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THE FIRST RECORD OF THE ORECTOLOBIFORM SHARK GENUS *CEDERSTROEMIA* (ELASMOBRANCHII, ORECTOLOBIDAE) IN ASIA (KASHIMA FORMATION, UPPER CRETACEOUS; OYUBARI AREA, HOKKAIDO, JAPAN)

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Abstract: We described fossil teeth assigned to the orectolobiform shark genus, *Cederstroemia* collected from the tuffaceous sandstone of the Kashima Formation (Santonian) in the Oyubari area, Hokkaido, Japan. This is the first report of fossil remains of *Cederstroemia* from Asia. Due to the small number of specimens and their poor preservation, we left the studied material in open nomenclature as *Cederstroemia* sp. At the same time, the studied material may belong to a new previously undescribed morphology of *Cederstroemia*. The occurrence of *Cederstroemia* fossils in Japan indicates that this genus dispersed to the northwestern part of the Pacific Ocean in the Late Cretaceous, which considerably extends the range and previously known habitat of this genus.

INTRODUCTION

Despite their wide geographical extent along the Pacific Ocean, selachian fossils are quite rare in Upper Cretaceous strata of the northwest Pacific. Nevertheless, elasmobranch fossils from the Upper Cretaceous of Japan have a long history of palaeontological research (e.g. Yabe 1902; Nishimoto & Morozumi 1979; Goto 1994; Yabumoto & Uyeno 1994; Uyeno & Suzuki 1995; Goto et al. 1996; Kitamura 2013a, b, 2019; Kanno et al. 2017, 2022).

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In particular, Nishimoto and Morozumi (1979) have briefly reported on the occurrence of several selachian taxa, including *Hexanchus* aff. *microdon* (Agassiz, 1835), *Odontaspis* sp., *Plicatolamna* sp., *Pristiophorus* sp., *Scapanorhynchus texanus* (Roemer, 1849), in the Campanian - Maastrichtian deposits in Honshu Island. Subsequently, Uyeno and Suzuki (1995) additionally recorded *Cretoxyrhina mantelli* (Agassiz, 1835) and *Squalicorax falcatus* (Agassiz, 1843) from Campanian strata of Honshu Island. In regards to the Campanian-Maastrichtian deposits of the Nemuro Group of eastern Hokkaido Island, Uyeno and Matsui (1993) recorded the occurrence of *Notidanodon* cf. *N. lanceolatus* (Woodward, 1886), *Sphenodus* sp., *Scapanorhynchus* sp., *Centrophoroides* cf. *C. latidens* Davis, 1887. Later, Yabumoto and Uyeno (1994) summarized information on the Upper Cretaceous elasmobranchs from Hokkaido and northeastern Honshu Islands based on previous studies. Regarding the Santonian deposits of Kyushu Island, Kitamura (2019) reported on the presence several elasmobranch taxa, including one squaliform, seven hexanchiforms, eight lamniforms, one synechodontiform, one echinorhiniform, and two ptychodontiforms.

In recent decades, the Upper Cretaceous Yezo Group, which is broadly exposed on the Hokkaido Island, has become one of the most important units for studying and understanding the elasmobranch assemblages in the Northwest Pacific region during the Late Cretaceous. A number of elasmobranch taxa have been reported from these successions, including one hybodontiform, three ptychodontiforms, seven hexanchiforms, one squaliform, five lamniforms, and two echinorhiniforms (e. g. Goto et al. 1996; Tomita & Kurihara 2011; Kanno et al. 2017, 2022).

Since 2009, one of the authors, (KM) has been investigating elasmobranch fossils in tuffaceous sandstone of the Santonian Kashima Formation (Yezo Group), which is distributed in the Shuparo River basin in the Kashima District, Yubari City, Hokkaido. Thirty-five taxa have been identified to date, including one echinorhiniform, twelve carcharhiniforms, nineteen lamniforms, two heterodontiforms, and one synechodontiform (Kaneko et al. 2012; Kaneko et al. 2015; Kaneko et al. 2019; Kaneko & Fujimoto 2022; Kaneko 2024).

In the present paper, we describe in detail the first occurrence of the orectolobiform shark genus *Cederstroemia* in Asia, based on isolated teeth from the Santonian Kashima Formation (Yezo Group) in Yubari City, Hokkaido, Japan.

Teeth assigned to the genus *Cederstroemia* were originally included in another orectolobiform shark genus, *Cretorectolobus* (Case, 1978). Later, Siverson (1995) established the genus *Cederstroemia* and included it along with *Cretorectolobus* in Orectolobiformes family *incertae sedis* (Siverson 1995; Guinot et al. 2013). According to Cappetta (2012), Ebersole et al. (2022), and Jambura et al. (2024), *Cederstroemia* belongs to the family Orectolobidae.

Currently, five valid species are believed to belong to *Cederstroemia*, namely *Cederstroemia havreensis* (Herman, 1977) from the Campanian of Belgium; *Cederstroemia nilsi* Siverson, 1995 from the Campanian of Sweden; *Cederstroemia siverssoni* Guinot, Underwood, Cappetta and Ward, 2013 from the middle Turonian of France; *Cederstroemia triangulata* Siverson, 1995 from the Campanian of Montana, USA; and *Cederstroemia ziaensis* Bourdon, Wright, Lucas, Spielmann and Pence, 2011 from the Santonian of New Mexico, USA.

