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# The oldest Gondwanan record of the extinct durophagous hybodontiform chondrichthyan, *Strophodus* from the Bajocian of Morocco

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## Abstract

*Strophodus* is a speciose and geographically widespread taxon of large durophagous hybodontiform chondrichthyan, with a stratigraphic range extending from Middle Triassic to the Early Cretaceous. Here, we describe a new species of *Strophodus*, *S. atlasensis* sp. nov., based on an incomplete articulated dentition recovered from marine Bajocian deposits of the eastern High Atlas Mountains in Morocco. The new species is diagnosed by a unique combination of dental characters that includes, among others, the presence of triangular first lateral teeth, mesio-distally wide and bulbous second lateral teeth without an occlusal crest or dome and uniquely shaped first posterior teeth that are shorter mesio-distally than being labio-lingually long, as well as small second posterior teeth whose roots protrude below the crowns to meet each other in an efficient interlocking manner. The holotype and only specimen of *Strophodus atlasensis* sp. nov. represents the hitherto oldest known record of *Strophodus* from Gondwana and the first record of that genus from the Bajocian, thus adding valuable novel information to our incomplete understanding of the evolutionary history of extinct hybodontiform chondrichthyans.

**Keywords** Chondrichthyes, Middle Jurassic, Taxonomic diversity, Palaeobiogeography

## Introduction

The Mesozoic marks a crucial episode of profound and persistent restructuring of marine communities (Sepkoski, 1984), driven largely by accelerating selection pressure of increasingly effective predators, particularly those adapted to durophagy (Vermeij, 1977; Vermeij et al., 1981), which quickly became abundant from the Middle

Triassic onwards following the recovery of life after the Permian–Triassic mass extinction (see Benton & Wu, 2022, and references therein). Among Mesozoic marine vertebrates, trophic specialisations towards durophagy are best documented for bony and cartilaginous fishes, which have evolved independently various morpho-functional adaptations for manipulating and processing hard-shelled prey prior to digestion (e.g., Amadori et al., 2020; 2022; Kriwet, 2001, 2005; Lane & Maisey, 2012; López-Arbarello et al., 2016; Smithwick, 2015; Thies et al., 2021).

The extinct hybodontiform chondrichthyan *Strophodus* Agassiz, 1838, with an estimated maximum body length of up to three meters and its massive, powerful jaws equipped with highly specialized crushing teeth suitable for breaking up various kinds of marine hard-shelled invertebrate prey, is one of the most iconic durophagous predators that ever roamed the Mesozoic seas (e.g., Cappetta, 2012; Szabó & Főzy, 2020). Extending for more than 130 million years, from the Middle Triassic

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(Anisian–Ladinian) to the Early Cretaceous (Albian) (Cappetta, 2012), *Strophodus* boasts an extensive fossil record that is mainly dominated by its characteristic teeth, which occur frequently in a wide variety of depositional environments, providing discrete combinations of dental characters for use in species identification and establishing reliable diagnoses (e.g., Carrillo-Briceño & Cadena, 2022; Leuzinger et al., 2017; Peyer, 1946; Rees & Underwood, 2008; Rigal & Cuny, 2016; Stumpf et al., 2022; Szabó, 2021; Szabó & Fözy, 2020).

Over the past two decades, records of *Strophodus* have been reported from an increasing number of Middle to Late Jurassic localities in Europe and Asia, which provided valuable new information for better understanding its palaeogeographic distribution and diversity dynamics (e.g., Citton et al., 2019; Cuny et al., 2005, 2009; Kumar et al., 2021; Leuzinger et al., 2017; Pfeil, 2011; Rigal & Cuny, 2016; Romano et al., 2018; Sharma & Singh, 2021; Stumpf et al., 2022; Szabó & Fözy, 2020; Vincent et al., 2013). However, records of *Strophodus* from Middle Jurassic strata of pre-Bathonian (Aalenian–Bajocian) age are still rare and restricted to a limited number of Aalenian occurrences from Europe (Quenstedt, 1858; Szabó, 2021; Szabó & Fözy, 2020; Vincent et al., 2013).

Here, we describe a new species of *Strophodus*, *S. atlasensis* sp. nov., based on a single incomplete dentition from the Bajocian of the eastern High Atlas Mountains

of Morocco. The new species, which constitutes the hitherto oldest known Gondwanan record of *Strophodus*, contributes towards filling the gap in understanding the early diversity and distribution of hybodontiforms during the Middle Jurassic.

## Materials and methods

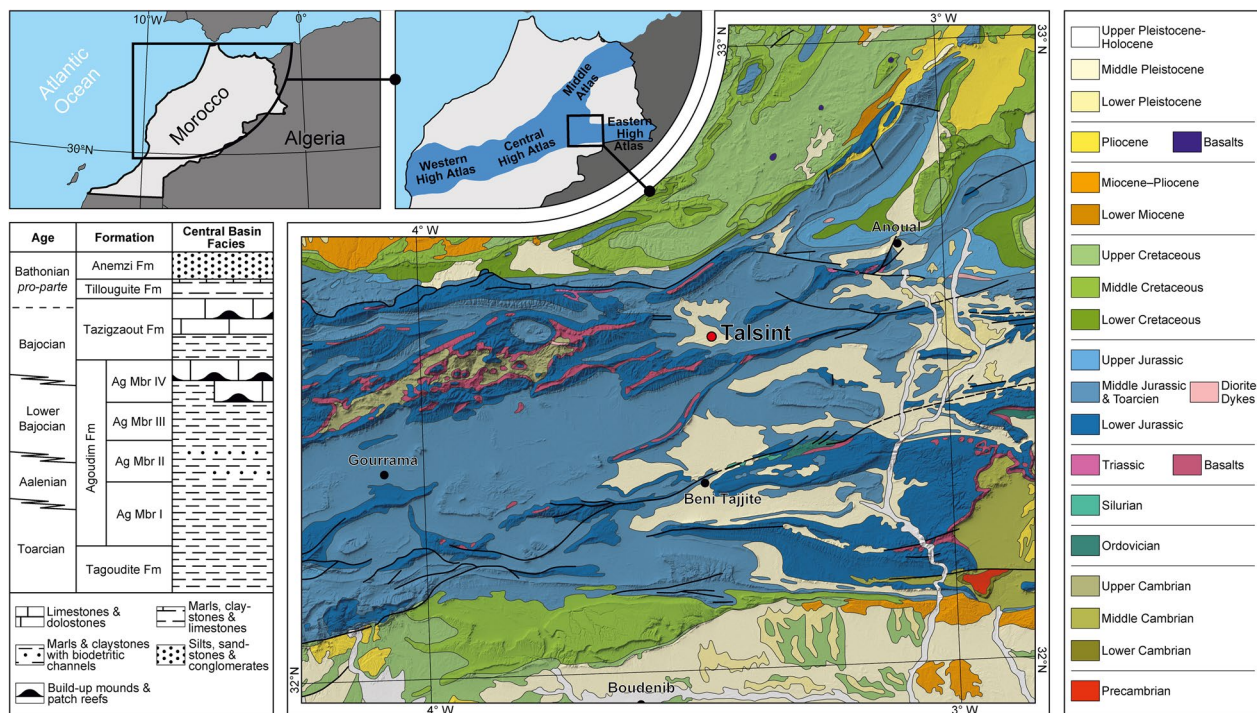
### Fossil material in this study

The articulated hybodontiform dentition that forms the focus of the present study was acquired by one of us (RK), who recently donated the specimen to the Palaeontological Institute and Museum of the University of Zurich, Switzerland, where it is curated and catalogued under the repository number PIMUZ A/I 5181. Currently the specimen is on loan and on public display in the 'Haimuseum und Sammlung R. Kindlimann' in Aathal-Seegräben, Switzerland.

