

Santonian-Campanian neoselachian faunas of the Upper Cretaceous Yezo Group in Nakagawa Town, Hokkaido, Japan

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ABSTRACT

Fifty-one fossil shark teeth, including Hexanchiformes, Echinorhiniformes, Squaliformes and Lamniformes, are described from two localities in Nishichirashinai and Omagari formations of the Yezo Group in Nakagawa Town, Hokkaido, Japan. They include the first occurrence of *Protosqualus* from the north-western Pacific and suggest the onset of the adaptation to deep-water environments of the Squaliformes in this region by early Campanian. Different sedimentary settings of the two localities may have caused different taxonomic compositions. The co-existence of Hexanchiformes and Lamniformes is also known in a contemporaneous Japanese fauna and those of southern high latitudes and suggests effects of paleogeographic settings on the global distribution of Upper Cretaceous neoselachian taxa.

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1. Introduction

The neoselachians (Chondrichthyes, Elasmobranchii) arose in the late Paleozoic and diversified extensively in the Jurassic and Cretaceous, and they are common components of Mesozoic marine faunas worldwide. Recent phylogenetic and quantitative assessments of their fossil record (e.g., Underwood, 2006; Guinot, 2013) revealed the chronology of neoselachian diversification patterns during the Mesozoic, and Guinot (2013) attempted to distinguish global and regional events by comparing European and North American Upper Cretaceous faunas. Information from other areas such as the Pacific is needed to further develop a global picture and as such, comprehensive studies on the selachian faunas in Japanese Cretaceous are important to fill the gap in our knowledge.

The Upper Cretaceous of Hokkaido, Japan, has a long history of palaeontological studies, but publications on fossil selachians had long been limited and sporadic. Goto et al. (1996) summarized

earlier works and reported the occurrences of genera *Hybodus*, *Ptychodus*, *Hexanchus*, *Notidanodon*, possible *Notorhynchus*, *Sphenodus* (*Orthacodus*), *Odontaspis*, *Scapanorhynchus*, *Cretolamna* and *Squalicorax* from different horizons of the Yezo Group ranging from Cenomanian to Campanian. Uyeno and Matsui (1993) reported the occurrences of *Notidanodon*, *Sphenodus*, *Scapanorhynchus*, *Centrophoroides*, indeterminate chlamydoselachid and squalid taxa, and *Schlerorhynchus* from the Campanian to Maastrichtian (possibly including the Danian) of Nemuro Group in eastern Hokkaido. Recent studies on the Santonian Kashima Formation in central Hokkaido has revealed the presence of diverse selachian faunas (e.g., *Cretodus* in Tomita and Kurihara, 2011; *Echinorhinus* in Kaneko et al., 2012; *Scyliorhinus*, *Pteroscylidium*, *Parasymbolus*, *Foumtizia*, *Palaeogaleus* and *Triakis* in Kaneko et al., 2015; *Carcharias*, *Johnlongia*, *Cretoxyrhina*, *Leptostyrax*, *Protolamna*, *Paranomotodon*, *Squalicorax* in Kaneko et al., 2019).

Our team reported the occurrence of well-preserved teeth of *Sphenodus* from the Upper Cretaceous in Nakagawa Town in northern Hokkaido (Kanno et al., 2017). Our continuing investigations revised the dating of the fossil-yielding strata in this locality based on additional molluscan fossils and obtained more

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neoselachian specimens from this and nearby localities, which include taxa previously unknown from Hokkaido. In this contribution, we discuss 1) the stratigraphic age and depositional setting of these localities, 2) describe the newly obtained neoselachian specimens and 3) compare the taxonomic composition of Nakagawa fossil shark fauna with those in and outside Japan.

2. Materials and methods

The shark teeth described in this study came from two localities: one at the Abeshinai River (locality *2 in Fig. 1C, 44°38'26.5"N, 142°03'40.1"E) and another at its tributary Rubeshibe River (locality *1 in Fig. 1C, 44°42'40.7"N, 142°00'29.5"E) in Nakagawa Town. In this paper, they are referred to as Abeshinai and Rubeshibe localities, respectively; note that the Abeshinai locality is marked in Kanno et al. (2017) slightly off from the correct position.

Dental measurements of shark teeth follow Shimada (2007, "TH" and "TW" in fig. 4), if not otherwise explained. NMV132 was photographed using scanning electron microscopy (SEM, Hitachi Miniscope®TM3000) without surface coating. Other specimens were coated with ammonium chloride before photographing them using Digital SLR (Nikon D7000).

Institutional abbreviations. — KCM, Kumamoto City Museum, Japan; MGUH, Geological Museum of the University of Copenhagen, Denmark; NMV, Nakagawa Museum of Natural History, Japan; PSMDHG, St. Petersburg State University - Paleontological and Stratigraphic Museum of the Department of Dynamic and Historical Geology, Russia; RBCM, Royal BC Museum at Victoria, British Columbia, Canada.

3. Geological Background

The mid-to Upper Cretaceous forearc basin deposits of the Yezo Group are widely distributed in central Hokkaido, Japan and western Sakhalin, Russian Far East (Fig. 1A, B; Matsumoto, 1954; Okada, 1983; Takashima et al., 2004; Shigeta and Maeda, 2005). This group shows significant lateral facies changes, and different stratigraphic divisions have been proposed in each area (e.g., Takashima et al., 2004). The Yezo Group in the Nakagawa area, northern Hokkaido, is one of the fundamental geological units in the establishment of Japanese Cretaceous stratigraphy (e.g., Nagao and Matsumoto, 1939; Matsumoto, 1942), and it has yielded abundant ammonoids and other invertebrate and vertebrate fossils (see Kanno et al., 2017 for a summary of the fossil content). The outcrops of this group are exposed along the Abeshinai River in the southwestern part of the Nakagawa area, and they consist of the Cenomanian Sakotandake Formation, Cenomanian to Turonian Sakugawa Formation, Turonian Saku Formation, Coniacian to Santonian Nishichirashinai Formation, Santonian to Campanian Omagari Formation and Campanian Osoushinai and Hakobuchi Formations (Fig. 1C, D; Takahashi et al., 2003, 2007). This study follows the local stratigraphic scheme proposed by Takahashi et al. (2003, 2007).

Although the exact locality and horizon cannot be specified, Uyeno (1972) reported *Hexanchus microdon* from Saku-gakko-no-sawa River of Nakagawa Town (Fig. 1C). Research Group for Mesozoic Fossil Shark (1977) also reported *Hexanchus microdon* from a muddy concretion float collected in Abeshinai River, supposedly derived from the base of Osoushinai Formation exposed upstream (locality *3 in Fig. 1C; Matsumoto, 1942). Their data are not included in our quantitative analysis.

3.1. Abeshinai locality

The Abeshinai locality is approximately 10 km south of the river mouth at the Teshio River and about 1 km upstream of the point where the tributary Wakkawenbetsu River flows in (Fig. 1C). The locality yielded the *Sphenodus* specimens reported earlier by our team (Kanno et al., 2017). These *Sphenodus* specimens and all other shark fossils from this site mentioned in the current study came from a large lens of poorly sorted conglomerate embedded in dark siltstone, which belongs to the Nishichirashinai Formation (Hashimoto et al., 1967; Takahashi et al., 2003; 2007). Based on the occurrence of the ammonoids *Anagaudryceras* cf. *yamashitai*, *Gaudryceras tenuiliratum*, *Yokoyamaoceras ishikawai*, *Menuites* sp., *Eupachydiscus* cf. *haradai*, *Protexanites?* sp. and *Polyptychoceras* sp. and the inoceramid *Sphenoceras naumanni*, this conglomerate is correlated with the Santonian to lower Campanian. Meanwhile, Takahashi et al. (2007) considered that the base of Campanian in the Nakagawa area is indicated by the lowermost occurrence of the bivalve *Inoceramus (Platyceramus) japonicus* in the upper part of the Omagari Formation, whose stratigraphic level is 500 m or more above the Abeshinai locality. Therefore, strata of this locality are referred to the Santonian.

The conglomerate lens contains abundant benthic molluscs (e.g., *Acila*, *Nanonavis*, *Glycymeris*, *Semifusus*), ammonoid shell fragments, crustacean elements, solitary corals, osteichthyan remains and the shark teeth described here mixed with abundant rip-up clasts and rounded pebbles. Of the shark teeth collected from this lens, hexanchiforms, *Echinorhinus* and *Sphenodus* specimens are relatively well-preserved and exhibit little evidence of pre-burial wear on tooth root and crown. However, most of the lamniform shark teeth from the same lens are severely damaged and taxonomically indeterminate. Overall, shark remains at the Abeshinai locality might be, at least in part, allochthonous material accumulated in submarine channel-fill sediment. Takahashi et al. (2003, 2007) noted low diversity and limited occurrences of macroinvertebrate fossils in the Nishichirashinai Formation, but they did not focus on this fossiliferous conglomerate.

3.2. Rubeshibe locality

The Rubeshibe locality is about 3 km southwest from the river mouth at the Abeshinai River, and all but one (NMV 106 was a float) specimens were collected from an outcrop on the riverbank (Fig. 1C). The lower part of the outcrop consists of sandy siltstone with a black mudstone layer on the top, whereas the upper part bears the poorly sorted massive sandstone; there is a 50-cm-thick layer of clast-supported pebble conglomerate between those upper and lower parts. The conglomerate cuts into the underlying sandy siltstone or black mudstone. The conglomerate layer includes cobble-to boulder-sized mud clasts in its uppermost part, displaying inverse-grading as a whole. This lithofacies matches the description of the Omagari Formation in Takahashi et al. (2003, 2007) and indicates a depositional setting of submarine channel-levee complex (Takahashi et al., 2007). The conglomerate yields abundant benthic molluscan shells, including *Acila* and oyster shells, whereas the sandstone includes various benthic molluscs, echinoids, ammonoids and fish debris. The shark teeth of the Rubeshibe locality came from the sandstone of the upper part, and they are not heavily worn before deposition in general.