The occurrence of the genus *Cederstroemia* is distributed in the Northern Hemisphere, including France (e.g., Landemain 1991; Biddle 1993; Guinot et al. 2013), Ukraine (Sokolsky & Guinot 2021), the UK (Guinot et al. 2013), European Russia (e.g., Ebersole et al. 2022; Solonin et al. 2023; Jambura et al. 2024), Sweden (Siverson 1995; Sørensen et al. 2013), and the USA (e.g., Bourdon et al. 2011). However, the occurrence of *Cederstroemia* has not been previously reported in the Asian Northwest Pacific.

The studied *Cederstroemia* material from the Kashima Formation provides us with important information for discussing the paleogeography of the genus *Cederstroemia* and its dispersal process in the Late Cretaceous.

GEOLOGICAL SETTING

The tuffaceous sandstone bed where the fossils were obtained is exposed on the riverbed of the Shuparo River near Titose-cho, Kashima District, Yubari City (Fig. 1). This area has been submerged by a lake due to the completion of the Yubari Shuparo Dam in 2015.

The geologic exposures at the riverbed of the Shuparo River near Titose-cho, Kashima District, Yubari City consist of the Upper Cretaceous Kashima Formation. In the river bed around this area, a dark gray mudstone bed with an almost vertical inclination direction is exposed, and a turbidite tuffaceous sandstone bed with parallel lamination is observed. Fossils shark teeth, including *Cederstroemia*, were found in a dense bed of shell bioclasts contained in a medium-grained sandstone bed with a thickness of about 1 m.

The dense layer is about 20 cm thick and consists mainly of bivalves and small gastropods presumed to be species of *Inoceramus*, *Ostrea*, and *Na-*

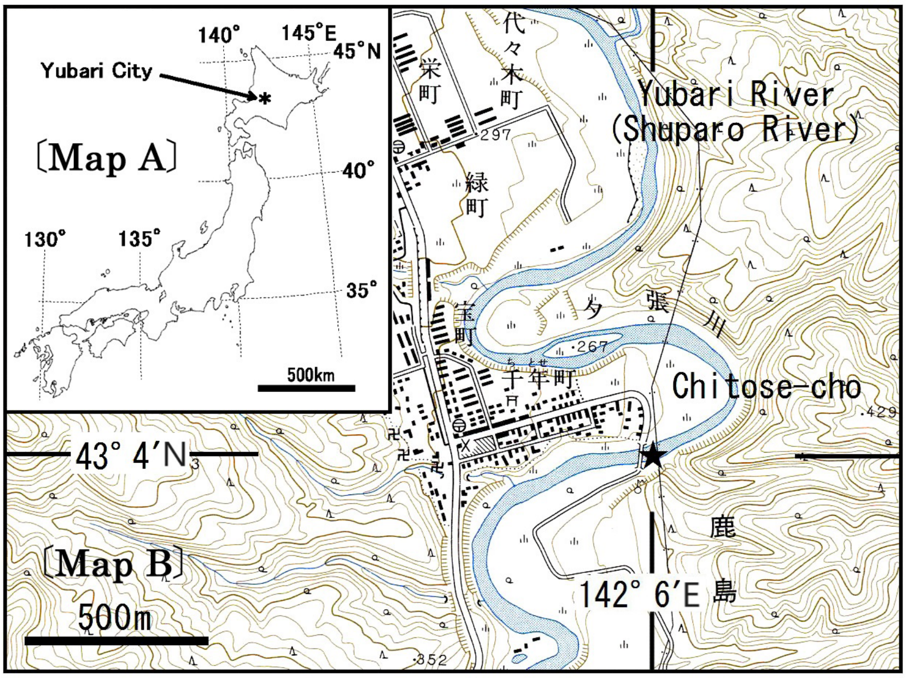

Fig. 1 - Geographic maps of Japan. Map A) map of Japan showing the location of the Yubari City (a black asterisk). Map B[1]): map of the region around Yubari City showing the position of the studied locality where the fossils of *Cederstroemia* were collected. [1]The topographical map of «Shuparo lake» scale 1:25000 published in 1989 by the Geospatial Information Authority of Japan.

nonavis, and many glauconite particles less than 0.2 cm in diameter. It also contains sporadically flat mudstone pseudo-pebbles of 2-20 cm in length.

Fragments of *Inoceramus* are usually less than 5 cm in size, but include relatively large fragments identified as *Inoceramus amakusensis* Nagao et Matsumoto, 1940, which are more than 20 cm in rare cases.

Fossilized shark teeth are scattered in this dense layer and are mostly well preserved without significant wear.

The Kashima Formation, named by Motoyama et al. (1991), is mainly composed of dark gray massive mudstone that has undergone strong bioturbation with numerous tuff sandstone beds or tuff layers with a thickness of less than 1 m (Takashima et al. 2004, 2018).