### Geological and stratigraphic framework

PIMUZ A/I 5181 was collected from Bajocian basal marine deposits referred to the upper Agoudim Formation accessible near the town of Talsint (32°32'7"N, 3°26'53" W), which is located in the eastern High Atlas Mountains of Morocco (Fig. 1).

Representing an ENE–WSW trending intracontinental fold-thrust belt, the High Atlas Mountain range was formed during the Cenozoic by the inversion of a



**Fig. 1** Geological location map (modified from Saadi et al., 1985 and Ait Addi & Chafiki, 2013)

Triassic–Jurassic rift system (Beauchamp et al., 1996; Frizon de Lamotte et al., 2008; Jacobshagen et al., 1988). The basal fill of this rift system, which was initiated by the opening of the North Atlantic Ocean as the result of the dislocation of Pangaea, mainly consists of Early and Middle Jurassic marls and limestones with intercalated carbonate build-ups referred to the Agoudim and Tazigzaout formations (Ait Addi, 2000, 2002; Ait Addi & Chafiki, 2013). The upper Agoudim Formation corresponds to the Agoudim Members III and IV, whose stratigraphic range is early to probably late Bajocian (Ait Addi, 2015; Bodin et al., 2017). While the Agoudim Member III consists of shaly marls with intercalated micritic and bioclastic limestones, the overlying Agoudim Member IV is composed of bioclastic limestones rich in brachiopods, serpulid worm tubes, bryozoans and algae, and shaly marls, marly limestones and limestones, as well as coral patch reefs with an abundant and diverse neritic biota, comprising bivalves, gastropods, brachiopods, echinoderms, serpulid tubes, sponges and bryozoans, as well as algae (Ait Addi, 2006, 2015).

## Methods

The hybodontiform dentition described herein was digitized using photogrammetry following the methodology outlined by Mallison and Wings (2014). The 3D model was generated using Agisoft Metashape Professional v1.7.4 by processing a total of 152 photographs that were acquired using a Fujifilm X-T3 digital camera equipped with a 16–50 mm f/3.5 lens. The 3D model was further processed utilizing Blender v3.0.0 to obtain ambient occlusion shading, which was combined with global illumination for soft lighting. The 3D model is available for download at the online repository figshare (<https://doi.org/10.6084/m9.figshare.21741020>).

All photographs presented in the text were obtained using a Nikon D5300 DSLR camera equipped with an AF-S DX Micro NIKKOR 40 mm f/2.8G lens and Adobe Photoshop CC 2021 was used for colour balance and contrast optimization. Palaeogeographic maps shown in Fig. 4A–F were created using the open source plate tectonic reconstruction software GPlates v2.2.0 (Boyden et al., 2011) and the data of Matthews et al. (2016). The stratigraphic chart shown in Fig. 4G was created utilizing the open source software TimeScale Creator v8.0, which is standardized to the age model of Gradstein et al. (2020). All figures presented in the text were finalized using Adobe Illustrator CC 2021.

The descriptive dental terminology employed in this study largely follows that of Cappetta (2012), whereas higher systematic relationships correspond to those of Maisey (1989), although we acknowledge that currently available phylogenetic hypotheses for hybodontiforms

are unsatisfactory (Rees, 2008; Stumpf et al., 2021a, 2021b).

## Systematic palaeontology

**Chondrichthyes** Huxley, 1880

**Hybodontiformes** Patterson, 1966

**Hybodontidae** Owen, 1846

**Acrodontinae** Casier, 1959 sensu Maisey, 1989

***Strophodus*** Agassiz, 1838

### Type species

*Strophodus longidens* Agassiz, 1838 from the Bathonian of France.

### Included species

*Strophodus longidens* Agassiz, 1838; *Strophodus magnus* Agassiz, 1838; *Strophodus reticulatus* Agassiz, 1838; *Strophodus subreticulatus* Agassiz, 1838; *Strophodus tenuis* Agassiz, 1838; *Strophodus medius* Owen, 1869; *Strophodus smithwoodwardi* (Peyer, 1946); *Strophodus udulfensis* (Leuzinger et al., 2017); *Strophodus dunaii* (Szabó & Fözy, 2020); *Strophodus indicus* Sharma & Singh, 2021; *Strophodus jaisalmerensis* Kumar et al., 2021; *Strophodus rebecca* Carrillo-Briceño & Cadena, 2022; *Strophodus atlasensis* sp. nov.

### Temporal distribution

Middle Triassic (Anisian–Ladinian) to Early Cretaceous (Albian).