Takahashi et al. (2003, 2007) correlated the Omagari Formation with the Santonian to lower Campanian. In this study, the

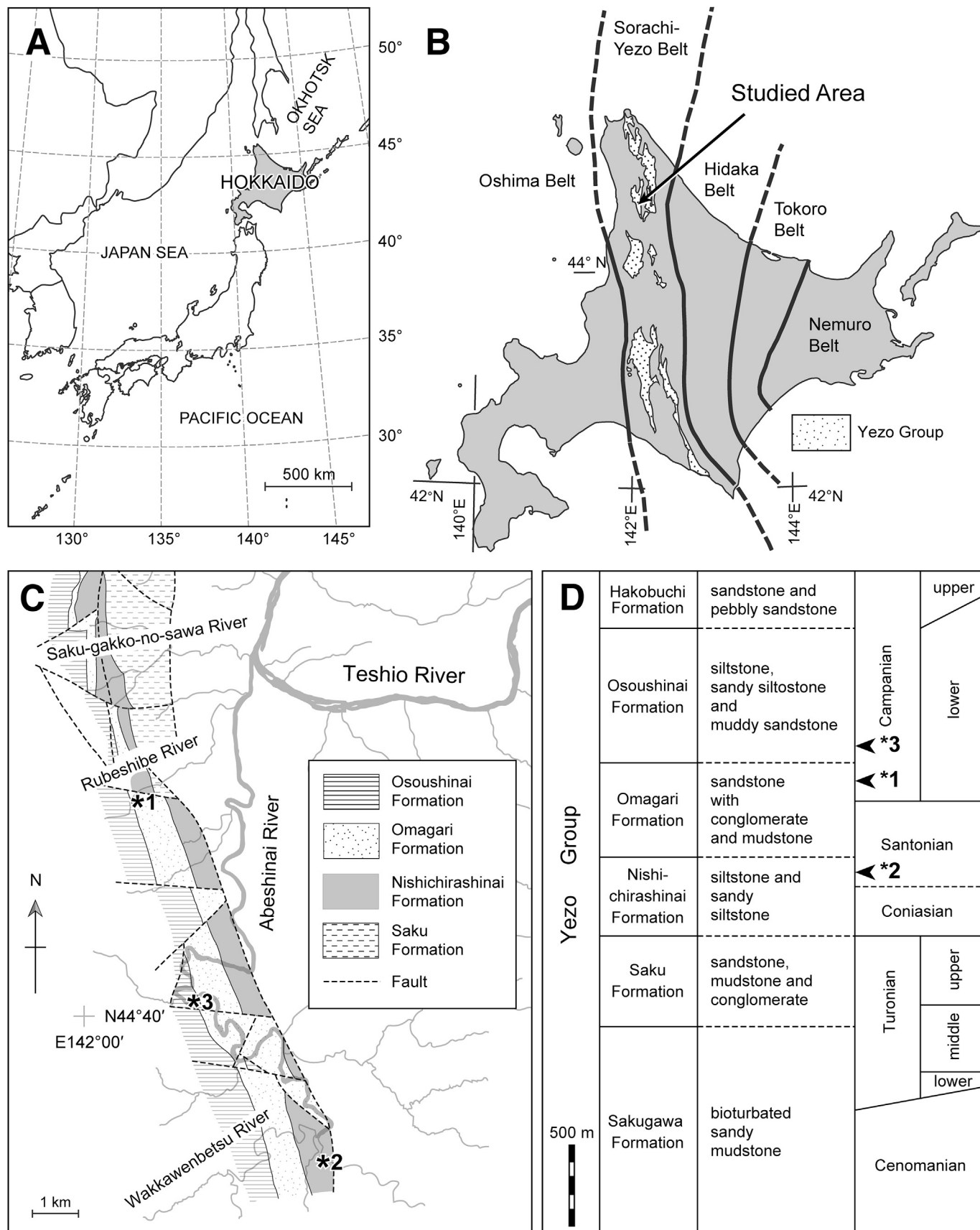


Fig. 1. Geological and stratigraphical setting of fossil localities. **A**, a wide-area map showing the location of Hokkaido Island. **B**, Tectonic divisions of Hokkaido Island and the distribution of the Cretaceous Yezo Group within the Sorachi-Yezo tectonic belt (redrawn from Takahashi et al., 2004). The location of studied area Nagakawa is indicated by an arrow. **C**, geological map of studied area based on Takahashi et al. (2007) and original observation data. Asterisks indicate localities of Rubeshibe (*1) and Abeshinai (*2) outcrops. **D**, Upper Cretaceous stratigraphy of the Nakagawa area based on Takahashi et al. (2007).

ammonoids *G. tenuiliratum*, *Y. ishikawai*, *Texanites* cf. *kawasakii* and *Polyptychoceras* sp. and the inoceramids *I. (P.)* cf. *japonicus* and *Sphenoceras* sp. were collected from the Rubeshibe locality. Only one specimen of *I. (P.)* cf. *japonicus* was found in this study, and definitive species identification is difficult for this specimen because of its fragmented condition. However, the concentric and divergent ribs of this specimen are similar to those of *I. (P.) japonicus*. Considering the occurrence of these molluscan fossils and the location close to the top of this formation (Fig. 1C), the strata exposed at this locality can be referred to the lower Campanian.

4. Systematic palaeontology

Table 1 lists the specimens described here. Descriptive tooth terminology largely follows that of Cappetta (2012) and Adnet and Cappetta (2001).

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Cohort Euserachii Hay, 1902
 Subcohort Neoserachii Compagno, 1977
 Order Hexanchiformes de Buen, 1926
 Family Hexanchidae Gray, 1851

Genus *Hexanchus* Rafinesque, 1810

Hexanchus sp.

Fig. 2A-D

Referred material and occurrences. NMV 100 and 103 from the lower Campanian Omagari Fm; NMV 101, 102 and 104 from the Santonian Nishichirashinai Fm.

Description. Lower teeth (Fig. 2A-C; NMV 100, 101, 102 and 104) are comb-like in shape and compressed labio-lingually. One principal cusp and two (NMV 104, distal part missing) to at least five (NMV 101) distal cusplets are present. The principal cusp is larger than the distal cusplets in all specimens. The distal cusplets diminish their height and width toward the distal end gradually, although this gradual change in size is subtle in NMV 102 tooth (Fig. 2B and C). The mesial cutting edge is serrated. The lingual face of the upper part of the root is strongly protuberant. The total height/total width ratio of the complete tooth is 0.74, and the slant height (maximum height when the tooth is tilted)/total width is 0.85 in NMV 100 (Fig. 2A). The root is rectangular and vertical ridges are observed on the lingual face of the root.

In the upper tooth (Fig. 2D; NMV 103), the main cusp and two cusplets are present, and the cusp is significantly larger than the cusplets. The root is labio-lingually compressed with vertical ridges on the labial surface.

Remarks. The teeth of *Hexanchus* are characterised by the presence of up to twelve distal cusplets in a large individual and the size of a distal cusplet that decreases gradually toward the rear (Cappetta, 2012). Two species of this genus are known from the Cretaceous deposit: *H. microdon* (Agassiz 1843) and *H. gracilis* (Davis 1887). However, as Cappetta (2012) pointed out, Cretaceous species of *Hexanchus* requires revision because *H. microdon* was diagnosed based on poor-quality figures of type species. We identify the *Hexanchus* specimens from Nakagawa as *Hexanchus* sp. to avoid further confusion.

There are subtle differences in morphology among the *Hexanchus* specimens from Nakagawa. For example, NMV 102 (Fig. 2B and C) has three similarly-sized cusplets while the other lower teeth have cusplets that clearly become smaller towards the rear. The serrations on the principal cusp are regular in size and shape in NMV 102, while those are irregular and slightly different in size in the other lower teeth specimens. Furthermore, the cutting edges of the principal

cusp and cusplets are almost straight in NMV 102, while they are curved in the other lower teeth. Those differences could be due to malformation or poor preservation of NMV 102, but they may also suggest the presence of at least two different species of the genus.

Genus *Xampylodon* Cappetta et al., 2019

Xampylodon dentatus (Woodward, 1886)

Fig. 2E

Referred material and occurrences. NMV 96 from the Santonian Nishichirashinai Fm.

Description. The fairly large tooth is labio-lingually compressed and mesio-distally wide (37.7 mm TW and 17.3 mm TH). Although the distalmost part is likely missing, at least twelve cusplets (including a possible main cusp) are present in this specimen. All the cusp and cusplets are cone-shaped and distally bent. The first five cusplets from the mesial side are relatively small, gradually increasing their height and width from mesial to distal; the fifth cusplet is the largest among the twelve (6.7 mm height from its base), and therefore, this probably is the main cusp. The sixth to the ninth are almost the same size. The seventh cusplet appears strongly bent (nearly horizontal) towards the distal end, but it may have been emphasised by the damage. The tenth to the twelfth cusplets gradually decrease their height and width towards the rear. The convex mesial cutting edge is longer than the nearly straight distal cutting edge in all cusplets, and the cutting edges are smooth without serration. The rectangular root is thin and deep, and there are numerous vertical furrows on the lingual face. The root-crown boundary is nearly straight and not distinctly convex.

Remarks. The genus *Xampylodon* was recently established by Cappetta et al. (2019) through the much-needed revision of the genus *Notidanodon* (e.g. Adolfsen et al., 2017; Cappetta and Grant-Mackie, 2018). Essentially, the “*Notidanodon*-like” teeth (i.e. a labio-lingually compressed tooth with well-developed, large mesial and distal cusplets and a rectangular non-bilobed root) with lower and more distally bent main cusp and cusplets were separated from *Notidanodon* and assigned to *Xampylodon* (Cappetta et al., 2019). The present specimen has the following characteristics of the genus: a main cusp and cusplets are distally bent and not high, the number of serrations on the mesial cutting edge of the main cusp (note: this is rather to be called mesial cusplets as they are well developed in this specimen) is four and in mesial cusplets, the mesial cutting edge is convex and longer than the distal one. Although NMV 96 does not have a straight root-crown boundary, a diagnostic characteristic of the genus, this convexity appears to be a variable feature depending on species in this genus (Cappetta et al., 2019); in fact, the lectotype specimen shows a rather straight boundary (Woodward 1886; pl. 6, fig. 18), and this probably represents heterodonty as teeth at the different positions show the difference in the convexity (e.g., compare the lower antero-lateral tooth RBCM P1188 and lower-lateral tooth RBCM P1190 in Cappetta et al., 2019).

Cappetta and Grant-Mackie (2018) and Cappetta et al. (2019) recognised at least four species in this genus: *X. dentatus* (Woodward, 1886) and *X. lanceolatus* (Woodward, 1886) from the Cretaceous and *X. brotzeni* (Siverson, 1995) and *X. loozi* (Vincent, 1876) from the Paleocene. NMV 96 is identified as *X. dentatus* because the diagnostic features of mesial and distal cusplets well match with the original description of well-preserved lectotype and paralectotype specimens (Woodward, 1886; pl. 6, figs. 17 and 18); NMV 96 shows the presence of distinct denticles (i.e. mesial cusplets) instead of serrations on the mesial cutting edge of the cusp and its morphology, an increase in the size of those mesial cusplets towards the cusp and a gradual decrease in size of the distal cusplets. Note that the present specimen resembles PSMDHG 374/33 described in Trikolidi (2014; fig. 13) that was provisionally referred

to *X. dentatus* by Cappetta et al. (2019); they share the similar number of cusplets (at least four mesial cusplets and five or six distal cusplets), distally inclined cusp and cusplets, the similarities in the size of distal cusplets (although gradually decreasing in size towards the distal end) and a rectangular root with straight root-crown boundary.

NMV 96 is distinguished from *X. lanceolatus* by the larger size and the presence of a short and relatively robust principal cusp with more cusplets (Woodward 1886; pl. 6, fig. 16), and from *X. loozi* by having well-developed mesial cusplets; *X. loozi* has serrations on the principal cusp (Vincent, 1876). The present specimen differs from *X. brotzeni* because the former is smaller in size and has well-developed mesial cusplets that are inclined distally rather than the apico-distally and straight root-crown boundary in *X. brotzeni* (Siverson, 1995).