The age of the Kashima Formation has been the subject of debate for several decades (Motoyama et al. 1991; Toshimitsu et al. 1995; Takashima et al. 2004). Traditionally, the age of this formation is considered as Turonian to the Campanian based on microfossils (Takashima et al. 2004). However, a number of studies consider the age of the Kashima Formation as Coniacian (Yamada 2009), as Coniacian – Santonian (Tanaka et al. 2017), or as the Santonian-Campanian boundary (Matsui & Karasawa 2020). In addition, Kaneko et al. (2012, 2015) found *I. amakusensis* in rocks where fossilized shark teeth were collected, which has been correlated with the Santonian (Toshimitsu et al. 1995). Following this, we consider the age of the sedimentary rocks of the Kashima Formation exposed on the riverbed of the Shuparo River near Titose-cho, Kashima District, Yubari City where the described material was collected as Santonian.

According to Kaneko et al. (2012) the fossil-dense layer in which the shark teeth were discovered is considered to be an allochthonous fossil group assemblage, with transported shells and other materials entwined in turbiditic sandstone. Based on the benthic foraminiferal assemblages the depositional environment of the Kashima Formation reflects the upper part of the upper bathyal environment with medium- to relatively high-oxygen levels (Takashima et al. 2004).

Material and methods

All of the specimens documented here were collected from the riverbed of the Shuparo River basin in the Kashima district of Yubari City, Hokkaido (Japan). This collection consists of four specimens in total, each comprising a slightly damaged to incomplete tooth. All specimens (MCM-A2575 to MCM-A2578) are housed in the Mikasa City Museum.

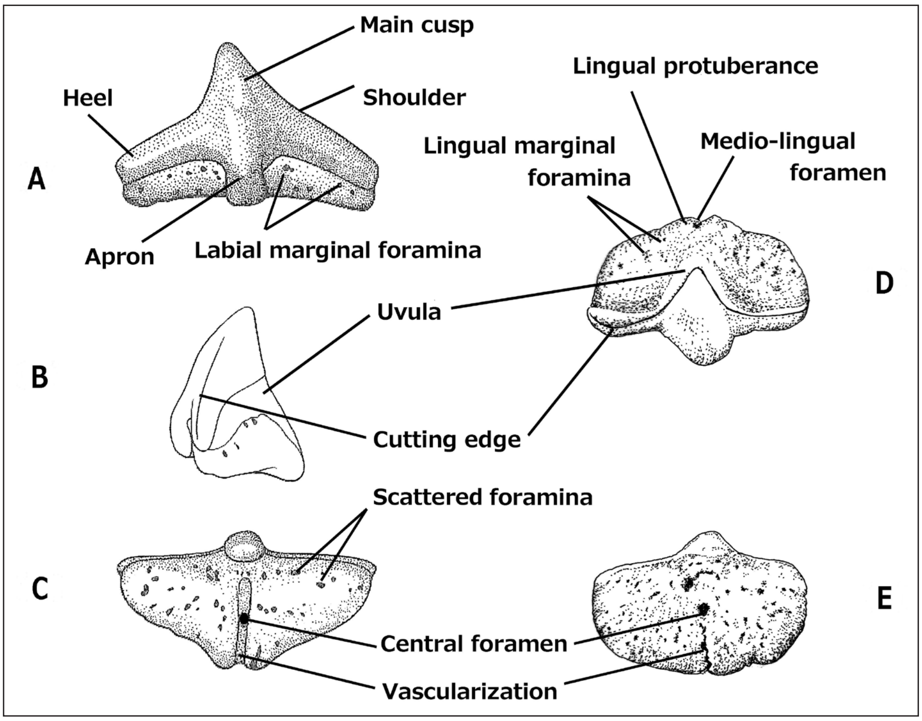

Fig. 2 - Dental terminology used for the morphological description of the teeth of *Cederstroemia*. The graphic drawings used here are modified from Cappetta (2012, fig. 144a-c) for A - C, and Siverson (1995, fig. 2) for D, E. Not to scale.

Formic acid treatment was carried out in order to extract the specimens from the host rock. Formic acid was used in a fume hood after diluting 78% industrial grade (Mitsubishi Gas Chemical Co., Ltd.) into a 5-7% aqueous solution. Kaneko et al. (2015), Kaneko and Fujimoto (2022) were used as references for the process of treatment with formic acid. The main component of the gas generated during the acid treatment work is carbon dioxide, but it also contains trace amounts of harmful components such as sulfur dioxide, so it was discharged through a water tank as a trap.

Photographs of the specimens were taken with a Nikon D300S DSLR mounted with an 80-400 mm lens as an imaging lens and a Mitutoyo M Plan Apo 5X as an objective lens. Illustrative drawings, images of the specimens and graphics were prepared using the Combine ZM stacking software, NX Studio (Ver. 1.3.2 Nikon Corporation) and Adobe Photoshop CC 2017 (v. 2017.04.25.r.252).

Systematics according to Ebersole et al. (2022). Tooth terminology follows Cappetta (1987, 2012), Siverson (1995), Yabe & Goto (1999), Guinot et al. (2013) and Ebersole et al. (2022). Based on that, we provide a general outline of dental terminology used for the morphological description of teeth of a species of *Cederstroemia* (Fig. 2).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Infraclass ELASMOBRANCHII Bonaparte, 1838
Order **Orectolobiformes** Applegate, 1972
Family Orectolobidae Jordan & Fowler, 1903
Genus *Cederstroemia* Siverson, 1995

Cederstroemia sp.