### Spatial distribution

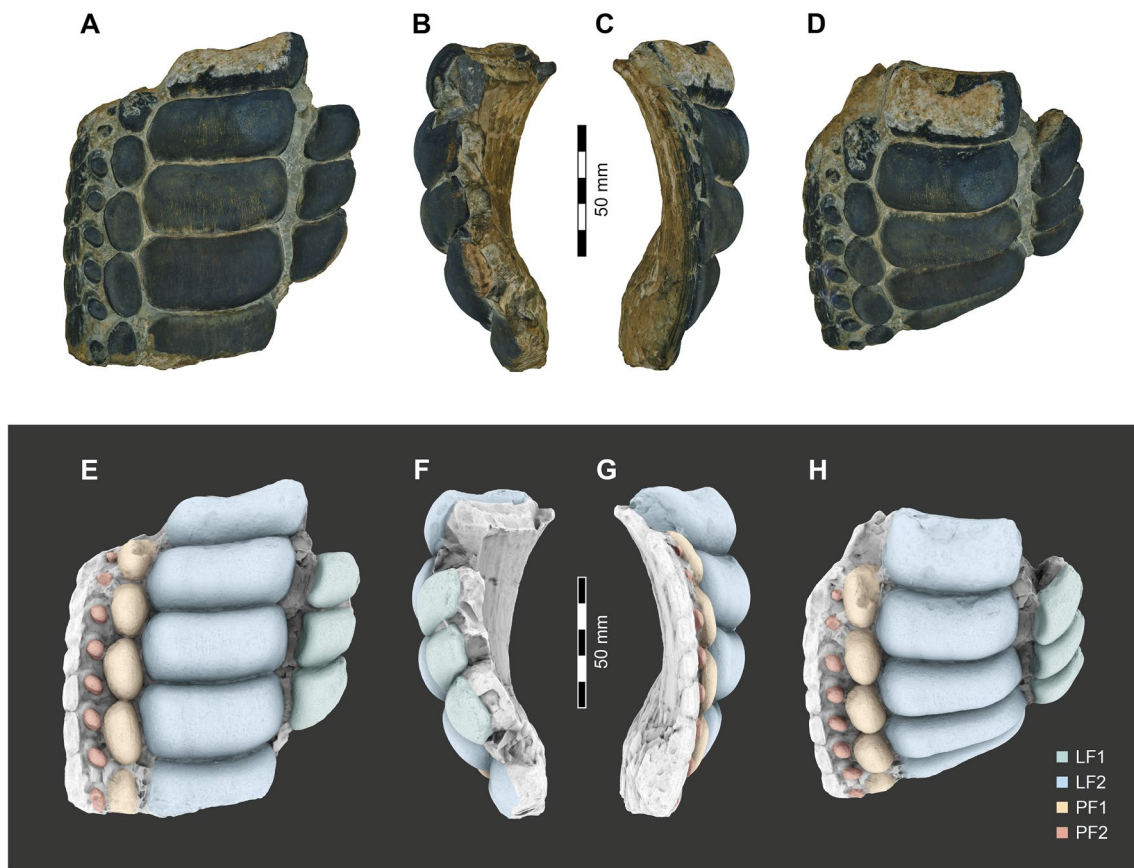
Europe, Asia, Africa, South America.

### *Strophodus atlasensis* sp. nov.

Figures 2, 3.

### Diagnosis

A species of *Strophodus* that is characterized by the following unique combination of dental characters: Presence of a well-developed, heterodont crushing-type dentition; teeth of first lateral file short mesio-distally and slightly domed in labio-lingual view, with a nearly triangular occlusal outline; tooth crowns of first lateral teeth without transverse occlusal crest, but covered with a finely reticulate pattern; teeth of the second lateral file wide mesio-distally and bulbous without a dome in labio-lingual view, displaying a subrectangular occlusal outline with a slightly concave labial and a gently convex lingual edge; tooth crowns of second lateral teeth without transverse occlusal crest and covered with a finely reticulate pattern that turns into labio-lingually aligned bands along the lingual part of the



**Fig. 2** *Strophodus atlasensis* sp. nov., PIMUZ A/I 5181, holotype, from the upper Agoudim Formation (Bajocian) near Talsint, Figuig Province, Morocco. Orthophoto (A–D) and ambient occlusion photogrammetric model with highlighted tooth crowns (E–H) in occlusal (A, E), mesial (B, F), distal (C, G) and oblique occlusal (D, H) views. Abbreviations: LF1, tooth crowns of first lateral file; LF2, tooth crowns of second lateral file; PF1, tooth crowns of first posterior file; PF2, tooth crowns of second posterior file

crown; teeth of first posterior file shorter mesio-distally than labio-lingually long and elliptical in occlusal outline; tooth crowns of first posterior teeth slightly elevated and ornamented with a finely reticulate pattern; tooth crowns of second posterior teeth small and oval in occlusal outline with their long axes oriented obliquely, exhibiting a finely reticulate ornamentation pattern; tooth roots of second posterior teeth parallel-gram-shaped in occlusal outline and protrude distally and slightly labio-lingually below the crown, meeting each other in an efficient interlocking manner.

#### **Holotype and only known specimen**

PIMUZ A/I 5181, an incomplete articulated dentition.

#### **Type locality and horizon**

Talsint, Figuig Province, Morocco; upper Agoudim Formation, Bajocian, Middle Jurassic.

#### **Etymology**

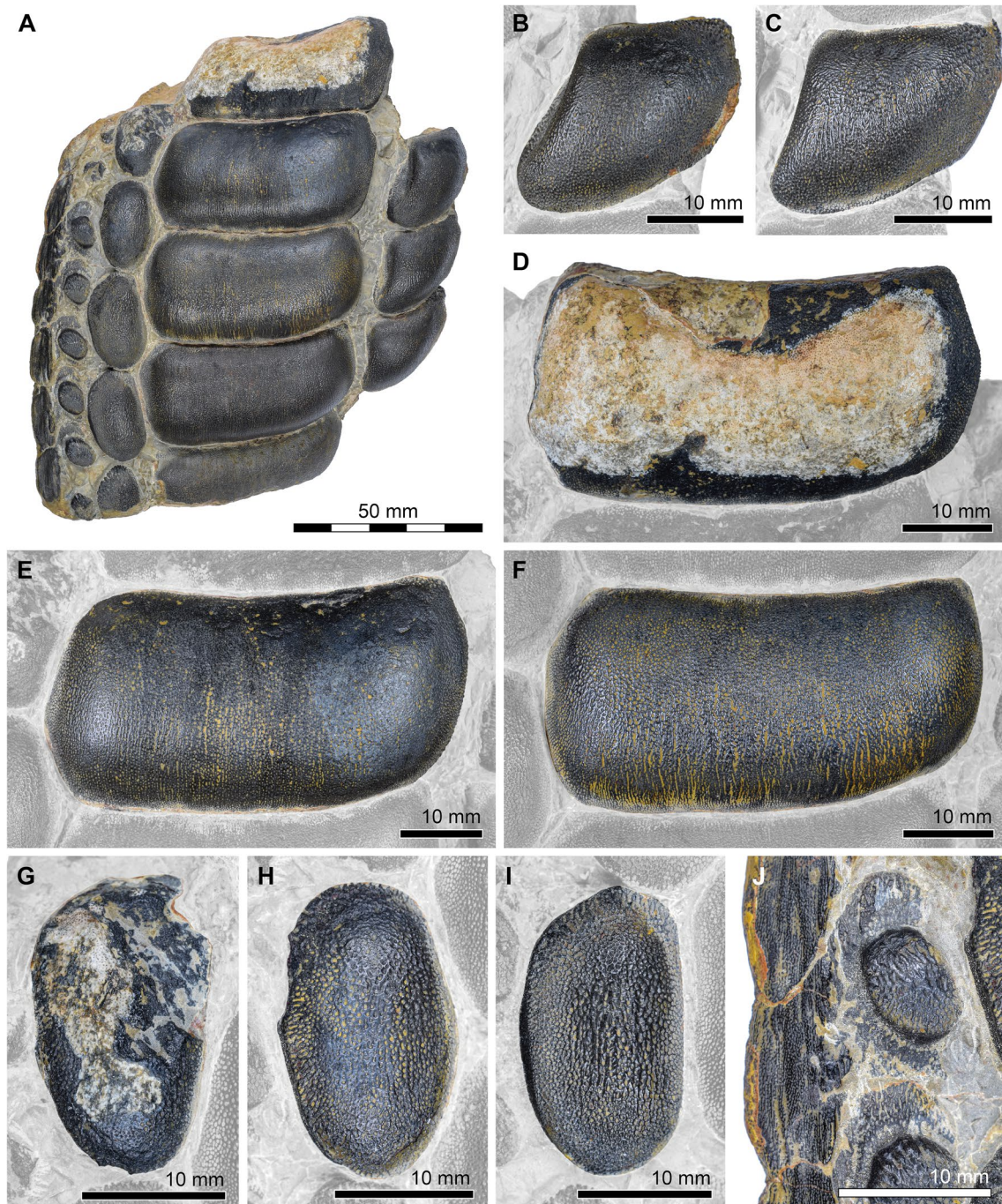
The specific epithet refers to the High Atlas Mountains from which the holotype originates.