A specimen of *Notidanodon* cf. *dentatus* in Kitamura and Kawasaki (2001; fig. 2) from the Santonian Hinoshima Formation in Kumamoto, Japan, was referred to as *X. dentatus* by Cappetta et al. (2019), and NMV 96 is the second report of this species from Japan. Another specimen from the Hinoshima Formation (KCM 12-000365 in Kitamura, 2019; fig. 3, 24) resembles NMV 96 and possibly represents another record of *Xampylodon* from the Upper Cretaceous in Japan. Remains of *Notidanodon* and *Xampylodon* have been reported from various stages of the Upper Cretaceous worldwide, such as the Campanian of Angola (Antunes and Cappetta, 2002), the lower Coniacian to Maastrichtian of Antarctica (Kriwet et al., 2006; Martin and Crame, 2006; Otero et al., 2014), the Cenomanian of South India (Underwood et al., 2011) and the Maastrichtian of Argentina (Bogan et al., 2016). From Japan, they have been reported from the Santonian and Turonian from Hokkaido (Yabumoto and Uyeno 1994), from the Maastrichtian in Osaka (Tanimoto et al., 2001), the lower Maastrichtian in Hyogo (*N. cf. dentatus*) (Tanimoto et al., 2001) and Santonian in Kumamoto (Kitamura and Kawasaki, 2001; Kitamura, 2019). Future research is required to re-examine those specimens following the emended diagnoses of *Notidanodon* and *Xampylodon* by Cappetta et al. (2019).

Hexanchidae gen. et sp. indet.

Referred material and occurrences. NMV 105 from the Santonian Nishichirashinai Fm.

Description. This specimen consists of two distal cusps and a compressed partial root. The remaining parts suggest a large size comparable to NMV 96, but they are too incomplete for further identification.

Table 1
List of specimens described in this study. Asterisks denote specimens described in Kanno et al. (2017).

Order	Family	Genus/species	Specimens and localities/horizons	
			Abeshinai locality/Nishichirashinai Fm	Rubeshibe locality/Omagari Fm
Hexanchiformes	Hexanchidae	<i>Hexanchus</i> sp.	NMV 101, 102, 104	NMV 100, 103
		<i>Xamphylodon dentatus</i>	NMV 96	—
		Hexanchidae indet.	NMV 105	—
	Orthacodontidae	<i>Sphenodus</i> cf. <i>lundgreni</i>	NMV 130, 131	—
		<i>S. sp. 1</i>	NMV 88*, 89*, 91*	—
		<i>S. sp.</i>	NMV 86*, 87*, 92*, 93*	—
	Hexanchiformes? family, genus and species indet.	NMV 90, 99	—	
Echinorhiniformes	Echinorhinidae	<i>Echinorhinus wadanohanaensis</i>	—	NMV108
		<i>E. sp.</i>	NMV 97	NMV 106, 107, 109
Squaliformes	Squalidae	<i>Protosqualus</i> sp.	—	NMV 132
Lamniformes	Otodontidae	<i>Cretalamna</i> cf. <i>borealis</i>	NMV 134	—
		<i>C. cf. ewelli</i>	NMV 111	—
		<i>C. sp.</i>	NMV 94, 110, 112, 113, 133, 135	—
	Carchariidae indet. Family, genus and species indet.	—	—	NMV 116
		—	NMV 95, 114, 115, 117, 118, 121–129, 136–138	NMV 115

Family Orthacodontidae Glikman, 1957

Genus *Sphenodus* Agassiz, 1843

Sphenodus lundgreni (Davis, 1890)

Sphenodus* cf. *lundgreni

Fig. 2F-H

Referred material and occurrences. NMV 130 and 131 from the Santonian Nishichirashinai Fm.

Description. NMV 130 and 131 are relatively small teeth for this genus (crown height 22.04 mm in NMV 130 and 24.85 mm in NMV 131). NMV 130 has a sharp and relatively wide cusp and a partly damaged root (Fig. 2F-H). The labial face is almost flat, while the lingual face is strongly convex. The cusp is sigmoidal in the profile view. Cutting edges are sharp, running towards the point where the root is damaged (Fig. 2F and H). Numerous short folds are present at the base of the cusp on the lingual face (Fig. 2G). The root surface has numerous short ridges which are deep and different in length (Fig. 2F). NMV 131 represents a partly cracked cusp and highly damaged root. The cusp is bent lingually, and both surfaces are convex. Very short folds are present at the base of the lingual face of the cusp. The root is highly damaged by cracks and covered with matrix, which makes it difficult to observe surface ornamentation. However, no ridges and grooves are present on the root.

Remarks. The assignment of *Sphenodus* and Orthacodontidae at the order level has been controversial for a long time; refer to Cappetta (2012; pp. 99–100) for a historical review. This study follows Cappetta's (2012) view that they are placed in the Hexanchiformes (contra Synecodontiformes in Kanno et al., 2017) so that a comparison with Kitamura (2019) on the taxonomic composition of a contemporaneous fauna in the Japanese Upper Cretaceous is possible.

Sphenodus lundgreni was first described by Davis (1890) with illustrated syntype specimens, but there is no designated holotype specimen. Although a majority of the figured syntypes are damaged teeth without complete roots, one specimen has a complete root and cusp with an attachment (MGUH 1406 in Davis 1890; pl. 39, fig. 9). Callahan et al. (2014) proposed this specimen as a candidate lectotype, and we agree with them given the presence of both root and cusp of MGUH 1406. NMV 130 and 131 share several characteristics with MGUH 1406 and the original description by Davis (1890): a slender cusp and a broad root, sharp cutting edges, vertical ridges on the labial face of the cusp and size. However, *Sphenodus*, particularly *S. lundgreni*, clearly needs a revision by using

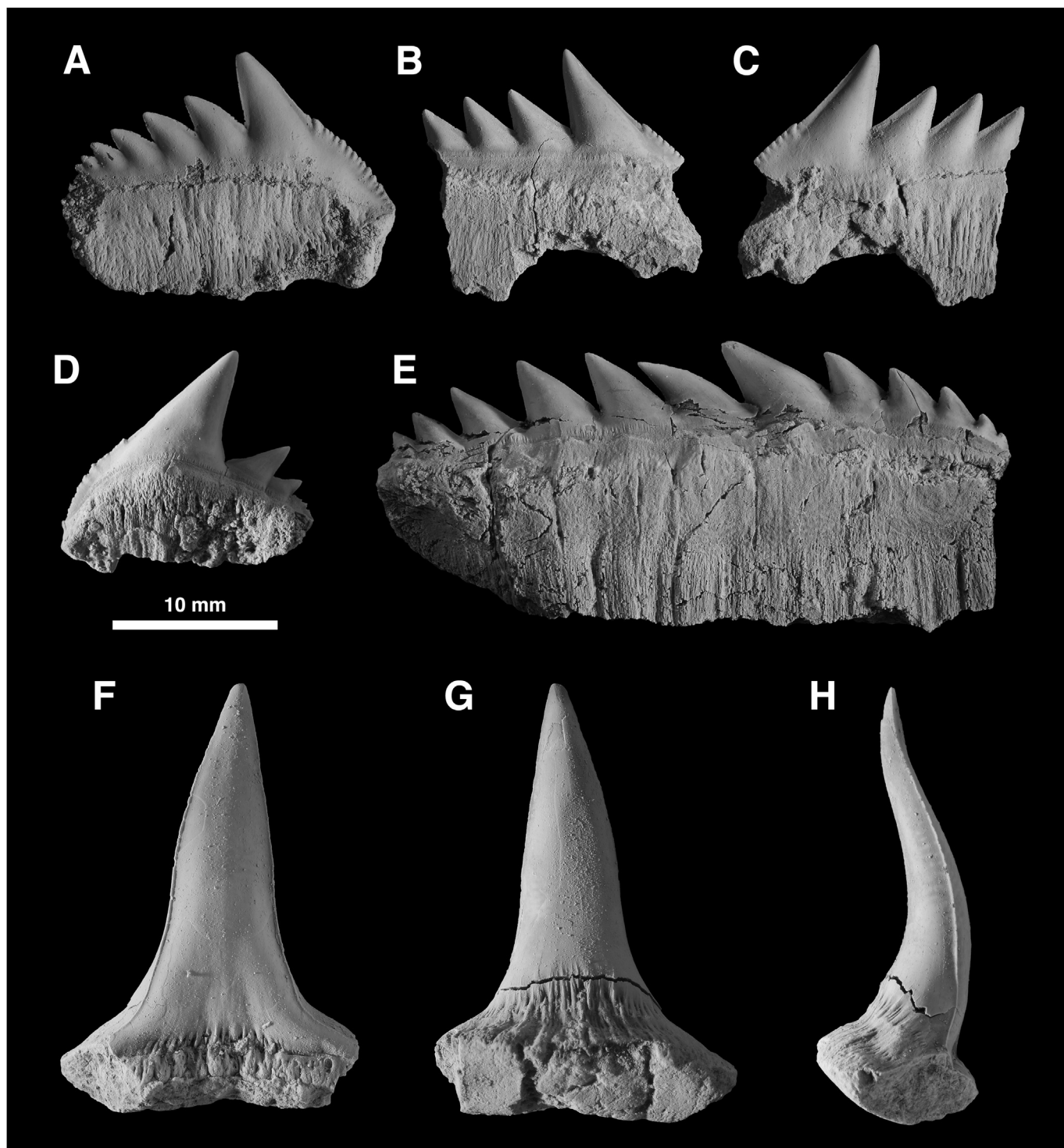


Fig. 2. Hexanchiformes from Nakagawa. **A–D**, *Hexanchus* sp.: **A**, labial view (NMV 100); **B**, lingual and **C**, labial views (NMV 102); **D**, labial view (NMV 103). **E**, *Xampylodon dentatus*, labial view (NMV 96). **F–H**, *Sphenodus* cf. *lundgreni*; **F**, labial, **G**, lingual and **H**, medial views (NMV 130).

complete specimens. Therefore, the present study assigns our specimens as *S* cf. *lundgreni*.

***Sphenodus* sp. 1**

Referred material and occurrences. NMV 88 and 89 (*S*. sp. 1 in Kanno et al., 2017) and NMV 91 (*S*. sp. 2 in Kanno et al., 2017) from the Santonian Nishichirashinai Fm.

Description. See Kanno et al. (2017; fig. 2D–G, K–M).

Remarks. NMV 91 lacks the basal part of cusp and the root and is differentiated from NMV 88 and 89 based on a few distinguishing characters (Kanno et al., 2017; tab. 1). However, the overall cusp is very similar to those of 88 and 89 (i.e. a slender cusp with sharp cutting edges, sigmoidal profile view and the degree of roundness of the cusp). Although the short ridges on the base of the cusp are missing in NMV 91, this is most likely due to a lack of the bottom part of the cusp.

NMV 88 and 89 are complete specimens with well-preserved cusp and root, allowing us to observe overall shape (i.e., a slender cusp, width and length nearly equal and a relatively thin root) and detailed surface ornament of the cusp and roots (short ridges and possible extension of cutting edges). The combination of those characteristics has not been reported in known species of the genus.

***Sphenodus* sp.**

Referred material and occurrences. NMV 86, 87, 92 and 93 in Kanno et al. (2017) from Santonian Nishichirashinai Fm.

Description. See Kanno et al. (2017).

Remarks. NMV 86 and 87 had been identified as *Sphenodus* cf. *lundgreni* and NMV 92 and 93 as *Sphenodus* sp. 2 by Kanno et al. (2017). However, the authors recognise a wide variation in morphology of syntype specimens of *S. lundgreni* as Davis (1890) mentioned earlier. The four specimens are too damaged to identify in the species level. Here, this study conservatively assigns those specimens to *Sphenodus* sp.

Hexanchiformes? fam., gen. et sp. indet.

Referred material and occurrences. NMV 90 and 99 from the Santonian Nishichirashinai Fm.