Fig. 3

Material: MCM-A2575 (slightly damaged anterior tooth, Fig. 3, 1a-1e), MCM-A2576 (slightly damaged lateral tooth, Fig. 3, 2a-1g), MCM-A2577 (partially preserved lateral tooth, Fig. 3, 3a-3e), MCM-A2578 (partially preserved antero-lateral tooth, Fig. 3, 4a-4d).

Description. The teeth have a maximum height of up to 2.75 mm and a width of up to 5.12 mm (in anterior tooth MCM-A2575). The teeth have a low cusp with high shoulders in MCM-A2575 and relative low shoulders in MCM-A2576-MCM-A2578. The cusps are slightly inclined distally. In comparison, the mesial shoulder is high and the distal shoulder is low. The cusp is thick labiolingually in lateral view and divided labiolingually by a clear cutting edge. The cutting edge does not form a blade. There are mesial and distal heels. The heels are very high and strongly inclined. There is a wide centrally located apron which extends beyond the base of the tooth root, with a missing lower part in MCM-A2575 and MCM-A2578. Both sides of the apron are concave in MCM-A2575 and rectangular in MCM-A2576- MCM-A2577 with slightly concave center of the apron's extremities. The enameloid of the crown is generally smooth, but in MCM-A2576 there are several rough, short, linear ornaments situated at the base of the lateral heels on lingual and labial sides (Fig. 3, 2c, 2f-g). An indistinct uvula that is not covered by enameloid from the lower center of the cusp to the end of the root. The root is thick in lingual view. Multiple lingual marginal foramina are situated between the border with the crown and the lingual protuberance, and a median lingual foramen opens at the lingual protuberance. The basal surface of the root is sub-rectangular, with a small centrally located foramen (hemiaulacorhize vascularization) and multiple small scattered foramina across the basal surface.

Remarks. The combination of morphological features of the fossil teeth described above allow us to attribute them to a species of *Cederstroemia*. The distinctive features of teeth of this genus are presented in detail below (see «Morphological features of *Cederstroemia, Cretorectolobus* and *Squatina* teeth» and Tab. 2). The specimens described here closely resemble the type material of late Campanian *C. havreensis* from Belgium and early Campanian *C. nilsi* from Sweden. Fossils of these chondrichthyan taxa are to date only known from Europe. *C. havreensis* mainly differs from *C. nilsi* in exhibiting a labial, rarely also lingual, ornamentation on the tooth crown, whereas *C. nilsi* is lacking any ornamentation on the crown (Guinot et al. 2013; Jambura et al. 2024, see «Distinctive features of the teeth of valid *Cederstroemia* species», and Tab. 3). The available *Cederstroemia* material is limited to four incompletely preserved teeth, three of which are lacking any ornamentation and are similar to *C. nilsi*. However, some subtle features, including ornamentation, may have worn away on these teeth. In addition, one tooth (MCM-A2576) is similar to *C. havreensis* in that it has a linear ornamentation on the tooth crown (Fig. 3, 2f-g). At the same time, it may be a previously undescribed new Asian species of this genus. Further detailed studies may confirm or refute this hypothesis. Due to the small number of specimens and poor preservation, we tentatively left this material in open nomenclature.

COMPARISON OF THE TOOTH MORPHOLOGY

Morphological features of *Cederstroemia, Cretorectolobus* and *Squatina* teeth

Squatina-type (Squatiniformes) morphology teeth have a main cusp that is triangular in labial view with lateral shoulders extending mesially and distally and with well-developed lateral heels, an apron on the labial side, a wide lingual protuberance, and a transversely elongated root with a flat and wide root base (Siverson 1995). This type is characteristic of the teeth of orectolobiform shark genera, *Cretorectolobus* and *Cederstroemia* in addition to those of the genus *Squatina* (Squatiniformes) (see Tab. 2).

Due to the high degree of similarity, teeth of *Cederstroemia* are often mistakenly attributed to the *Squatina* (e.g. Ebersole et al. 2022). This is particularly probable if fossil teeth come from the same locality, and it is highly likely that *Cederstroemia* tooth fossils are included in the reported *Squatina* tooth fossil record. Identification is possible, although extremely difficult, especially when considering incomplete specimens.

In the current paper we have summarized the data on the tooth characteristics of the three genera, *Squatina*, *Cretorectolobus*, and *Cederstroemia*, based on available literatures sources and personal observations.

The combination of features described below allows us to identify these taxa more confidently. In basal view, the root of the *Squatina* teeth are more often triangular to diamond-shaped with a clear central foramen on basal face. The root has a large depression from the center to the labial side with hemiaulacorhize vascularization but never holaulacorhize vascularization. The root of the *Cretorectorobus* and *Cederstroemia* teeth on the other hand is triangular to rectangular in shape, with holaulacorhize or hemiaulacorhize vascularization with a strongly oblique profile. The teeth of the *Cederstroemia* and *Cretorectolobus* have the low cusps, relatively high and more oblique lateral shoulders and more elongated and parallel-sided labial protuberance, whereas the cusps of the *Squatina* teeth is high and the lateral shoulders relatively low and straighter. In addition, some teeth of *Cretorectorobus* have lateral shoulders with cusplets. The cuspidate lateral shoulders are missing in *Squatina* and *Cederstroemia* teeth (Case 1978; Siveson 1996; Cappetta 2012; Guinot et al.