#### **Nomenclatural act**

The 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 resolved 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:C987BC7F-F855-410D-9B62-7245A40F42E3.

#### **Description**

The holotype and only specimen of *Strophodus atlasensis* sp. nov., PIMUZ A/I 5181, is represented by an incomplete articulated dentition that contains a total of 21 crushing-type teeth, which are closely arranged in four well-defined tooth files, including two lateral and two



**Fig. 3** *Strophodus atlasensis* sp. nov., PIMUZ AVI 5181, holotype, from the upper Agoudim Formation (Bajocian) near Talsint, Figuig Province, Morocco. Complete specimen (A) with close-up views of first lateral (B, C), second lateral (D–F) and first posterior teeth (G–I), plus close-up of second posterior tooth (J)

posterior files (Fig. 2). The dentition, which exhibits a high degree of heterodonty, is here tentatively separated into comprising both functional and replacement teeth based on the presence or absence of dental wear patterns (see below). The dentition is gently convex along

its labio-lingual axis (Fig. 2B, C, E, G) and slightly twisted (Fig. 2D, H). The tooth roots are still embedded in rock matrix or are just partially exposed. Whether the dentition belongs to the upper or lower jaw cannot be determined due to its incomplete preservation.

### First lateral teeth

The first lateral tooth file preserves one functional and two replacement teeth. The tooth crown is short mesio-distally and slightly domed, displaying an almost triangular outline in occlusal view (Figs. 2A, E; 3A–C). The tooth crown ornamentation shows a finely reticulate pattern consisting of very fine, more or less regularly arranged pits (Fig. 3B, C). An occlusal crest is absent. The functional tooth is slightly worn along the labial edge of the crown (Fig. 3B), while the replacement teeth are free of dental wear (Fig. 3C).

### Second lateral teeth

The second lateral tooth file encompasses two functional and three replacement teeth, the lingual-most tooth being incomplete and broken lingually. The teeth, which are larger than any of those positioned in the first lateral or the posterior tooth files, are wider mesio-distally than labio-lingually long and conspicuously bulbous, exhibiting a somewhat bean-shaped occlusal outline with a slightly concave labial and a gently convex lingual edge (Figs. 2A, E; 3A, D–F). The crown does not form a dome-like elevation in labio-lingual view and lacks a transverse occlusal crest. It shows a finely reticulate ornamentation pattern consisting of very small, densely packed pits, which turn into fine labio-lingually aligned bands along the lingual part of the crown (Fig. 3F). Extensive wear patterns can be observed in the labial-most functional tooth, in which even the enameloid has been worn off across most part of the occlusal surface of the crown (Fig. 3D). This contrasts with the next following functional tooth, which has been less affected by dental wear, showing a slightly worn occlusal surface along the labial half of the crown (Fig. 3E). The replacement teeth lack any signs of dental wear (Fig. 3F).

### First posterior teeth

The first posterior tooth file preserves two functional and three replacement teeth, with the youngest replacement tooth being incomplete and broken lingually. The tooth crowns are short mesio-distally with an elliptical outline in occlusal view, with their long axes oriented labio-lingually (Figs. 2A, E; 3G–I). The occlusal surface of the crown is slightly elevated (Fig. 2C, G) and lacks an occlusal crest, displaying a dense, minutely reticulate ornamentation pattern (Fig. 3I). The labial-most functional tooth has strongly suffered from dental wear as shown by severe damage to the enameloid and the underlying dentinal core of the crown (Fig. 3G). The next following functional tooth is slightly worn along the labial

edge of the crown (Fig. 3H), unlike the replacement teeth, which display no signs of dental wear (Fig. 3I).

### Second posterior teeth

The second lateral tooth file preserves eight teeth, comprising three functional and five replacement teeth, the youngest replacement tooth being incomplete. The tooth crowns are small and have an oval outline in occlusal view, with their long axes obliquely oriented (Fig. 2A, E; 3J). The crown is flat and ornamented with a finely reticulate ornamentation pattern. The tooth root has a somewhat parallelogram-shaped outline in occlusal view and protrudes distally and slightly labio-lingually below the crown. The labial and lingual margins of the root are obliquely oriented in occlusal view, so that they meet in an efficient interlocking manner.

### Comparison

The dental traits displayed by specimen PIMUZ A/I 5181 from the Bajocian of the Moroccan High Atlas Mountains are consistent with referral to the genus *Strophodus*, whose stratigraphic range spans from the Middle Triassic to the Early Cretaceous. *Strophodus* has frequently been reported from numerous localities across the globe (compare Carrillo-Briceño & Cadena, 2022; Rees & Underwood, 2008; Stumpf et al., 2022; Szabó & Főzy, 2020), making it one of the most common and geographically widespread Mesozoic hybodontiforms to ever have lived.

*Strophodus*, as currently understood, encompasses at least 13 species, 12 of which have been named to date. These are (in stratigraphic order; please see Table 1 for detailed bibliographical information): (1) *S. cf. reticulatus* from the Anisian–Ladinian of Switzerland, (2) *S. smithwoodwardi* from the Toarcian of Switzerland, (3) *S. dunaii* from the Aalenian of Hungary, (4) *S. tenuis* from Aalenian–Bathonian of Germany and England, (5) *S. longidens* (type species) from the Bathonian of France, (6) *S. magnus* from the Bathonian of England, France and India, (7) *S. indicus* and (8) *S. jaisalmerensis*, both from the Bathonian of India, (9) *S. medius* from the Bathonian–Callovian of France, England and possibly India, (10) *S. reticulatus* from the Bathonian–Tithonian of England, France, Switzerland, Germany and Hungary, (11) *S. subreticulatus* from the Kimmeridgian of Switzerland, (12) *S. udulfensis* from the Kimmeridgian of Switzerland, Poland and possibly England and (13) *S. rebecae* from the Valanginian–Hauterivian of Colombia.