Description. See Kanno et al. (2017) for the previously described NMV 90 (fig. 2H-J). NMV 99 lacks the root and the basal part of the cusp. The apex of the cusp is damaged and partly worn. The cusp is curved lingually but not sigmoidal. Both faces of the cusp are smooth without vertical folds and are equally rounded, making the basal view of the cusp oval rather than bell shape. The cutting edge is sharp.

Remarks. NMV 90 was identified as *Sphenodus* sp. 2 by Kanno et al. (2017) using characteristics of the cusp. However, Cappetta et al. (2019) recently described *Komoksodon kwutchakuth* and established a new family (Komoksodontidae, Hexanchiformes?), which has a similar elongate cusp with a smooth surface without any vertical ridges and two cusplets on the root. NMV 99 is also missing the basal part of the cusp and cannot confirm the presence of short vertical folds or ridges. It is impossible to determine whether the two NMV specimens belong to the orthacodontid *Sphenodus* or komoksodontid *Komoksodon*.

Order Echinorhiniformes de Buen, 1926

Family Echinorhinidae Gill, 1862

Genus *Echinorhinus* Blainville, 1816

***Echinorhinus wadanohanaensis* Kitamura, 2013a**

Fig. 3A, B

Referred material and occurrences. NMV 108 from the Santonian Nishichirashinai Fm.

Description. The specimen bears some cracks and lacks a mesial part of the root. The tooth is extremely thin and remarkably compressed labio-lingually, and it is broader than tall. A single main cusp is covered with enameloid, and the root has a flat basal face. The lingual face of the crown is convex, whereas some part of the labial face is slightly convex. The main cusp is relatively high and strongly bent towards the distal end. The apex of the main cusp does not extend beyond the demarcation of the heel. The mesial margin of the cusp is straight whereas the distal margin is slightly curved apically. A smooth cutting edge on the mesial margin of the main cusp extends from the apex of the cusp to the crown-root boundary. The heel is well developed on the distal end of the crown. The root is rectangular, and its lingual and labial faces are flat; the lingual face is mostly smooth without any pores, but there is a vertical groove on the middle part which extends from the base of the crown to the bottom of the incomplete root. The crown-root

boundary is horizontal, and the lingual protuberance is slightly developed. Short vertical ridges are partly seen along the mesial part of the boundary on the labial face of the root, whereas no ridges are present on the lingual face.

Remarks. The specimen is identified as *Echinorhinus* by having the following characteristics: the labio-lingually compressed crown and root, anaulacorhize root and a strong distal orientation of the triangular cusp (Pfeil, 1983). The fossil record of *Echinorhinus* is limited to isolated teeth, but they are morphologically similar to those of recent species (Cappetta, 2012). Kitamura (2013a) recently reviewed the fossil species of *Echinorhinus* and described a new species *E. wadanohanaensis* from the Upper Cretaceous of Japan. Subsequently, two new species were added to this genus from the Lower and Upper Cretaceous (e.g., Guinot et al., 2014; Bogan et al., 2017). Consequently, there are 19 nominated species in this genus ranging from the Valanginian to Recent.

NMV 108 is identified as *E. wadanohanaensis*, because the tooth is relatively large but extremely thin, a single cusp has a smooth cutting edge, its apex does not extend beyond the heel and the root is high and rectangular (see detailed comparison with other Cretaceous species in Kitamura 2013a). It however has a nutrient groove whose absence is one of the key diagnostic features of *E. wadanohanaensis* (Kitamura, 2013a). The presence/absence of a nutritive groove and multiple cusplet(s) have been used as a diagnosis of some species of *Echinorhinus* (e.g. Kitamura, 2013a; Bogan et al., 2017). However, these features are most likely ontogenetically variable (Adnet et al., 2012; Adolfssen and Ward, 2014) and even monognathic heterodonty (S. Kanno, personal observation). Therefore, using the nutritive groove in taxonomic identification may be unreliable. Further study is required to investigate monognathic, dignathic and ontogenetic heterodonty of *Echinorhinus* teeth using both extinct and recent species specimens.

***Echinorhinus* sp.**

Fig. 3C-F

Referred material and occurrences. NMV 97 from the Santonian Nishichirashinai Fm.; NMV 106, 107 and 109 from the lower Campanian Omagari Fm.

Description. All specimens are poorly preserved, and the main cusp (NMV 97 and NMV 106; Fig. 3A and B) or distal part(s) (NMV 97, NMV 107 and NMV 109; Fig. 3E and F) are missing. The teeth are compressed labio-lingually, and the lingual face is convex, whereas the labial face is almost flat but slightly concave. NMV 97 and NMV 109 are robust and thick with fairly convex lingual surfaces when compared to other *Echinorhinus* specimens from Nakagawa (i.e., NMV 106, NMV 107 and NMV 108). The partly preserved main cusp of NMV 107 and NMV 109 are curved apically, and the apex is nearly erect. The apex of NMV 109 extends beyond the distal heel but not in NMV 107. The root is compressed labio-lingually, and especially those of NMV 106 and NMV 107 are extremely flat. Irregular foramina are present on the labial face of the root in NMV 106 and NMV 109 (Fig. 3C-F). In NMV 107, the labial face is smooth, and the neckband is present.

Remarks. These incomplete teeth are identifiable as *Echinorhinus* by having the characteristics of *Echinorhinus* stated earlier. Since the main cusp and the root are incompletely preserved, it is impossible to assign them to particular species. There is a remarkable morphological variability among the present specimens, however, and they could be attributed to sexual and/or ontogenetic heterodonty, or different species. The extant Family Echinorhinidae is a small group composed of only one genus and two species, but a total of 14 nominal extinct species of the genus have been reported (Kitamura, 2013a). Considering the possible variability due to the heterodonty and other intraspecific factors, the large number of extinct species may include *nomina dubia*.

Order Squaliformes [Goodrich, 1909](#)

Family Squalidae [Bonaparte, 1834](#)

Genus *Protosqualus* [Cappetta, 1977](#)

***Protosqualus* sp.**

Fig. 4

Referred material and occurrences. NMV 132 from the lower Campanian Omagari Fm.

Description. The specimen lacks the distal parts of crown and root, and it is slightly compressed labio-lingually. The tooth is much longer than tall, and the single cusp is strongly bent towards the distal end. The mesial cutting edge is smooth and almost straight. The apron is well developed on the labial side and detached from the crown ([Fig. 4A](#)). The extremity of the triangular apron is rounded, extending to (but not beyond) the base of the root. On the lingual face, the uvula is not inclined distally; it possesses a relatively sharp extremity, projecting lingually and extending basally ([Fig. 4B](#) and [C](#)). The root is low and not deep. The crown extends out- and downwards over the root. No foramina are present on

labial or lingual surfaces of the root or on the crown-root boundary. The mesial and distal parts of the lingual face are strongly concave, forming shallow hollows. An infundibulum is present, and the base of the root is concave ([Fig. 4D](#)).

Remarks. NMV 132 is the first record of *Protosqualus* from the northwestern Pacific region, and the Campanian occurrence is relatively late for the genus. The genus is known from the Lower Cretaceous to the Paleocene of Europe and Southern high latitudes ([Appendix 1](#)) and distinguished from the closely related *Squalus* by having a poorly labio-lingually compressed crown, a wide and rather triangular apron with the rounded extremity not distinctly separated from the labial limit of the enamel band and a thick and low root ([Müller and Diedrich, 1991](#); [Adnet et al., 2008](#); [Cappetta, 2012](#); [Cappetta et al., 2019](#)).

Within the genus *Protosqualus*, five nominal species are recognised to date: *P. sigei* [Cappetta, 1977](#), *P. albertsi* [Thies, 1981](#), *P. pachyrhiza* [Underwood and Mitchell, 1999](#), *P. glickmani* [Averianov, 1997](#), *P. barringtonensis* [Guinot et al., 2013](#) and *P. (or S.) argentinensis* [Bogan et al., 2016](#) (see [Cappetta et al., 2019](#)). They are often distinguished based

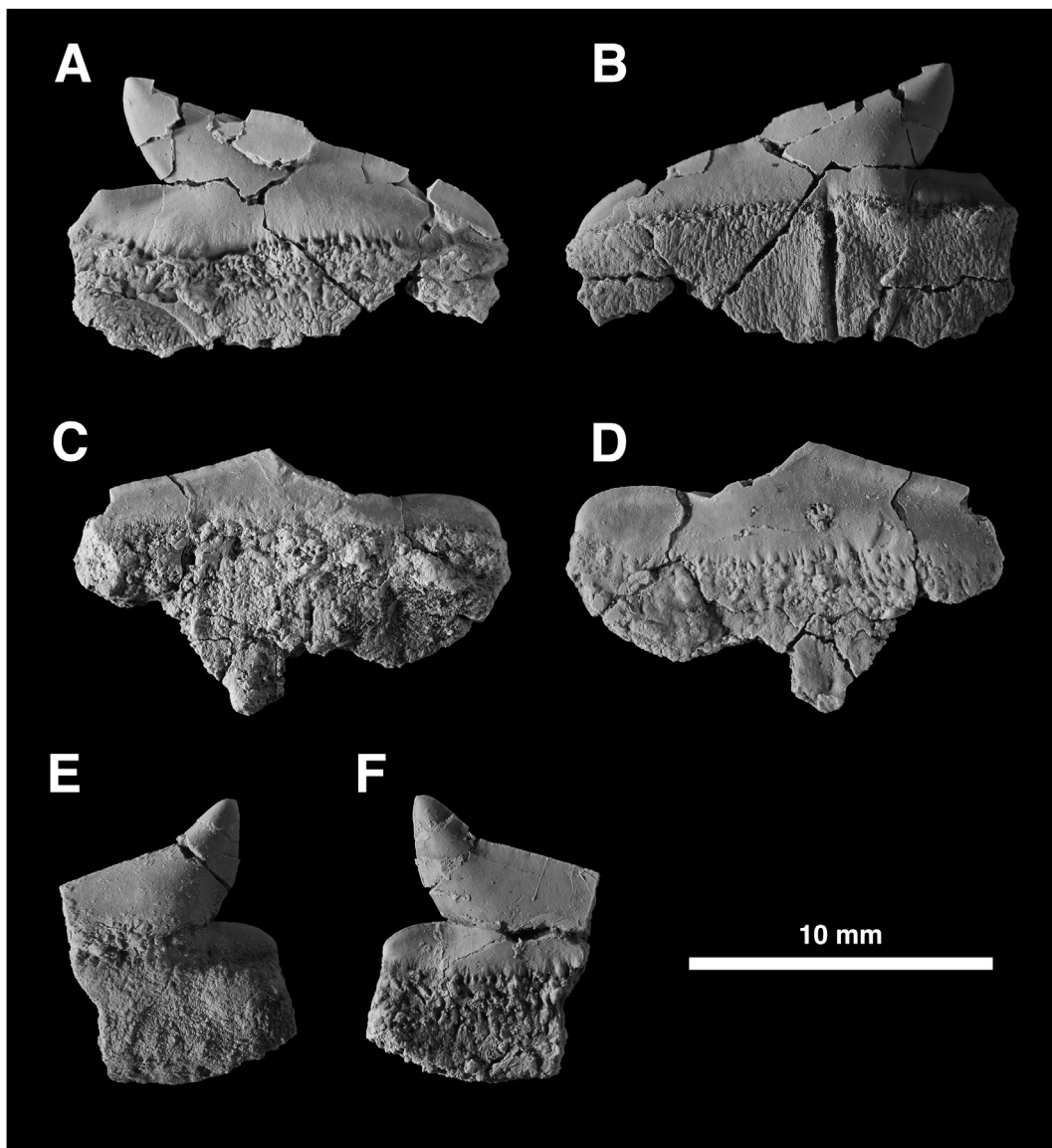


Fig. 3. *Echinorhinus* from Nakagawa. **A–B**, *E. wadanohanaensis*: **A**, labial and **B**, lingual views (NMV 108); **C–F**, *E. sp.*: **C**, labial and **D**, lingual views (NMV 106); **E**, labial and **F**, lingual views (NMV 109).