2012; Guinot et al. 2013; Siverson et al. 2016; Hoganson et al. 2019; Ebersole et al. 2022; Jambura et al. 2024). It should be underlined that a combination of a number of the characteristics listed above is required for reliable identification.

Distinctive features of the teeth of valid *Cederstroemia* species

As mentioned above, the genus *Cederstroemia*, consists of five valid species: *Cederstroemia siverssoni*, *C. ziaensis*, *C. nilsi*, *C. triangulata* and *C. havreensis*. However, with the exception of *C. havreensis*, which was described based on the examination of about one hundred fossil teeth, each description was based on a small number of specimens, including incomplete specimens. Consequently, identification is potentially open to consideration.

In this paper, we compared the morphological characteristics of the five species based on comprehensive literatures sources and personal observations and summarized their distinguishing features (see Tab. 3) that are described below.

Teeth of *C. siverssoni* and *C. havreensis* are large in size, with a maximum width of 13-15 mm, and their teeth have the vertical ridges on the lateral extremities of the lingual face of the heels or rarely also on the labial face in *C. havreensis* (Guinot et al. 2013). However, the maximum size of the other three species is less than 10 mm, and the crown surfaces of all tooth types are smooth (Siverson 1995; Bourdon et al. 2011; Guinot et al. 2013). Meanwhile the medio-lingual foramen of *C. siverssoni* is wide and oval, whereas the medio-lingual foramen of *C. havreensis* is small and round (Guinot et al. 2013). Additionally, teeth of the *C. havreensis* can be separated from *C. siverssoni* on the basis of their lingually oriented lateral extremities of the cutting edges, less densely arranged and less organized marginolingual foramina, more elongate lingual protuberance of the crown and generally more bulky and shorter apron (Guinot et al. 2013). Teeth of *C. havreensis* and *C. nilsi* closely resemble each other. Nevertheless, *C. havreensis* mainly differs from *C. nilsi* in exhibiting a labial, rarely also lingual, ornamentation on the tooth crown, whereas *C. nilsi* is lacking any ornamentation on the crown (Guinot et al. 2013; Jambura et al. 2024). Teeth of the *C. triangulata* and *C. ziaensis* have a basal face of the root that is subtriangular in outline with a straight labial bord, thereby differentiating this taxon from other species. However, in the teeth of *C. ziaensis* the cusp and mesial shoulders of lateral positions merge much more smoothly than those of *C. triangulata* or *C. nilsi* (Bourdon et al. 2011).

The variation of the root vascularization seems to be a poor character to distinguish species (Jambura et al. 2024). Nevertheless, we will briefly note this in order to have a comprehensive understanding of morphological features and variability. The holotype anterior tooth of *C. havreensis* is intermediate between the hemiaulacorhize and holaulacorhize stage, with a labiolingually very elongated central foramen (Siverson 1995). The root vascularization of *C. triangulata* is at the hemiaulacorhize or at the holaulacorhize, but the furrows are very deep, making it clearly distinguishable from the other four species. The root vascularization in *C. nilsi* teeth is characterized by a hemiaulacorhize stage in all teeth, with a small circular central foramen located slightly lingually of the center of the root (Siveson 1995). *C. ziaensis* has a hemiaulacorhize root in all specimens and a large central foramen located labially at the base of the tooth, whereas the other four species have numerous scattered foramina (Bourdon et al. 2011).

DISCUSSION

Palaeobiogeographic implications and significance of the occurrence of *Cederstroemia* in the Asian North Pacific region.

There are still few reports of fossil occurrences for *Cederstroemia*, of which all previous reports were limited to Europe and North America (Fig. 4 and Tab. 1) forming many gaps in the spatiotemporal and geographical distribution of this genus.

Fig. 3 - *Cederstroemia* sp. teeth from the Yubari City in Hokkaido, Japan. 1a-1e) MCM-A2575, anterior tooth: 1a, labial view, 1b, lingual view, 1c, profile view, 1d, occlusal view, 1e, basal view. 2a-2g) MCM-A2576, lateral tooth: 2a, labial view, 1b, lingual view, 2c, profile view, 2d, occlusal view, 2e, basal view, 2f, close-up of the labial side of the heel, 2g, close-up of the lingual side of the heel. 3a-3e) MCM-A2577, lateral tooth, 3a, labial view, 3b, lingual view, 3c, profile view, 3d, occlusal view, 3e, basal view. 4a-4d) MCM-A2578, antero - lateral tooth, 4a, labial view, 4b, lingual view, 4c, profile view, 4d, occlusal view. All scale bars represent 1 mm.