Given the lack of suitable skeletal material, morphological features for use in species identification mainly focus on dental traits. There are currently just a few *Strophodus* species that are known by articulated or at least associated dentitions, including *S. smithwoodwardi*, *S. medius*, *S. magnus* and *S. reticulatus* (Peyer, 1946; Rees

**Table 1** The fossil record of *Strophodus*

Epoch	Stage	Occurrence	Species	Material	References
Middle Triassic	Anisian–Ladinian	Switzerland	<i>S. cf. reticulatus</i>	Associated teeth	Rieppel, 1981
Early Jurassic	Hettangian	Japan	<i>Strophodus</i> sp.	Single tooth	Goto et al., 1991, 1996; Goto, 1994
	?	Japan	<i>Strophodus</i> sp.	Single tooth	Takakuwa & Gunma Fossil Club, 2011
Middle Jurassic	Toarcian	Switzerland	<i>S. smithwoodwardi</i>	Jaws with associated teeth	Peyer, 1942, 1946
	Toarcian	Italy	<i>Strophodus</i> sp.	Isolated teeth	Romano et al., 2018
	Aalenian	Germany	<i>S. tenuis</i> , <i>Strophodus</i> sp.	Isolated teeth	Quenstedt, 1858
	Aalenian	Hungary	<i>S. dunaii</i>	Isolated teeth	Szabó & Főzy, 2020; Szabó, 2021
	Aalenian	France	<i>Strophodus</i> sp.	Single tooth	Vincent et al., 2013
	Bajocian	Morocco	<i>S. atlasensis</i> sp. nov	Articulated dentition	This study
	Bathonian	France	<i>S. longidens</i> , <i>S. medius</i> , <i>S. magnus</i> , <i>Strophodus</i> sp.	Articulated and associated teeth, isolated teeth	Owen, 1869; Kriwet et al., 1997; Rees & Underwood, 2008; Knoll & López-Antoñanzas, 2014; Rigal & Cuny, 2016
	Bathonian	UK	<i>S. magnus</i> , <i>S. medius</i> , <i>S. reticulatus</i> , <i>S. tenuis</i> , <i>Strophodus</i> sp.	Isolated teeth	Woodward, 1889b, 1890; Rees & Underwood, 2008; Wills et al., 2019
	Bathonian	India	<i>S. magnus</i> , <i>S. medius</i> , <i>S. indicus</i> , <i>S. jaisalmerensis</i> ,	Isolated teeth	Sharma & Singh, 2021; Kumar et al., 2021
	?Bathonian–Callovian	Thailand	<i>Strophodus</i> sp.	Teeth and cephalic spine fragment	Cuny et al., 2009
Late Jurassic	Callovian	Germany	<i>Strophodus</i> sp.	Isolated teeth	Heller, 1955; Michelis et al., 1996
	Callovian	UK	<i>S. reticulatus</i>	Jaw fragments and associated teeth, fin spines	Woodward, 1888, 1889b; Martill, 1991; Stumpf et al., 2021b
	Callovian	Hungary	<i>S. reticulatus</i>	Single tooth	Szabó & Főzy, 2020
	Oxfordian	France	<i>S. reticulatus</i>	Isolated teeth	Priem, 1911
	Oxfordian	Switzerland	<i>Strophodus</i> sp.	Isolated teeth	Peyer, 1946
	Oxfordian	India	<i>Strophodus</i> sp.	Isolated teeth	Kumar et al., 2021
	Oxfordian	Madagascar	<i>Strophodus</i> sp.	Isolated teeth	Priem, 1907, 1924
	Oxfordian–Kimmeridgian	Japan	<i>Strophodus</i> sp.	Single tooth	Yabe, 1902; Goto, 1994; Goto et al., 1996
	Kimmeridgian	France	<i>S. reticulatus</i> , <i>Strophodus</i> sp.	Isolated teeth	Dollfus, 1863; Candoni, 1995
	Kimmeridgian	Germany	<i>Strophodus</i> sp.	Isolated teeth	Quenstedt, 1858
	Kimmeridgian	Germany	<i>S. reticulatus</i>	Isolated teeth	Fricke, 1876
	Kimmeridgian	Switzerland	<i>S. subreticulatus</i> , <i>S. udulfensis</i> , <i>Strophodus</i> sp.	Isolated teeth	Peyer, 1946; Müller, 2011; Leuzinger et al., 2017
	Kimmeridgian	Portugal	<i>Strophodus</i> sp.	Single tooth, fin and cephalic spines	Kriwet, 1995, 1998
	Kimmeridgian	Poland	<i>S. udulfensis</i>	Isolated teeth	Stumpf et al., 2022
	Kimmeridgian	Lebanon	<i>S. cf. magnus</i>	Isolated teeth	This study
	Kimmeridgian–Tithonian	UK	<i>S. reticulatus</i>	Isolated teeth	Underwood, 2020
	Kimmeridgian–Tithonian	Italy	<i>S. cf. magnus</i>	Associated teeth	Citton et al., 2019
Tithonian	Italy	<i>Strophodus</i> sp.	Isolated teeth	Zittel, 1870; Bassani, 1885	
Tithonian	Germany	<i>Strophodus</i> sp.	Jaws with associated teeth	Pfeil, 2011; Kriwet & Klug, 2015; Villalobos-Segura et al., 2023	
Tithonian	Hungary	<i>S. reticulatus</i>	Isolated teeth	Szabó & Főzy, 2020	
Tithonian	Thailand	<i>Strophodus</i> sp.	Single tooth	Cuny et al., 2005	
?	Thailand	<i>Strophodus</i> sp.	Single tooth	Cuny et al., 2005	

**Table 1** (continued)

Epoch	Stage	Occurrence	Species	Material	References
Early Cretaceous	Valanginian	France	<i>Strophodus</i> sp.	Isolated teeth	Pictet & Campiche, 1858; Priem, 1912; Guinot et al., 2014
	Valanginian–Hauterivian	Switzerland	<i>Strophodus</i> sp.	Isolated teeth	Peyer, 1946
	Valanginian–Hauterivian	Colombia	<i>S. rebecca</i> , <i>Strophodus</i> sp.	Isolated teeth	Carrillo-Briceño & Cadena, 2022
	Albian	France	<i>Strophodus</i> sp.	Single tooth	Priem, 1912
	Albian	Tunisia	<i>Strophodus</i> sp.	Isolated teeth	Tabaste, 1963

& Underwood, 2008; Rigal & Cuny, 2016; Szabó & Főzy, 2020). All these species share very similar dental patterns characterized by five to six tooth files on each side of the jaws, which can be further separated into two files of rather high anterior teeth, two files of wide lateral teeth and one or two files of small posterior teeth. In addition, there is a single file of high symphyseal teeth that is restricted to the lower dentition, as can be seen in a yet undetermined species from the Late Jurassic of Germany (Pfeil, 2011). By contrast, the stratigraphically oldest representative of *Strophodus*, which is known from a single associated dentition from the Anisian–Ladinian of Switzerland (referred to as *S. cf. reticulatus* by Rieppel, 1981), appears to be readily differentiated from younger species by its smaller size and higher number of anterior tooth files (Rees & Underwood, 2008).