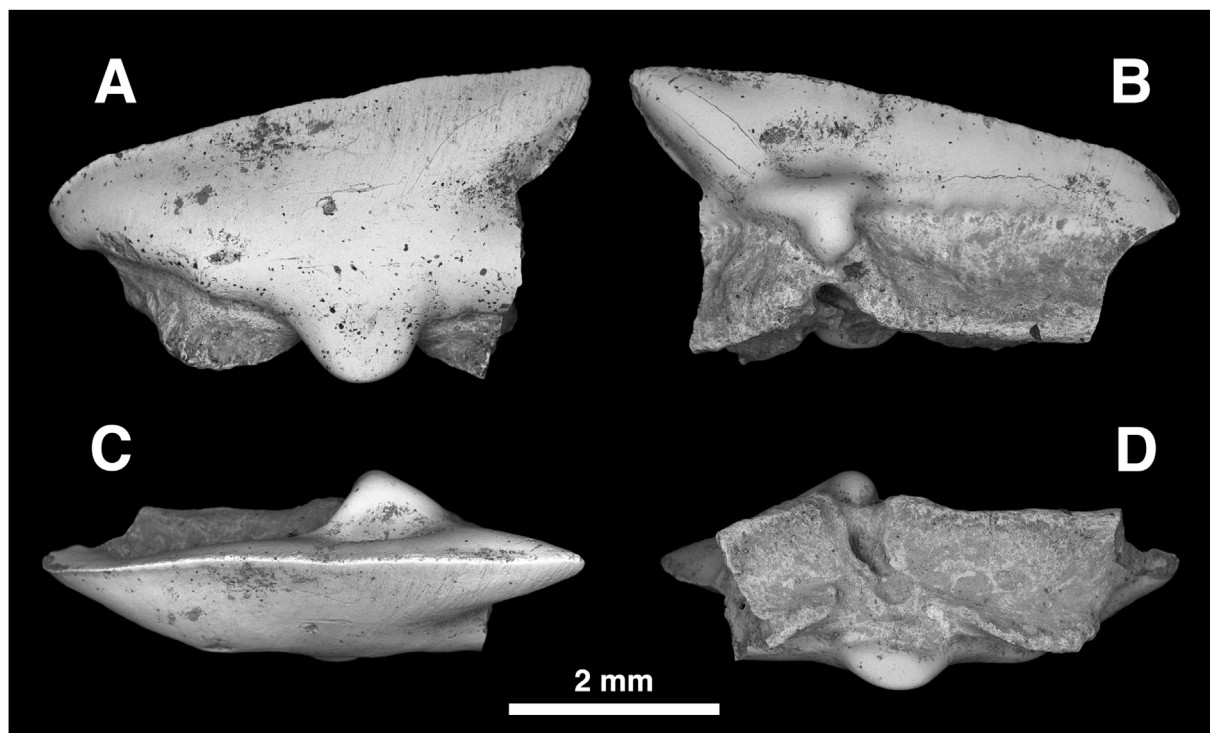


Fig. 4. SEM photographs of *Protosqualus* sp. from Nakagawa. A, labial, B, lingual, C, occlusal and D, basal views (NMV 132).

on the morphology of apron, the presence of infundibulum and axial foramen and size. However, recent studies on recent *Squalus acanthias* Linnaeus, 1758 (Adnet and Cappetta, 2001; Kriwet and Klug, 2009; Guinot et al., 2013) indicate significant heterodonty and variability attributed to ontogeny and sexual dimorphism. For example, the morphology of the apron and the infundibulum and the presence/absence of the fusion of the axial foramen into an infundibulum are different depending on tooth positions both in fossil and extant *Squalus* (e.g., Kriwet and Klug, 2009; Adolfsson and Ward, 2014). Additionally, the morphology of apron seems to be variable even within the same species (e.g., Müller and Diedrich, 1991; Siverson, 1993; Adolfsson and Ward, 2013).

NMV 132 is moderate in size (maximum crown length 5.5 mm, maximum root width 1.9 mm) for *Protosqualus*, but it differs from previously described species in having the following characteristics: cutting edge is smooth and almost straight, the apron is well developed and only slightly detached from the cusp, and it does not extend below the level of the basal part of the root, uvula is fairly large but not inclined distally, the infundibulum is present, no lateral foramen is present on the root, and the basal part of the root is concave. However, considering that further study on the heterodonty of *Protosqualus* is required for the species identification, our identification remains conservative.

The occurrence of this genus from Hokkaido is consistent with the anti-tropical distribution pattern of this genus suggested by Underwood et al. (2011). *Protosqualus* is one of the earliest known squalid genera (Adnet and Cappetta, 2001; Cappetta, 2012), and the earliest occurrences are from the Barremian (Thies, 1981; Underwood, 2004). They are not common from Santonian and upper strata, suggesting a possible collection bias favoring European middle Cretaceous records (Appendix 1).

Early records of extinct squaliformes such as *Protosqualus* are common in relatively shallow water environments (Siverson, 1993; Adnet and Cappetta, 2001; Kriwet and Klug, 2009). Adnet and Cappetta (2001) suggested that the adaptation of Squaliformes to

deep-water environments occurred after the Cenomanian-Turonian mass extinction, whereas Klug and Kriwet (2010) predicted earlier timing based on phylogenetic analysis. Although it is hard to determine the exact timing of this adaptation based on fossil records because of the rarity of their occurrences (Klug and Kriwet, 2010), the Campanian occurrence of NMV 132 from a deep-water environment of Japan (see Discussion) is evidence of the survival of the genus in the northern part of the Pacific and possibly indicate that the adaptation of the Squaliformes to the deep-water environment was achieved at least by the Campanian in this region. A close examination of Cretaceous records of the Squaliformes outside Europe is necessary to gain a broader picture of their evolutionary history of adaptation to deep-water environments.

Order Lamniformes Berg, 1958
Family Otodontidae Glikman, 1964

Genus *Cretalamna* Glikman, 1958

Cretalamna borealis (Priem, 1897)

C. cf. borealis

Fig. 5A-D

Referred material and occurrences. NMV 134 from the Santonian Nishichirashinai Fm.

Description. NMV134 is a large anterior tooth missing apical portion of the cusp and the edge of the distal lobe, and it is estimated to be about or over 30 mm tall if complete. The lingual face of the cusp is convex, while the labial face is almost flat (Fig. 5A-C). The remaining part of the cusp is recurved lingually with sharp cutting edges. The cusplets are sharp and located more lingually than the cutting edge of the main cusp. The neck band is present on the base of the labial face of the cusp. The bilobed root is thick, and the lingual protuberance of the root is pronounced in profile and basal views (Fig. 5C). The basal edge of the root is moderately (not tightly) curved. The root is fairly symmetrical in basal view (Fig. 5D).

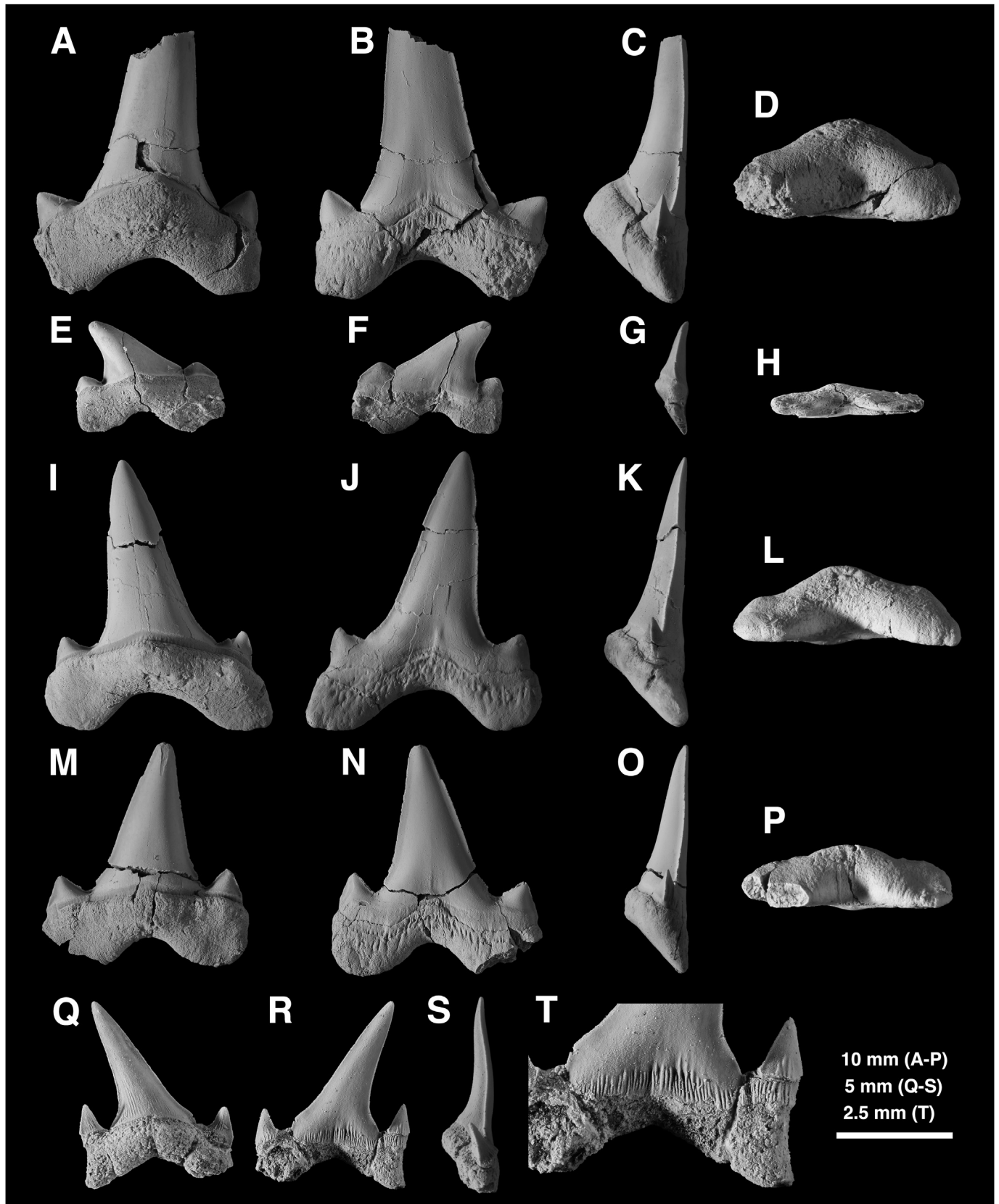


Fig. 5. Lamniformes from Nakagawa. **A–D**, *Cretalamna cf. borealis*: A, lingual, B, labial and C, profile views and D, the basal view of root (NMV 134); **E–H**, *Cretalamna cf. ewelli*: E, lingual, F, labial and G, profile views and H, the basal view of root (NMV 111); **I–L**, *Cretalamna* sp.: I, lingual, J, labial and K, profile views and L, the basal view of root (NMV 94); **M–P**, *Cretalamna* sp.: M, lingual, N, labial and O, profile views and P, the basal view of root (NMV 113); **Q–T**, Carchariidae indet.: Q, lingual, R, labial and S, profile views and T, close-up of vertical folds on labial side (NMV 116).