FIGURE 3

Tab. 1 - The localities of the occurrences of fossils of *Cederstroemia*. Notes: [1]originally Biddle (1993) described material as «*Squatina mülleri*» and *Cretorectolobus* sp; [2]originally Landemaine (1991) described material as *Cretorectolobus* cf. *mülleri* and *Cretorectolobus* sp.; [3]originally Reuss (1846) described material as *Squatina muelleri.;* [4]originally Case (1978) described material as *Cretorectolobus olsoni.*

Species	**Locality**	**Age**	**References**
Cederstroemia siverssoni	Grand Est, France	Albian	[1]Biddle (1993)
—	Nouvelle-Aquitaine, France	Cenomanian	[2]Landemaine (1991)
—	Grand Est, France	Middle Turonian	Guinot et al. (2013)
—	Czech Republic	?Cretaceous	[3]Reuss (1846)
Cederstroemia cf. *siverssoni*	Cherkasy Oblast, Ukraine	Albian	Sokolskyi, T. & Guinot, G. (2021)
—	East of England, England	Early Cenomanian	Guinot et al. (2013)
—	South East England, England	Middle Cenomanian	Guinot et al. (2013)
—	Antrim, North Irland	Early Coniacian	Guinot et al. (2013)
Cederstroemia ziaensis	New Mexico, USA	Santonian	Bourdon et al. (2011)
Cederstroemia nilsi	Orenburg Oblast, Russia	Santonian-Campanian	Jambura et al. (2023)
—	Skane, Sweden	Early Campanian	Siverson (1995); Sørensen et al. (2013)
Cederstroemia triangulata	Montana, USA	Late Campanian	Siverson (1995); [4]Case (1978)
Cederstroemia havreensis	South East England, England	Late Santonian	Guinot et al. (2013)
—	South East England, England	Early Campanian	Guinot et al. (2013)
—	Hauts-de-France, France	Early Campanian	Guinot et al. (2013)
—	Grand Est, France	Early Campanian	Guinot et al. (2013)
—	Belgium	Campanian	Herman (1977)
Cederstroemia sp.	Kursk Oblast, Russia	Albian-Cenomanian	Solonin et al. (2023)
—	Ryazan Oblast, Russia	Cenomaian-Santonian	Solonin et al. (2020)
—	**Hokkaido, Japan**	**Santonian**	**This paper**
—	Saratov Oblast, Russia	Late Campanian	Ebersole et al. (2022)
—	Wyoming, USA	Maastrichtian	Wroblewski (2004)

Tab. 2 - Morphological features of *Cederstroemia, Cretorectorobus* and *Squatina* teeth.

Features	***Cederstroemia***	***Cretorectolobus***	***Squatina***
Outline of teeth (labial view)	triangular	triangular	triangular
Outline of cusp	triangular	predominantly cone-shaped	cone-shaped or triangular
Cusp height	relatively low	relatively low	relatively high
Lateral shoulders shape	more oblique	more oblique	more straight
Lateral shoulders height	relatively high	relatively high	relatively low
Heels	well-develop	well-develop	well-develop to almost non-existing
Cusplets	non-existing	one pair present on some teeth	non-existing
Cutting edge	well-developed, sharp (not blade), the cutting edges of the heels join up very progressively the cutting edges of the cusp	well-developed, not sharp	well-developed, sharp (blade)
Apron	robust, elongated, with rectangular extremities	relatively short and narrow with rounded extremities	relatively short with rounded extremities
Lingual protuberance of the crown	particularly high and oblique	broad and rather high	well-develop, low and often strongly elongated
Lingual protuberance of root	high and short	relatively short	low, broad, often strongly elongated
Ornamentation	short subvertical ridges are often present on labial and rare lingual face of the heels (in some species)	non-existing	weak labial ornamentation of the heel in some teeth
Outline of basal face	triangular to rectangular	triangular to rectangular	triangular to diamond-shaped
Root profile	strongly oblique	strongly oblique	not oblique, elongated
Bulkiness of the root	stouter	relatively thin	relatively thin
Root vascularization	hemiaulacorhize or holaulacorhize	hemiaulacorhize or holaulacorhize	hemiaulacorhize
Central foramen	opens in hemiaulacorhize teeth	opens in hemiaulacorhize teeth	clearly expressed in most teeth
Median lingual foramen	well develop in most teeth	well develop in most teeth	well develop in most teeth
Lingual marginal foramina	numerous	numerous	numerous
Scattered foramina	numerous	numerous	numerous

Tab. 3 - Distinctive features of the teeth of valid *Cederstroemia* species.

