretaceous Research* **117**:104603 DOI [10.1016/j.cretres.2020.104603](https://doi.org/10.1016/j.cretres.2020.104603).
- Soto M, Perea D, Toriño P. 2012.** New remains of *Priohybodus arambourgi* (Hybodontiformes: Hybodontidae) from Late Jurassic–earliest Cretaceous deposits in Uruguay. *Cretaceous Research* **35**:118–123 DOI [10.1016/j.cretres.2011.12.001](https://doi.org/10.1016/j.cretres.2011.12.001).

- Stromer E. 1927.** Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 9. Die Plagiostomen mit einem Anhang über Käno- und mesozoische Rückenflossenstacheln von Elasmobranchiern. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Math.–naturwiss. Abt* **31**:51–64.
- Stumpf S, López-Romero FA, Kindlimann R, Lacombat F, Pohl B, Kriwet J. 2021.** A unique hybodontiform skeleton provides novel insights into Mesozoic chondrichthyan life. *Papers in Palaeontology* **7**(3):1479–1505 DOI [10.1002/spp2.1350](https://doi.org/10.1002/spp2.1350).
- Stumpf S, Meng S, Kriwet J. 2022.** Diversity Patterns of Late Jurassic Chondrichthyans: new insights from a historically collected hybodontiform tooth assemblage from Poland. *Diversity* **2022**(14):85 DOI [10.3390/d14020085](https://doi.org/10.3390/d14020085).
- Szabó M, Fózy I. 2020.** *Asteracanthus* (Hybodontiformes: Acrodontidae) remains from the Jurassic of Hungary, with the description of a new species and with remarks on the taxonomy and paleobiology of the genus. *Neues Jahrbuch Geol Paläontol. Abhandlung* **297**(3):295–309 DOI [10.1127/njgpa/2020/0926](https://doi.org/10.1127/njgpa/2020/0926).
- Vincent P, Martin JE, Fischer V, Suan G, Khalloufi B, Suchéras-Marx B, Léna A, Janneau K, Rousselle B, Rulleau L. 2013.** Marine vertebrate remains from the Toarcian–Aalenian succession of southern Beaujolais, Rhône, France. *Geological Magazine* **150**(5):822–834 DOI [10.1017/S0016756812000982](https://doi.org/10.1017/S0016756812000982).
- Werner C. 1989.** Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica* **5**:1–112.
- Wills S, Bernard EL, Brewer P, Underwood CJ, Ward DJ. 2019.** Palaeontology, stratigraphy and sedimentology of Woodeaton Quarry (Oxfordshire) and a new microvertebrate site from the White Limestone Formation (Bathonian, Jurassic). *Proceedings of the Geologists Association* **130**(2):170–186 DOI [10.1016/j.pgeola.2019.02.003](https://doi.org/10.1016/j.pgeola.2019.02.003).
- Woodward AS. 1888.** Notes on some vertebrate fossils from the Province of Bahia, Brazil, collected by Joseph Mawson Esq. F.G.S. *Annals and Magazine of Natural History* **2**(8):132–136 DOI [10.1080/00222938809460891](https://doi.org/10.1080/00222938809460891).
- Woodward AS. 1889.** *Catalogue of the fossil fishes in the British Museum. Part. I.* London: British Museum (Natural History).
- Yabe H. 1902.** Notes on some shark's teeth from Mesozoic formations of Japan. *Journal of the Geological Society of Japan* **9**:399–404.
- Zittel KA. 1870.** Die Fauna der älteren cephalopoden-führenden Tithonbildungen. *Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates* **2**(2):192–194.