Remarks. *Cretalamna* is one of the most common sharks from the Upper Cretaceous. Recently [Siversson et al. \(2013\)](#) extensively revised its taxonomy and recognised three groups, i.e., *C. appendiculata* group, *C. borealis* group and *C. hattini* group; NMV 134 belongs to the *C. borealis* group in [Siversson et al. \(2013\)](#) because of its slender cusp and symmetry of the basal view of the root.

The emended diagnosis of *C. borealis* by [Siversson et al. \(2013\)](#) lists “commonly rounded and strongly divergent cusplets,” but those of NMV 134 are sharp. Reference to this species remains provisional due to limited and damaged material and the morphological difference of the cusplets and not tightly curved basal edge of the root. The present specimen is different from *C. bryanti* (*C. borealis*-like species) ([Ebersole and Ehret 2018](#)) because the specimen does not have long root lobes and deep U-shaped basal concavity. The Nakagawa specimen is from Santonian and stratigraphically older than the *C. borealis* specimens described by [Siversson et al. \(2013\)](#) from the Campanian in Sweden.

***Cretalamna* cf. *ewelli* Siversson, 2013**

Fig. 5E–H

Referred material and occurrences. NMV 111 from the Santonian Nishichirashinai Fm.

Description. NMV 111 is a lateroposterior tooth (TH 10.1 mm) with slight damage to the mesial lobe of the root (Fig. 5E and F). The tooth is labio-lingually compressed (Fig. 5G). The distally inclined cusp is short and weakly lingually curved at the apex. A pair of relatively large cusplets are not high but divergent. The root is asymmetric in basal view, where the distal lobe is shorter than the mesial one (Fig. 5H). The median indentation of the basal edge of the root is U-shaped and not deep.

Remarks. NMV 111 belongs to the *C. borealis* group in [Siversson et al. \(2013\)](#) because of its slender cusp and symmetry of the basal view of the root. Morphological features of NMV 111, such as the inclined cusp and the strongly labiolingually compressed root with U-shaped medial indentation (rather than V-shaped), are comparable to the upper lateroposterior teeth of *C. ewelli*. However, the inner and outer cutting edge of cusplets are almost equally convex, which is different from one of the diagnostic features of *C. ewelli*. Additionally, material from Nakagawa is limited, and identification of a *Cretalamna* species based on one lateroposterior tooth can be misleading. Therefore, the identification of this specimen is provisional. The tooth is very thin in profile view, suggesting a more posterior position or a younger individual (c.f. juvenile *C. borealis* specimen in [Siversson et al. \(2015: fig. 9D\)](#)).

***Cretalamna* sp**

Fig. 5I–P.

Referred material and occurrences. NMV94, 110, 112, 113, 133 and 135 from Santonian Nishichirashinai Fm.

Description. All specimens share the following characteristics: (1) a pair of large cusplets, (2) the well-developed neck band at the border line between cusp and root on the labial face, which is curved along with the curvature of the median indentation of the basal edge of root (i.e., the curvatures of the neck band and the median indentation are almost parallel), (3) spherical-shaped (“waterdrop” like shape) pores on the root lobes, (4) a U-shaped median indentation of the basal edge of the root, (5) asymmetric root in basal view and (6) rounded interface between cusp and cusplets except NMV 112.

These specimens exhibit a range of size variation: NMV 94 (TH 23.9 mm), NMV 110 (TH c. 23 mm: missing the tip of the cusplet and the distal cusplet and distal lobe of the root), NMV 135 (TH 22.0 mm), NMV 112 (damaged cusp, TH c. 14 mm), NMV 113 (damaged cusp, TH c. 21 mm) and NMV 133 (TH 11.0 mm: a latero-posterior tooth with a short and distally inclined cusp missing the apex, and is

apico-basally compressed). NMV 94 (Fig. 5I–L), 110 and 135 have a relatively slender cusp, whereas 112 and 113 (Fig. 5M–P) have a wider cusp. The cusp is slightly inclined labially in NMV 94, while slightly sigmoidal in NMV 110 and NMV 113 in profile. Cusplets in NMV 110 have a concave cutting edge in both inner and cutting edges, while those in the other specimens have convex edges.

The teeth are divided into two groups based on the development and direction of the lingual protuberance, although their taxonomic significance is unclear (see “Remarks” below). The protuberance in NMV 94, NMV 112, NMV 133 and NMV135 (hereafter, the group A; Fig. 5I–L as a representative) projects horizontally and is higher than that in NMV 110 and NMV 113 (hereafter, the group B; Fig. 5M–P as a representative). The lingual protuberance in the group B extends somewhat basally and shows a dome-shaped rather than projecting horizontally.

Remarks. All specimens are identified as *Cretalamna* because they are more similar to this genus than *Kenolamna* [Siversson et al. \(2013\)](#) or other lamnid genera in [Cappetta \(2012\)](#). Groups A and B are distinguished by the features of lingual protuberance, but it is unknown if this is due to heterodonty (i.e., dignathic, sexual, ontogenetic etc.) or interspecific difference. Given that they share many morphological features, both groups are assigned to the same species here.

However, none of the described specimens satisfies the diagnosis of any known *Cretalamna* species because of the following features; the cusp is slenderer in labial or lingual view, the bottom of the gap between the cusp and cusplet is wide and rounded, and the well-developed neck band shows the similar curve with the median indentation of the basal edge of the root. Their unique features of the cusp and the gap between the cusp and cusplet suggest the existence of an unknown species, but we think it is premature to establish a new taxon based on available specimens.

Family Carcharhiidae [Müller and Henle, 1838](#)

Carcharhiidae indet.

Fig. 5Q–T

Referred material and occurrences. NMV 116 from the lower Campanian Omagari Fm.

Description. The specimen is a relatively well-preserved upper lateral tooth with some cracks. The main cusp is slender, thin and slightly sigmoidal in profile (Fig. 5Q–S). The lingual face is moderately convex, while the labial face is rather flat. Cutting edges are sharp and reach the base of the cusp; the mesial cutting edge is almost straight, although it is incomplete near the crown base, whereas the distal cutting edge is convex, extending to the distal cusplet. A pair of cone-shaped lateral cusplets are fairly large, sharp and inclined lingually in profile view. On the lingual face, the enameloid surfaces of the lateral cusplets are separated from the cutting edges of the main cusp by notches; on the labial face, they are continuous. Numerous very short, parallel vertical folds are well developed on the basal part of the cusp and cusplets on the labial side (Fig. 5T). Very weak striations are present, extending from the neck to the basal third of the cusp on the lingual side (Fig. 5Q). The neck is slightly curved on the lingual face that is almost parallel to the basal curvature of the root. The bilobed root is relatively thin and low, and its lobes are short. The base of the root is angular rather than curved. The nutritive groove is present but not deep.

Remarks. Taxonomy of fossil odontaspids requires a revision because recent studies indicate non-monophyly of the traditional Odontaspidae and resurrection of the Carchariidae (e.g., [Shimada et al., 2015](#); [Stone and Shimada 2019](#)). Due to limited material and the difficulty of identification using a single lateral tooth, here we provisionally classify NMV 116 as Carchariidae indet. Overall profile of the tooth resembles some previously reported specimens of

Scapanorhynchus and *Carcharias* in Becker et al. (2004), Bourdon et al. (2011), Cappetta (2012) and Bice and Shimada (2016). The present specimen is distinguished from the genus *Scapanorhynchus* by not having vertical folds on the cusp (Hamm and Shimada, 2002; Cappetta, 2012). It may be in fact referable to the resurrected *Carchariidae* because the tooth has some similarities with *Carcharias*, such as a sigmoidal cusp and two lingually-bent sharp cusplets.

Order Lamniformes Berg, 1958

Family uncertain

gen. et sp. indet.

Referred material. NMV 95, 114, 115, 117, 118, 121–129, 136–138.

Description. These teeth represent damaged crowns missing all or much of the root, and apparently, most of them had been damaged prior to the fossilization. They share general characteristics of Lamniformes; a triangular cusp, razor-like cutting edges running toward the basal part of the main cusp and holoaulacorhize root (Cappetta, 2012). The poor preservation does not allow identification at lower taxonomic levels.

5. Discussion

5.1. Comparison of Abeshinai and Rubeshibe assemblages

The sample size differs considerably between the two Nakagawa localities ($N = 42$ at Abeshinai locality and $N = 9$ at Rubeshibe locality), and it is unreasonable to draw a statistically meaningful conclusion. However, a notable point is that the commonest taxa in one locality are very rare or absent in the other (Table 1). The hexanchiform Orthacodontidae (26%) and lamniform Otodontidae (24%) are the two commonest families at the Abeshinai locality, but they are absent at the Rubeshibe locality, whereas the Echinorhinidae (44%) is the commonest at Rubeshibe, but it is the rarest (2%) at Abeshinai. Ages of the two shark faunas differ but only slightly; the fossil-yielding unit in Abeshinai is inferred to be Santonian and that in Rubeshibe the early Campanian (see Geological Background). The difference in taxonomic composition likely reflects factor(s) other than the age.

An obvious difference between the two localities is in the depositional environment. Kitamura (2019) distinguished three different selachian faunas in the Santonian Hinoshima Formation of Himenoura Group in Kumamoto, southwest Japan and related them to depositional environments and shark ecology. The abundance or rarity of certain taxa at the Nakagawa localities may allow a similar interpretation. As mentioned earlier, the assemblage at Abeshinai locality is likely allochthonous and was accumulated in a submarine channel fill situated in a continental slope to the bathyal environment; many damaged and indeterminate lamniform teeth also suggest physical disturbance prior to fossilization. It is reasonable that the remains of large-bodied fast-swimming lamniforms living in coastal to offshore surface environments are common in such sediments, and they suffer from damage due to physical disturbance before burial. On the other hand, the assemblage at Rubeshibe came from a sandstone unit deposited in a submarine channel-levee complex and shows little evidence of significant transportation. The teeth of *Echinorhinus* from the Rubeshibe locality are very thin and fragile, indicating that there was little stressful transportation to cause damage. Given the rarity of lamniform remains and the abundance of Echinorhinidae at the Rubeshibe locality, the Rubeshibe assemblage seems to represent neoselachians with deeper water habitats. According to this interpretation, the occurrence of *Protosqualus* from the same Rubeshibe locality suggests the deep-water adaptation of the Squaliformes, as mentioned earlier.