Features	***C. siverssoni***	***C. nilsi***	***C. havreensis***	***C. triangulata***	***C. ziaensis***
Maximum width (mm)	up to 15	up to 9	up to 15	up to 10.5	up to 7.5
Cusp	triangular in shape, low and bulky, broadly united to heels	conical in shape, bulky, erect and better demarcated from the	conical in shape, bulky, erect and better demarcated	triangular in shape, relatively low and poorly demarcated	triangular in shape, thick, lingually directed
Lateral shoulders	high, elongate	high, relatively short	high, relatively short	high, relatively short	high, elongate, merge much more smoothly with the cusp than in
Heels	high, elongate, sub-horizontal in anterior teeth and strongly	relatively short, high and oblique, softly rounded	relatively short, high and oblique	relatively short, high and oblique	relatively elongate
Cutting edge	sharp, labial oriented	sharp, lingual oriented	sharp, lingual oriented	sharp	smooth
Apron	subrectangular in shape, very elongate (reaching or overtking	subtriangular in shape, bulky, short (not reaching baseline of	parallel-sided, bulky, wide, rounded lower extremity reaching	bulky, elongate (reaching reaching baseline of root)	elongate (reaching or overtking the baseline of tooth),
Lingual protuberance	short	elongate	elongate	elongate	relatively short
Ornamentation	vertical ridge on the lingual surface of the heels in some teeth	smooth	subvertical ridges on lingual face and sometimes on labial	smooth	smooth
Outline of basal face	rectangular	subrectangular	subrectangular	subtriangular	subtriangular
Root vascularization	hemiaulacorhize to partially holaulacorhize	hemiaulacorhize and holaulacorhize in some teeth	intermediate between the hemiaulacorhize and holaulacorhize	holaulacorhize and hemiaulacorhize in some teeth	hemiaulacorhize
Central foramen	clear, lingually oriented	clear, circular, labially oriented	clear, elongated	clear and large, mostly elongated	clear, labially oriented
Median lingual foramen	broad, elliptical in shape	small, circular	small, circular	circular to elongate	very small, circular
Lingual marginal foramina	smaller, more numerous and well organized	smaller, less densely arranged and less organized	smaller, less densely arranged and less organized, elliptical	relatively large in size, rare	rare
Scattered foramina	numerous	numerous	numerous	numerous	rare

Fossil teeth of this genus have only been found at relatively high paleolatitudes between 30° and 65° north latitude, including the Anglo-Paris Basin (UK and France), the peri-Tethys sea (Ukraine, Russia), the Western Interior Seaway (New Mexico, Wyoming, Montana), and presently the Asian North Pacific (Japan) (e.g., Siverson 1995; Bourdon et al. 2011; Guinot et al. 2013; Ebersole et al. 2022; Solonin et al. 2023). In addition, the fossil teeth of *Cederstroemia* sp. described in this paper of this genus from Japan (Hokkaido) were discovered at approximately 43°N, and as mentioned above, the paleoenvironment between 30° to 65°N palaeolatitudes is suitable for this genus to live. The origin of this genus is unknown, but there are clues to its origin from the Anglo-Paris Basin to the peri-Tethys sea in Russian platform area. The oldest known fossils of this genus are from Albian of France (Grand Est), Ukraine (Cherkasy Oblast) and Russia (Kursk Oblast) (Guinot et al. 2013; Sokolsky & Guinot 2021; Solonin et al. 2023). The position of the epicontinental seas from the Anglo-Paris Basin to the western part of Russian platform area during the Late Cretaceous would have greatly favored a subsequent spread of elasmobranchs throughout the entire peri-Tethys (Amadori et al. 2022). In the Late Cretaceous *Cederstroemia*, like other elasmobranchs (e.g., *Ptychodus*), probably exploited this epicontinental seaway to migrate along the peripheral areas of the Neo-Tethys Ocean (e.g., Asian peri-Tethys) and to access the northwestern margin of the paleo-Pacific Ocean.

At the same time, the dispersal of the fish fauna was not restricted exclusively to this route. Biogeographic trends for dispersal between northeast Asia and North America were previously reported for bony fishes (Cavin 2008). Therefore, the dispersal of elasmobranchs may have a similar biogeographic trend in the most favorable periods, when elasmobranchs could disperse between epicontinental seas of Northeast Asia and North America. This hypothesis though needs further detailed study and verification.

As previously reported by Kitamura (2019), the characteristics of the Late Cretaceous shark fauna of the Japanese Islands are similar to those of the contemporaneous Southern Hemisphere fauna (e.g. Angola, Australia, and Antarctica). Kitamura (2019) concluded that the typical Southern Hemisphere shark taxa (e.g. *Notidanodon den-*