The single incomplete dentition PIMUZ A/I 5181 shares with *S. medius* and *S. reticulatus* two files of posterior teeth (Rees & Underwood, 2008), a condition deviating them from *S. magnus* and *S. smithwoodwardi*, as well as *Strophodus* sp. from the lower Tithonian of Germany (probably conspecific with *S. smithwoodwardi*), which all share a single file of posterior teeth (Peyer, 1946; Pfeil, 2011; Rigal & Cuny, 2016).

On the other hand, PIMUZ A/I 5181 is rather more similar to *S. magnus* and *S. smithwoodwardi* than to other species, particularly in possessing first lateral teeth with a nearly triangular occlusal outline and finely reticulate ornamentation (Peyer, 1946; Rigal & Cuny, 2016). First lateral teeth with a triangular occlusal outline also occur in the poorly known species *S. subreticulatus* (Agassiz, 1838). However, second lateral teeth of *S. subreticulatus* are slightly domed mesially and appear to have reached wider mesio-distal dimensions, attaining a parallelogram-shaped occlusal outline (Agassiz, 1838). Likewise, lateral teeth of quite similar morphology are also present in *S. magnus*. In general, second lateral teeth of *S. magnus* are uniformly reticulate and tend to have rather wide and flat, less mesially domed dental morphologies with angled extremities, which gives them

a parallelogram-shaped to almost rectangular outline in occlusal view (Rees & Underwood, 2008; Rigal & Cuny, 2016; Sharma & Singh, 2021). This contrasts with PIMUZ A/I 5181, in which the teeth of the second lateral file are conspicuously bulbous and somewhat bean-shaped in occlusal view. *Strophodus magnus* and the recently proposed species *S. jaisalmerensis*, which both co-occur in the Bathonian of India (Kumar et al., 2021; Sharma & Singh, 2021), appear to have been characterized by strikingly similar teeth that are very difficult to distinguish from one another. According to Kumar et al. (2021), posterior teeth of *S. jaisalmerensis*, which are only known from isolated crowns, bear a quadrangular occlusal outline and a reticulate ornamentation, contrasting with *S. magnus*, whose posterior teeth are virtually identical to those of the second posterior file of PIMUZ A/I 5181 except for having more strongly ornamented crowns. Teeth approaching the peculiar morphology of first posterior teeth of PIMUZ A/I 5181 are unknown in any other *Strophodus* species.

Second lateral teeth of *S. smithwoodwardi*, although morphologically similar, are readily distinguished from those of PIMUZ A/I 5181 by possessing a more complex ornamentation, which displays a prominent reticulate pattern that turns into frequently branching folds towards the edges of the crown (Peyer, 1946). *Strophodus rebecca* from the Valanginian–Hauterivian of Colombia, which is the stratigraphically youngest known *Strophodus* species, is easily distinguishable from PIMUZ A/I 5181 in having smaller and less elongated second lateral teeth with a parallelogram-shaped occlusal outline and rather low and flat crowns (Carrillo-Briceño & Cadena, 2022). In addition, first lateral teeth of *S. rebecca* have a trapezoidal rather than triangular outline in occlusal view. The remaining species currently included in *Strophodus* (viz., *S. longidens*, *S. reticulatus*, *S. medius*, *S. udulfensis* and *S. dunaii*) are clearly separated from PIMUZ A/I 5181 due to the presence of lateral teeth that are generally wider mesio-distally and more heavily and even more complexly ornamented (see Szabó & Főzy, 2020). Posterior



teeth, which are known in *S. reticulatus*, *S. medius* and *S. udulfensis*, are also fairly different from those of PIMUZ A/I 5181 (Leuzinger et al., 2017; Rees & Underwood, 2008).

In summary, given the unique combination of dental characters displayed by the herein described specimen PIMUZ A/I 5181 from the Bajocian of the Moroccan High Atlas Mountains, it is evident that it can be readily distinguished from any other *Strophodus* species known so far, thus justifying the erection of a new species, *S. atlasensis* sp. nov.

## Discussion

### Historical background and validity of *Strophodus*

The genus *Strophodus* has a long history of taxonomic study, but it was only recently that its taxonomic status has been clarified. *Strophodus* was initially erected by Agassiz (1838) on the basis of low-crowned durophagous crushing teeth from Triassic to Cretaceous strata of Europe. Later, after the discovery of *Strophodus* teeth associated with dorsal fin spines reminiscent of *Asteracanthus* Agassiz, 1837, originally founded upon isolated dorsal fin spines ornamented with stellate tubercles, *Strophodus* became a junior synonym of *Asteracanthus* (1889a; Woodward, 1888). This long accepted taxonomic scheme has recently been challenged by Stumpf et al. (2021b), who reported a hybodontiform skeleton from the Late Jurassic of Germany with tuberculated dorsal fin spines most similar to those of *Asteracanthus* and well-defined multicuspid grasping teeth that distinctly differ from the durophagous crushing teeth previously assigned to this genus. Consequently, given this unique combination of morphological characters, Stumpf et al. (2021b) proposed to resurrect *Strophodus* from synonymy with *Asteracanthus*. The genus *Asteracanthus*, whose stratigraphic range, as now understood, is Middle Jurassic (Bathonian) to Early Cretaceous (Valanginian), is currently considered monotypic to accommodate the single species *A. ornatissimus* Agassiz, 1837 only (for more details, see Stumpf et al., 2021b, 2022).