5.2. Characteristics of Nakagawa faunas

The order Lamniformes is a small group today with only 15 extant species, but the group was highly diverse during the Cretaceous, with more than 360 fossil species described (Condamine et al., 2019). Stratigraphically oldest fossil records of nine lamniform families *sensu* Cappetta (2012) date back to the Early and mid-Cretaceous, and the remaining seven families are known only from the Cenozoic. Although most of the present lamniform specimens are too damaged to identify at genus- and/or species-level, the fossils shark teeth from the Upper Cretaceous of Nakagawa represent a variety of lamniform teeth, which is not inconsistent with the previous finding that Lamniformes had high species diversity until K/Pg boundary (Kriwet and Benton, 2004; Condamine et al., 2019). Upper Cretaceous records of Lamniformes in Japan often include Mitsukurinidae and Otodontidae (Yabumoto and Uyeno, 1994; Goto et al., 1996; Kitamura, 2019), whereas remains of *Carchariidae* are rare (Kitamura, 2013b), despite that this family is quite common in coeval deposits elsewhere in the world (e.g., Siverson, 1992; Cumbaa et al., 2010; Underwood and Cumbaa, 2010; Otero et al., 2014). All but one lamniform teeth from Nakagawa identifiable at lower taxonomic ranks are attributed to the otodontid *Cretalamna*. This high occurrence of otodontids is not inconsistent with previous records from other localities in the Japanese Upper Cretaceous in general, although abundant indeterminate teeth do not allow a firm conclusion on the family-level taxonomic composition.

Kitamura (2019) noted the co-existence of Lamniformes and Hexanchiformes in Japanese Santonian fauna and regarded the presence of the elements of Weddellian fauna in the Japanese Cretaceous reflect the spread of these taxa that are characteristic to the southern high latitudes into the mid latitude regions in Northern Hemisphere. In our study of Nakagawa fauna, lamniforms such as *Cretalamna* and hexanchiform *Sphenodus* co-exist in the Santonian Abeshinai fauna as in other Japanese Santonian faunas. *Sphenodus* has previously been reported from the Jurassic to Lower Cretaceous and Paleocene in various localities in Europe, but not from the mid-Cretaceous (Kanno et al., 2017), and this taxon has not been reported from the Upper Cretaceous in Western Interior Seaway (WIS) of North America either, despite the well-known fossiliferous nature of the latter. Meanwhile, lamniform remains are common from the Upper Cretaceous in Europe or North America. The Upper Cretaceous strata of western Europe and WIS largely represent the sedimentation in epicontinental seas, unlike the areas such as northwestern Pacific (i.e., Japan) or southern high latitudes (home for Weddellian Province), which were directly facing the deeper ocean. Little is known about the paleoecology of *Sphenodus*, but the different geographic distributions of this genus and other lamniforms suggest that they could co-exist but had different paleoecological/paleogeographic preferences. Further studies on the relative abundance of Hexanchiformes and Lamniformes at various stratigraphic levels in the Japanese Cretaceous will give us a clue to track their waxing and waning at a global scale.

6. Conclusions

Hexanchiformes, Echinorhiniformes, Squaliformes and Lamniformes are described from Abeshinai (Santonian, Nishichirashinai Formation) and Rubeshibe (lower Campanian, Omagari Formation) localities in Nakagawa Town, Hokkaido, Japan. The lithology suggests an accumulation in a submarine channel-fill setting in the former locality, whereas a submarine channel-levee complex for the latter; the difference may have contributed to the different taxonomic compositions. A single tooth of the squalid *Protosqualus* sp. is the first occurrence of this genus from northwestern Pacific,

implying the onset of the adaptation of the Squaliformes to deep-water habitat at least by early Campanian. Occurrences of Hexanchiformes (Hexanchidae and Orthacodontidae) and their co-existence with the Lamniformes are also observed in a contemporaneous Japanese fauna reported by Kitamura (2019) and Weddellian fauna of the southern high latitudes, demonstrating the effects of paleogeographic settings on the global distribution of Upper Cretaceous neoselachian taxa.

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References

- Adnet, S., Cappetta, H., 2001. A palaeontological and phylogenetical analysis of squaliform sharks (Chondrichthyes: Squaliformes) based on dental characters. *Lethaia* 34, 234–248.
- Adnet, S., Cappetta, H., Mertiniene, R., 2008. Re-evaluation of squaloid shark records from the Albian and Cenomanian of Lithuania. *Cretaceous Research* 29, 711–722.
- Adnet, S., Guinot, G., Cappetta, H., Welcomme, J.L., 2012. Oldest evidence of bramble sharks (Elasmobranchii, Echinorhinidae) in the Lower Cretaceous of southeast France and the evolutionary history of orbitostylic sharks. *Cretaceous Research* 35, 81–87.
- Adolfsson, J.S., Ward, D.J., 2013. Neoselachians from the Danian (Early Paleocene) of Denmark. *Acta Palaeontologica Polonica* 60, 313–338.
- Adolfsson, J.S., Ward, D.J., 2014. Crossing the boundary: an elasmobranch fauna from Stevns Klint, Denmark. *Palaeontology* 57, 591–629.
- Adolfsson, J., Milán, J., Friedman, M., 2017. Review of the Danian vertebrate fauna of southern Scandinavia. *Bulletin of the Geological Society of Denmark* 65, 1–23.
- Agassiz, L., 1833–1843. *Recherches sur les poissons fossiles*. Petitpierre, Neuchâtel.
- Antunes, M.T., Cappetta, H., 2002. Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. *Palaeontographica Abteilung A* 264, 85–146.
- Averianov, A.O., 1997. Additions to the Selachian fauna of the Russian Cretaceous. I. A new species of *Protosqualus* Cappetta, 1977 (Chondrichthyes: Squalidae). *Zoosystematica Rossica* 5, 319–320.
- Becker, M.A., Chamberlain, J.A., Terry, D.O., 2004. Chondrichthyans from the Fairpoint Member of the Fox Hills Formation (Maastrichtian), Meade County, South Dakota. *Journal of Vertebrate Paleontology* 24, 780–793.
- Berg, L.S., 1958. *System der rezenten und fossilen Fischartigen und Fische*. Verlag der Wissenschaften, Berlin.
- Bice, K.N., Shimada, K., 2016. Fossil marine vertebrates from the Codell Sandstone Member (middle Turonian) of the Upper Cretaceous Carlile Shale in Jewell County, Kansas, USA. *Cretaceous Research* 65, 172–198.
- Blainville, H.M.D.d., 1816. Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin des Sciences, par la Société Philomatique de Paris* 8, 105–124.
- Bogan, S., Agnolin, F.L., Novas, F.E., 2016. New selachian records from the Upper Cretaceous of southern Patagonia: paleobiogeographical implications and the description of a new taxon. *Journal of Vertebrate Paleontology* 36.
- Bogan, S., Agnolin, F.L., Otero, R.A., Egli, F.B., Suárez, M.E., Soto-Acuña, S., Novas, F.E., 2017. A new species of the genus *Echinorhinus* (Chondrichthyes, Echinorhiniformes) from the Upper Cretaceous of southern South America (Argentina-Chile). *Cretaceous Research* 78, 89–94.
- Bonaparte, C.L.J.L., 1832–1841. *Iconografia della fauna italiana per le Quattro classi degli animali vertebrati*. Tip. Salviucci, Roma.
- Bonaparte, C.L.J.L., 1838. *Selachorum tabula analytica*. *Nuovi Annali delle Scienze Naturali* 1, 195–214.
- Bourdon, J., Wtight, K., Lucas, S.G., Spielmann, J.A., Pence, R., 2011. Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone, central New Mexico. Part of Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone. *Central New Mexico* 52, 1–54.
- Callahan, W.R., Mehling, C.M., Denton, R.K., Parris, D.C., 2014. *Vertebrate Paleontology and Stratigraphy of the Late Cretaceous Holmdel Park Site, Monmouth County, New Jersey*. *Dakoterra* 6, 163–169.
- Cappetta, H., 1977. Observations sur quelques sélaciens du Crétacé supérieur d'Angleterre avec la description d'un genre nouveau. *Géobios* 10, 479–485.
- Cappetta, H., 2012. *Handbook of Paleichthyology*, vol. 3E. Verlag Dr. Friedrich Pfeil, München. Chondrichthyes – Mesozoic and Cenozoic Elasmobranchii: Teeth.
- Cappetta, H., Grant-Mackie, J., 2018. Discovery of the most ancient *Notidanodon* tooth (Neoselachii: Hexanchiformes) in the Late Jurassic of New Zealand. *New considerations on the systematics and range of the genus. Palaeovertebrata* 42.
- Cappetta, H., Morrison, K., Adnet, S., 2019. A shark fauna from the Campanian of Hornby Island, British Columbia, Canada: an insight into the diversity of Cretaceous deep-water assemblages. *Historical Biology* 33, 1121–1182.
- Compagno, L.J.V., 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17, 303–322.
- Condamine, F.L., Romieu, J., Guinot, G., 2019. Climate cooling and clade competition likely drove the decline of lamniform sharks. *Proceedings of the National Academy of Sciences, USA* 116, 20584–20590.
- Cumbaa, S.L., Shimada, K., Cook, T.D., 2010. Mid-Cenomanian vertebrate faunas of the Western Interior Seaway of North America and their evolutionary, paleobiogeographical, and paleoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295, 199–214.
- Davis, J.W., 1887. The fossil fishes of the chalk of Mount Lebanon, in Syria. *Scientific Transactions of the Royal Dublin Society* 2, 457–636.
- Davis, J.W., 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society* 2, 363–434.
- de Buen, F., 1926. *Catálogo ictiológico del Mediterráneo español y de Marruecos: recopilando lo publicado sobre peces de las costas mediterránea y próximas del Atlántico (Mar de España)*. Ministerio de Marina, Dirección General de Pesca, Instituto Español de Oceanografía.
- Ebersole, J.A., Ehret, D.J., 2018. A new species of *Cretalamna sensu stricto* (Lamniiformes, Otodontidae) from the Late Cretaceous (Santonian–Campanian) of Alabama, USA. *PeerJ* 6, e4229.
- Gill, T., 1862. On the classification of the families and genera of the Squali of California. *Proceedings of the Academy of Natural Sciences of Philadelphia* 14, 483–501.
- Glikman, L.S., 1957. Genetic relations of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous. *Trudy Geologicheskogo Muzeja Imeni A. P. Karpinskogo/Akademija Nauk SSSR* 1, 110–117.
- Glikman, L.S., 1958. Rates of evolution in lamnoid sharks. *Doklady Akademii Nauk SSSR* 123, 568–571.
- Glikman, L.S., 1964. *Sharks of the Paleogene and their stratigraphic significance*, vol. 229. Nauka Press, Moscow.
- Goodrich, E.S., 1909. *Vertebrata Craniata (First fascicle: Cyclostomes and Fishes)*. In: Lankester, R. (Ed.), *A Treatise on Zoology*, vol. 9. A. Adam and Charles Black, London, pp. 1–518.
- Goto, M., Uyeno, T., Yabumoto, Y., 1996. Summary of Mesozoic elasmobranch remains from Japan. In: A. G., Viohl, G. (Eds.), *Mesozoic Fishes—Systematics and Palaeoecology*. Verlag Dr. Friedrich Pfeil, München, pp. 73–82.
- Gray, J.E., 1851. List of the specimens of fish in the collection of the British Museum. Part. 1. Chondropterygii. *British Museum (Natural History)*, London.
- Guinot, G., 2013. Late Cretaceous elasmobranch palaeoecology in NW Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 388, 23–41.
- Guinot, G., Underwood, C.J., Cappetta, H., Ward, D.J., 2013. Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK. *Journal of Systematic Palaeontology* 11, 589–671.
- Guinot, G., Cappetta, H., Adnet, S., 2014. A rare elasmobranch assemblage from the Valanginian (Lower Cretaceous) of southern France. *Cretaceous Research* 48, 54–84.
- Hamm, S.A., Shimada, K., 2002. Associated tooth set of the Late Cretaceous lamniform shark, *Scapanorhynchus raphiodon* (Mitsukurinidae), from the Niobrara Chalk of Western Kansas. *Transactions of the Kansas Academy of Science* 105, 18–26.
- Hashimoto, W., Nagao, S., Kanno, S., Asaga, M., Otomo, R., Koyakai, T., Tono, S., Kitamura, K., Taira, K., Wajima, M., 1967. Geology and underground resources in Nakagawa-cho, p. 48. Hokkaido. Nakagawa-cho.
- Hay, O., 1902. *Bibliography and catalogue of the fossil vertebrata of North America*. *Bulletin of United States Geological Survey* 179, 1–868.
- Huxley, T.H., 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* 649–662.
- Kaneko, M., Fujimoto, T., Kano, M., 2012. The first record of bramble shark *Echinorhinus* sp. in the North Pacific region, from the Upper Cretaceous Kashima Formation (Santonian), Hokkaido, Japan. *Bulletin of the Mikasa City Museum* 16, 1–8.
- Kaneko, M., Fujimoto, T., Kano, M., 2015. The first record on fossil shark teeth of the order Carcharhiniformes (Scyliorhinidae and Triakidae) in Northwest Pacific