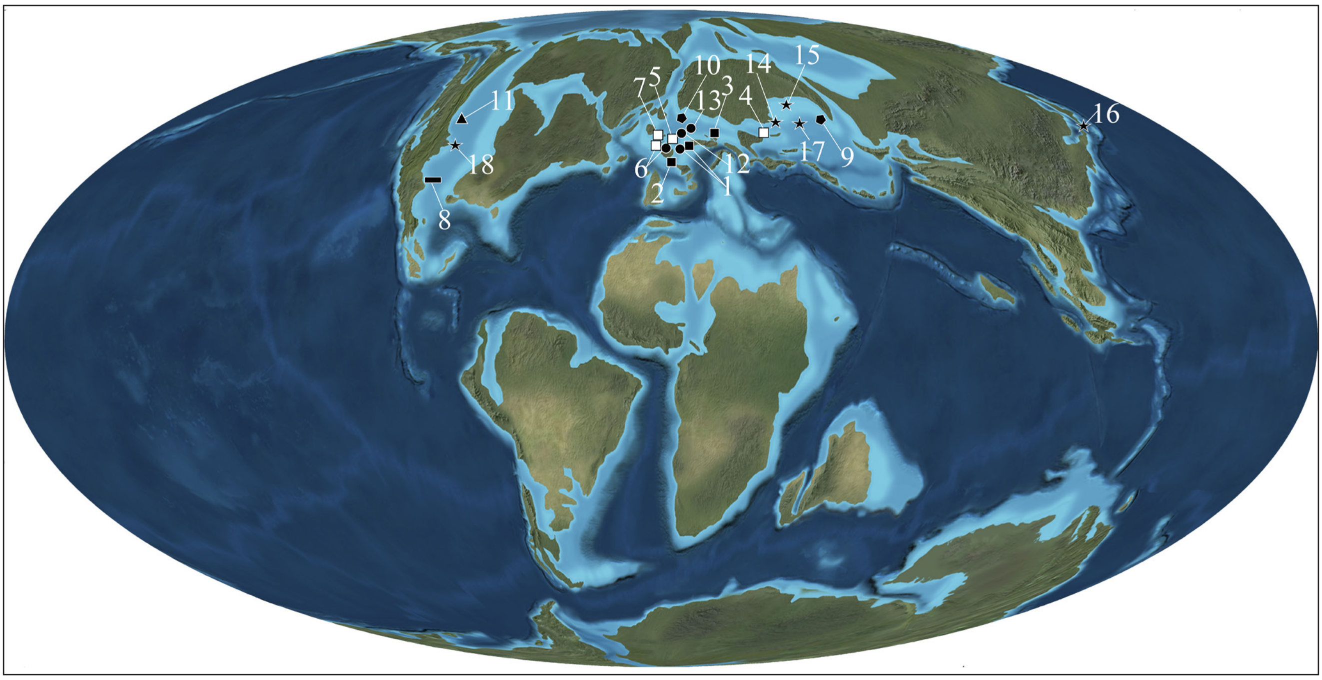

Fig. 4 - Reconstruction of the paleogeography during the Santonian, with indication of the localities of the cited *Cederstroemia* fossils occurrences. 1. Grand Est, France; 2. Nouvelle-Aquitaine, France; 3. Czech Republic; 4. Cherkasy Oblast, Ukraine; 5. East of England, England; 6. South East England, England; 7. Antrim, North Irland; 8. New Mexico, USA; 9. Orenburg Oblast, Russia; 10. Skane, Sweden; 11. Montana, USA; 12. Hauts-de-France, France; 13. Belgium; 14. Kursk Oblast, Russia; 15. Ryazan Oblast, Russia; 16. Yubari, Japan; 17. Saratov Oblast, Russia; 18. Wyoming, USA. Symbols: black square – *Cederstroemia siverssoni*, white square - *Cederstroemia* cf.*siverssoni*, black rectangle – *C. ziaensis*, black pentagon – *Cederstroemia nilsi*, black triangle – *Cederstroemia triangulata*, black circle - *Cederstroemia havreensis*, black star – *Cederstroemia* sp. Map modified from Byrum & Lieberman 2021; Solonin et al. 2021.

tatus (Woodward, 1886), *Chlamydoselachus* sp.) had the opportunity to spread to the middle latitudes of the Northern Hemisphere by the Late Cretaceous (Kitamura 2019). At the same time, based on the currently available data, the north-south distribution of elasmobranchs faunas was not predominant and taxonomic coincidence between elasmobranchs fauna of the Japanese Islands and assemblages of elasmobranchs of the Southern Hemisphere is less pronounced. In particular, previous studies of elasmobranchs of the Japanese Islands (e.g. Goto et al. 1996; Kaneko et al. 2015, 2019; Kanno et al. 2022) show a significant taxonomic overlap between the Upper Cretaceous elasmobranchs of Europe, North America and Japanese islands, which may indicate a practically unhindered dispersal between these regions of the Northern Hemisphere in the Late Cretaceous, meanwhile apparently in different directions.

Further detailed studies of marine faunas, including elasmobranchs, in Northeast Asia and in the whole paleo-Pacific region will help to clarify and improve our understanding of these events.

Conclusion

This report results from the examination of four fossil teeth recovered from the Kashima Formation (Santonian) of the Upper Cretaceous Yezo Group, Hokkaido, belonging to the orectolobid shark genus, *Cederstroemia*. This study represents the first report of the occurrence of this genus in Asia and in the Western Pacific region as a whole. Due to the small number of specimens and poor preservation, we left this material in open nomenclature as *Cederstroemia* sp. At the same time, the material described here may belong to a new previously undescribed morphology of *Cederstroemia*, although further materials is needed to test this hypothesis.

Following Cappetta (2012), Ebersole et al. (2022), and Jambura et al. (2024), we currently consider *Cederstroemia* as belonging to the family Orectolobidae. The teeth of the orectolobid shark genera, *Cretorectolobus* and *Cederstroemia* are characterized by a *Squatina*-type morphology, which is observed in the squatiniform shark genus *Squatina*. Meanwhile, the teeth of the orectolobid shark genera

Cederstroemia and *Cretorectolobus* differ from the teeth of *Squatina* in a number of distinctive features as a higher and more oblique lateral shoulder, much lower cusps, a strongly oblique root profile, and more elongated and parallel-sided labial protuberance. Here, we have examined the distinctive features of five valid *Cederstroemia* species, although we identify problems with differentiating between certain species if in the absence of well-preserved material.

The Japanese *Cederstroemia* fossils record fills the gap between its European and North American contemporaries, further improving our understanding of the distribution of *Cederstroemia* in particular, and of elasmobranchs in general in the Late Cretaceous seas of the Northern Hemisphere.

Further sampling of the fossil teeth of *Cederstroemia* from Kashima Formation will improve and clarify the identification of the fossil material, including the one we described in the present paper.

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