### Palaeoecology and distribution of *Strophodus*

*Strophodus* is certainly among the largest hybodontiforms to have ever lived, probably reaching a maximum body length between two and three meters, as inferred from its massive Meckel's cartilages, which may reach up to about 30 cm in maximum length (Woodward, 1888), similar to those seen in better known taxa, such as *Hybodus* Agassiz, 1837 and *Asteracanthus* (Stumpf et al., 2021b). The robust teeth of *Strophodus* form an effective crushing dentition that is consistent with a durophagous diet. Hard prey consumption is further supported by high degrees of dental wear (e.g., Rees & Underwood, 2008;

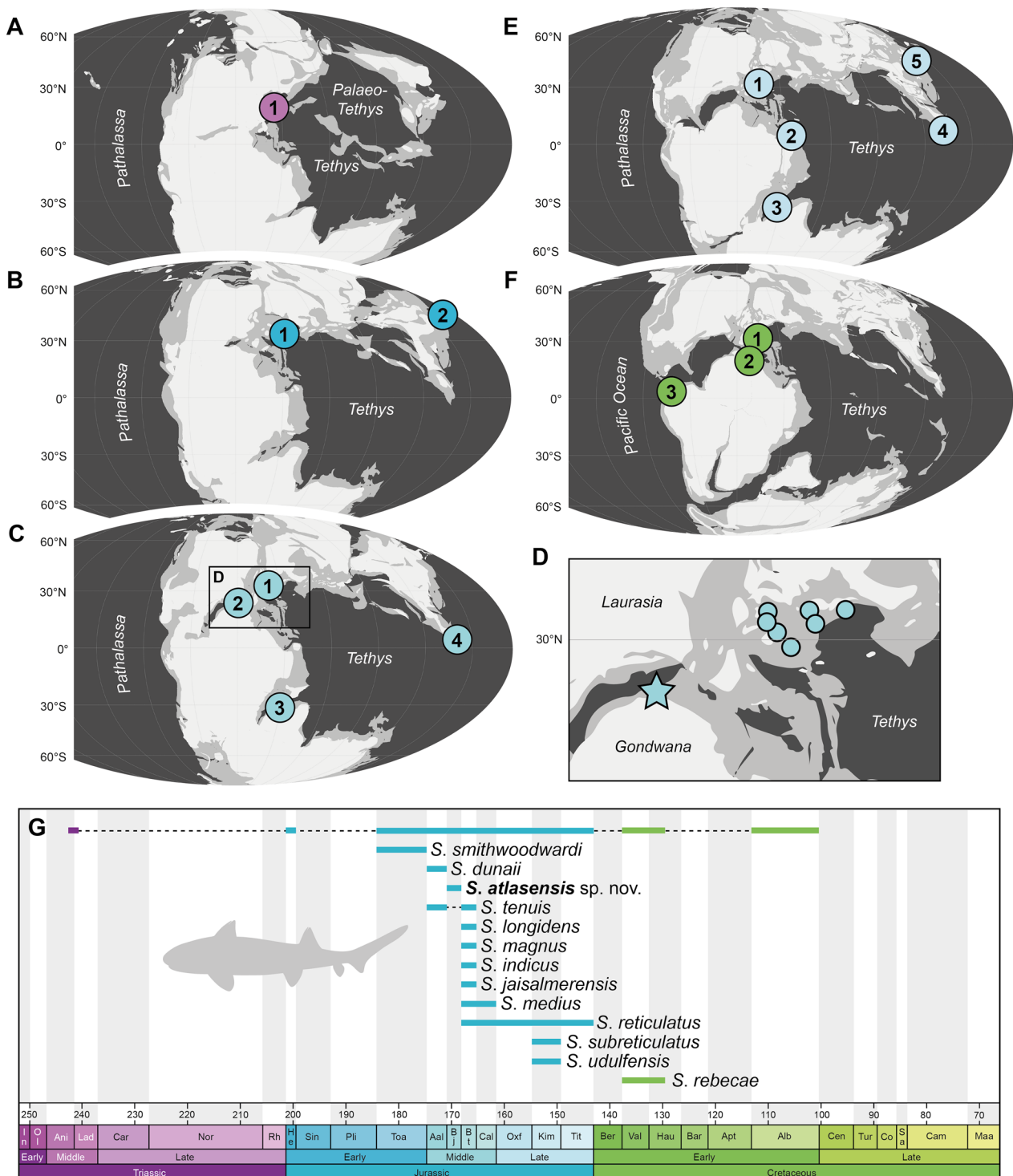
Rigal & Cuny, 2016), indicating that *Strophodus* have been capable of exploiting a wide variety of hard-shelled invertebrates.

*Strophodus* has generally been interpreted to be a bottom-dwelling taxon that predominantly preyed upon epifaunal hard-shelled invertebrates (Cappetta, 1987, 2012; Rees & Underwood, 2008), although isotopic data suggest an epipelagic rather than nektobenthic life-style (Anderson et al., 1994; Dromart et al., 2003; Lécuyer et al., 2003). In addition, isotopic data also provided evidence for a stress-tolerant euryhaline ecology, indicating that *Strophodus* have been well capable of migrating into low-salinity environments, possibly for reproduction (Leuzinger et al., 2015).

The fossil record of *Strophodus*, which extends for more than 130 million years, from the Middle Triassic (Anisian–Ladinian) to the late Early Cretaceous (Albian), suggests that the genus may have had a pan-tropical distribution, given that all reported occurrences are limited to palaeolatitudes between 60°N and 60°S (Fig. 4). This apparent pattern implies that the palaeogeographic distribution of *Strophodus* may have been temperature-controlled, which consequently would have hampered migration across the polar regions.

The western Tethys region may have acted as centre of origin (Fig. 4A), considering the oldest and hitherto only known Triassic record of *Strophodus* from the Monte San Giorgio Lagerstätte of Switzerland (Rieppel, 1981). From the Middle Triassic onwards, *Strophodus* apparently began to spread eastwards, reaching the western Panthalassa region by the Early Jurassic at the latest (Fig. 4B), as can be deduced from a single, badly preserved tooth from the Hettangian of Japan (Goto et al., 1991). An additional record from the Early Jurassic of Japan (Takakuwa & Gunma Fossil Club, 2011), together with rare reported occurrences from the Middle and Late Jurassic of Thailand (Cuny et al., 2005, 2009), suggest that *Strophodus* may have been a widespread inhabitant of Jurassic marine ecosystems along the eastern Eurasian shelf, although more evidence is needed to confirm this.