- region from Upper Cretaceous Kashima Formation, (Santonian) Hokkaido, Japan. *Bulletin of the Mikasa City Museum* 18, 27–49.
- Kaneko, M., Fujimoto, T., Kano, M., 2019. Fossil shark teeth of the order Lamniformes in from the Upper Cretaceous Kashima Formation (Santonian), Hokkaido, north Japan. *Bulletin of the Mikasa City Museum* 22, 1–43.
- Kanno, S., Nakajima, Y., Hikida, Y., Sato, T., 2017. *Sphenodus* (Chondrichthyes, Neoselachii) from the Upper Cretaceous in Nakagawa Town, Hokkaido, Japan. *Paleontological Research* 21, 122–130.
- Kitamura, N., 2013a. Description of a new species of the family Echinorhinidae (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous Himenoura Group in Kumamoto Prefecture, Southwestern Japan. *Paleontological Research* 17, 189–195.
- Kitamura, N., 2013b. “*Carcharias*”*amonensis* (Chondrichthyes, Odontaspidae) from the Upper Cretaceous Mifune Group in Kumamoto, Japan. *Paleontological Research* 17, 230–235.
- Kitamura, N., 2019. Features and paleoecological significance of the shark fauna from the Upper Cretaceous Hinoshima Formation, Himenoura Group, Southwest Japan. *Paleontological Research* 23, 110–130.
- Kitamura, N., Kawasaki, S., 2001. New specimens of elasmobranch fossils from the Upper Cretaceous Hinoshima Formation of the Himenoura Group, in Kumamoto Prefecture, Japan. *Bulletin of the Kumamoto City Museum* 13, 41–49.
- Klug, S., Kriwet, J., 2010. Timing of deep-sea adaptation in dogfish sharks: insights from a supertree of extinct and extant taxa. *Zoologica Scripta* 39, 331–342.
- Kriwet, J., Benton, M.J., 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous–Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 181–194.
- Kriwet, J., Klug, S., 2009. Fossil record and origin of squaliform sharks (Chondrichthyes, Neoselachii). In: Gallucci, V., McFarlane, G., Bargmann, G. (Eds.), *Biology and Management of dogfish sharks*. American Fisheries Society, Maryland, pp. 19–38.
- Kriwet, J., Lirio, J.M., Nuñez, H.J., Puceat, E., Lécuyer, C., 2006. Late Cretaceous Antarctic fish diversity, vol. 258. Geological Society, London, Special Publications, pp. 83–100.
- Linnaeus, C., 1758. *Systema naturae*, tenth ed. Salvi, Stockholm.
- Martin, J.E., Crame, J.A., 2006. Palaeobiological significance of high-latitude Late Cretaceous vertebrate fossils from the James Ross Basin, Antarctica. *Geological Society, London, Special Publications* 258, 109.
- Matsumoto, T., 1942. Fundamentals in the Cretaceous stratigraphy of Japan, Part 1. *Memoirs of the Faculty of Science, Kyushu Imperial University, Series D, Geology* 1, 129–280.
- Matsumoto, T., 1954. The Cretaceous System in the Japanese Islands. *Japan Society for the Promotion of Science, Tokyo*, p. 324.
- Müller, A., Diedrich, C., 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoburger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen* 20, 3–105.
- Müller, J., Henle, F.G.J., 1838–1841. *Systematische Beschreibung der Plagiostomen*. Veit und Comp., Berlin, Berlin, p. 29–10.
- Nagao, T., Matsumoto, T., 1939. A Monograph of the Cretaceous *Inoceramus* of Japan. *Journal of the Faculty of Science* 4, 241–299. Hokkaido Imperial University, Ser. 4, Geology and mineralogy.
- Okada, H., 1983. Collision orogenesis and sedimentation in Hokkaido, Japan. In: Hashimoto, M., Uyeda, S. (Eds.), *Accretion Tectonics in the Circum-Pacific Regions*. Terra Scientific Publishing Company, Tokyo, pp. 91–105.
- Otero, R.A., Gutstein, C.S., Vargas, A., Rubilar-Rogers, D., Yury-Yañez, R., Bastias, J., Ramírez, C., 2014. New Chondrichthyans from the Upper Cretaceous (Campanian–Maastrichtian) of Seymour and James Ross Islands, Antarctica. *Journal of Paleontology* 88, 411–420.
- Pfeil, F.H., 1983. Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. *Palaeoichthyologica* 1, 1–315.
- Priem, F., 1897. Sur des dents d’élasmobranches de divers gisements Sénoniens (Villedieu, Meudon, Folx-les-Caves). *Bulletin de la Société Géologique de la France* 25, 40–56.
- Rafinesque, C.S., 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia: con varie osservazioni sopra i medesimi. Per le stampe di Sanfilippo, Palermo.
- Research Group for Mesozoic Fossil Shark (RGMFS), 1977. Cretaceous fossil elasmobranchs from Japan (First report). *Bulletin of the Mizunami Fossil Museum* 4, 119–138.
- Shigeta, Y., Maeda, H., 2005. Yezo Group research in Sakhalin—a historical review. *National Science Museum Monographs* 31, 1–24.
- Shimada, K., 2007. Skeletal and dental anatomy of lamniform shark, *Cretalamna appendiculata*, from Upper Cretaceous Niobrara Chalk of Kansas. *Journal of Vertebrate Paleontology* 27, 584–602.
- Shimada, K., Popov, E.V., Siverson, M., Welton, B.J., Long, D.J., 2015. A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States. *Journal of Vertebrate Paleontology* 35, e981335.
- Siverson, M., 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology* 35, 519–554.
- Siverson, M., 1993. Maastrichtian squaloid sharks from southern Sweden. *Palaeontology* 36, 1–19.
- Siverson, M., 1995. Revision of the Danian cow sharks, sand tiger sharks, and goblin sharks (Hexanchidae, Odontaspidae, and Mitsukurinidae) from southern Sweden. *Journal of Vertebrate Paleontology* 15, 1–12.
- Siverson, M., Lindgren, J., Newbrey, M.G., Cederström, P., Cook, T.D., 2013. Campanian (Late Cretaceous) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. *Acta Palaeontologica Polonica* 60, 339–384.
- Stone, N.R., Shimada, K., 2019. Skeletal Anatomy of the Bigeye Sand Tiger Shark, *Odontaspis noronhai* (Lamniformes: Odontaspidae), and Its Implications for Lamniform Phylogeny, Taxonomy, and Conservation Biology. *Copeia* 107, 632–652.
- Takahashi, A., Hirano, H., Sato, T., 2003. Stratigraphy and fossil assemblage of the Upper Cretaceous in the Teshionakagawa area, Hokkaido, northern Japan. *The Journal of the Geological Society of Japan* 109, 77–95.
- Takahashi, A., Hikida, Y., Jenkins, R.G., Tanabe, K., 2007. Stratigraphy and megafauna of the Upper Cretaceous Yezo Supergroup in the Teshionakagawa area, northern Hokkaido, Japan. *Bulletin of the Mikasa City Museum* 11, 25–59.
- Takahashi, R., Kawabe, F., Nishi, H., Moriya, K., Wani, R., Ando, H., 2004. Geology and stratigraphy of forearc basin sediments in Hokkaido, Japan: Cretaceous environmental events on the north-west Pacific margin. *Cretaceous Research* 25, 365–390.
- Tanimoto, M., Sato, M., Tani, M., 2001. *Notidonodon* (Chondrichthyes, Hexanchidae) from the Upper Cretaceous Maastrichtian Izumi Group, Southwest Japan. *Journal of Geosciences Osaka City University* 49, 223–227.
- Thies, D., 1981. Vier neue Neoselachier-Haiarten aus der NW-deutschen Unterkreid. *Neues Jahrbuch für Geologie und Paläontologie - Monatshefte* 8, 475–486.
- Tomita, T., Kurihara, K.I., 2011. First record of a large lamniform shark *Cretodus semiplicatus* in the Pacific Region, from the Mikasa Formation (lower Cenomanian), Hokkaido, Japan. *Paleontological Research* 15, 181–184.
- Trikolidi, F.A., 2014. Cow sharks (Hexanchiformes) from the Cretaceous deposits of the Crimea. *Proceedings of the Zoological Institute RAS* 318, 76–97.
- Underwood, C.J., 2004. Barremian and Aptian (Cretaceous) sharks and rays from Speeton, Yorkshire, north-east England. *Proceedings of the Yorkshire Geological Society* 55, 107–118.
- Underwood, C.J., 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology* 32, 215–235.
- Underwood, C.J., Cumbaa, S.L., 2010. Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. *Palaeontology* 53, 903–944.
- Underwood, C.J., Mitchell, S.F., 1999. Albian and Cenomanian selachian assemblages from North East England. *Palaeontology* 60, 9–59.
- Underwood, C.J., Goswami, A., Prasad, G.V.R., Verma, O., Flynn, J.J., 2011. Marine vertebrates from the ‘middle’ Cretaceous (early Cenomanian) of South India. *Journal of Vertebrate Paleontology* 31, 539–552.
- Uyeno, T., 1972. On Cretaceous and Tertiary fish remains from the Hidaka and Yubari districts in Hokkaido, Japan. *Memoirs of the National Museum of Nature and Science* 5, 223–226.
- Uyeno, T., Matsui, N., 1993. Late Cretaceous fish fossils from Nemuro, Hokkaido, Japan. *Memoirs of the National Museum of Nature and Science* 26, 39–46.
- Vincent, G., 1876. Description de la faune de l’étage Landénien inférieur de Belgique. *Annales de la Société royale malacologique de Belgique* 11, 111–160.
- Woodward, A.S., 1886. On the Palaeontology of the selachian genus *Notidanus*, Cuvier. *Geological Magazine* 3, 205–217.
- Yabumoto, Y., Uyeno, T., 1994. Late Mesozoic and Cenozoic fish faunas of Japan. *Island Arc* 3, 255–269.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105139>.