The European Early Jurassic record of *Strophodus* is rare and limited to a small number of specimens from Switzerland and Italy (Peyer, 1946; Romano et al., 2018). This is remarkable in that hybodontiforms have frequently been reported from numerous Early Jurassic localities across Europe since the nineteenth century (e.g., Charlesworth, 1839; Delsate & Duffin, 1993; Fraas, 1896; Kindlimann, 1990; Maisch & Matzke, 2016; Quenstedt, 1882; Rees, 1998; Stumpf & Kriwet, 2019; Woodward, 1889b). This apparent discrepancy may be explained by abiotic stress and/or biotic constraints, such as the availability of preferred food resources, which might have had an impact on *Strophodus* and its



**Fig. 4** Palaeogeographic maps (A–F) and stratigraphic chart (G) illustrating the spatial and temporal distribution of *Strophodus* (see Table 1 for more information). **A** Middle Triassic: 1, Switzerland. **B** Early Jurassic: 1, Switzerland and Italy; 2, Japan. **C** Middle Jurassic: 1, Europe; 2, Morocco; 3, India; 4, Thailand. **D** Western Tethys region during the Middle Jurassic depicting the reported occurrences of *Strophodus* from Europe (indicated by dots) and the type locality of *Strophodus atlasensis* sp. nov. near Talsint, Morocco (indicated by a star). **E** Late Jurassic: 1, Europe; 2, Lebanon; 3, India and Madagascar; 4, Thailand; 5, Japan. **F** Early Cretaceous: 1, France and Switzerland; 2, Tunisia; 3, Colombia

dispersal ability as opposed to more generalist feeding taxa, such as *Hybodus*, which is one of the most common hybodontiforms encountered in Early Jurassic strata from Europe (Delsate et al., 2002; Duffin, 1993, 1997, 2010).

*Strophodus* is rare in strata of early Middle Jurassic age, comprising rare teeth from the Aalenian of Europe (Quenstedt, 1858; Szabó, 2021; Szabó & Főzy, 2020; Vincent et al., 2013) as well as the herein described dentition from the Bajocian of the Moroccan High Atlas Mountains, whose stratigraphic age and paleogeographic positioning (Fig. 4C, D) renders *S. atlasensis* sp. nov. the oldest documented record of *Strophodus* from Gondwana known up to now. This suggests that *S. atlasensis* sp. nov. might have been endemic to the northern Gondwanan shelf, but more likely reflects a lack of sampling. By the late Middle Jurassic, *Strophodus* seems to have become more common and widespread, particularly in Europe from where it has been frequently reported (e.g., Knoll & López-Antoñanzas, 2014; Martill, 1991; Michelis et al., 1996; Rees & Underwood, 2008; Rigal & Cuny, 2016; Wills et al., 2019). Migrating southwards, probably along the eastern Gondwanan shelf, *Strophodus* must have reached the south-western Tethys region by the Bathonian at the latest (Kumar et al., 2021; Sharma & Singh, 2021), the time when *Strophodus* also reached its highest species diversity (Fig. 4G).

*Strophodus* is well represented by many teeth in Late Jurassic strata of Europe (see Stumpf et al., 2022, and references therein), followed by those from Asia (Cuny et al., 2005; Goto, 1994; Kumar et al., 2021) and two teeth from Madagascar (Priem, 1907, 1924) (Fig. 4E). Several teeth were also recovered from the Kimmeridgian of Lebanon (GC, pers. obs.).

Following a fluctuating trend during the Late Jurassic, the species diversity of *Strophodus* has significantly dropped by the Early Cretaceous, which parallels with a low number of reported occurrences from the Valanginian to Hauterivian of Europe and Colombia (Carrillo-Briceño & Cadena, 2022; Guinot et al., 2014; Peyer, 1946; Pictet & Campiche, 1858; Priem, 1912) (Fig. 4F). The Colombian records, which have recently been described by Carrillo-Briceño and Cadena (2022), are of special interest as they expand the known spatial distribution of *Strophodus* to the north-western Gondwanan shelf. As such, it appears reasonable to suggest that the Hispanic Corridor, initially established during the earliest Jurassic (see Sha, 2019, and references therein), might have served as a migration route, allowing *Strophodus* to expand westwards, from the western Tethys region to the eastern Panthalassa region. The youngest fossil records of *Strophodus* are represented by rare dental material from

the Albian of France and Tunisia (Priem, 1912; Tabaste, 1963).

Potential causes underlying the species decline and subsequent demise of *Strophodus* remain elusive but are likely to be multifactorial, perhaps involving both fluctuations in the relative availability of preferred food resources (note that marine hard-shelled invertebrates declined across the Jurassic/Cretaceous boundary; see Tennant et al., 2017, and references therein) and an increasing competitive overlap with crown group elasmobranchs (i.e., sharks and rays), which rapidly diversified during the Jurassic and Cretaceous (Guinot & Cavin, 2016; Kriwet et al., 2009; Underwood, 2006). Interestingly, the final demise of *Strophodus* coincides with the appearance of the giant durophagous shark *Ptychodus* Agassiz, 1834 (see Cappetta, 2012, and references therein), which quickly diversified into many different species soon after it first appeared during the Albian to become the most dominant Cretaceous durophagous predator to have ever lived (e.g., Shimada et al., 2009, 2010; Amadori et al., 2020, 2022, 2023; Jambura & Kriwet, 2020). This suggests that *Ptychodus* might have benefitted from the freed ecospace that was left in the wake of *Strophodus*' extinction.

## Conclusion

*Strophodus* is a diverse and widespread genus of extinct hybodontiform chondrichthyans, characterized by a unique heterodont dentition well-adapted to durophagy. First appearing in the Middle Triassic, *Strophodus* attained an almost global distribution by the late Middle and Late Jurassic, before finally vanishing at the close of the Early Cretaceous. However, as with other hybodontiforms, records of *Strophodus* from the early Middle Jurassic are poorly represented, and to date, only a few isolated teeth of *Strophodus* have been reported from the Aalenian of Europe. *Strophodus atlasensis* sp. nov., which is here recognized based on a single articulated dentition from the Bajocian of the Moroccan High Atlas Mountains, represents the hitherto oldest known record of *Strophodus* from Gondwana, and the first record of that genus from deposits of Bajocian age, casting new light on our understanding of Middle Jurassic hybodontiforms. Predating recently described occurrences from the Bathonian of India, the discovery of *S. atlasensis* sp. nov. suggests that *Strophodus* may have reached the southern Tethyan realm earlier than currently anticipated. Therefore, the search for fossil chondrichthyan remains in Jurassic, especially Early to Middle Jurassic strata of northern Africa, but also other regions of Africa, should be intensified in the future for better understanding the early evolutionary history of this enigmatic durophagous

chondrichthyan. The holotype and only specimen of *S. atlasensis* sp. nov. displays high degrees of dental wear, indicating that the new species was a highly specialized durophagous predator that hold a high trophic position in the Middle Jurassic Gondwanan marine food web.

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#### Author contributions

SS designed the study, wrote the manuscript, analysed the data and prepared the figures. CK generated the photogrammetric model and prepared the figures. All authors contributed and approved the initially submitted version of the manuscript. All authors read and approved the final manuscript.

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#### Availability of data and materials

The specimen shown in Figs. 2, 3 is housed in the Palaeontological Institute and Museum of the University of Zurich, Switzerland, and catalogued under the repository number PIMUZ A/I 5181. The 3D model of PIMUZ A/I 5181 is available on the online repository figshare (<https://doi.org/10.6084/m9.figshare.21741020>).

#### Declarations

#### Competing interests

The authors declare that they have no competing interests.

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