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Author: Kitamura, Naoshi

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Features and paleoecological significance of the shark fauna from the Upper Cretaceous Hinoshima Formation, Himenoura Group, Southwest Japan

NAOSHI KITAMURA

4-8-7 Motoyama, Chuo-ku Kumamoto, Kumamoto 860-0821, Japan (e-mail: shark5963yama@jcom.zaq.ne.jp)

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Abstract. The shark fauna of the Upper Cretaceous Hinoshima Formation (Santonian: 86.3–83.6 Ma) of the Himenoura Group (Kamiamakusa, Kumamoto Prefecture, Kyushu, Japan) was investigated based on fossil shark teeth found at five localities: Himedo Park, Kugushima, Wadanohana, Higashiura, and Kotorigoe. A detailed geological survey and taxonomic analysis was undertaken, and the habitat, depositional environment, and associated mollusks of each locality were considered in the context of previous studies. Twenty-three species, 15 genera, 11 families, and 6 orders of fossil sharks are recognized from the localities. This assemblage is more diverse than has previously been reported for Japan, and Lamniformes and Hexanchiformes were abundant. Three categories of shark fauna are recognized: a coastal region (Himedo Park; probably a breeding site), the coast to the open sea (Kugushima and Wadanohana), and bottom-dwelling or near-seafloor fauna (Kugushima, Wadanohana, Higashiura, and Kotorigoe). The shark fauna of the Hinoshima Formation is similar to that of the Yezo and Futaba groups, and also to faunas from Angola, Australia, and Antarctica. However, based on the composition of taxa, the fauna differs from that of the Upper Cretaceous shark fauna of the Western Interior Seaway and Europe. The Upper Cretaceous shark fauna of Japan, including the Hinoshima Formation, contained active pelagic (*Squalicorax* and *Cretoxyrhina mantelli*) and bentho-pelagic (e.g. *Notidanodon*, *Chlamydoselachus*, *Sphenodus*) predators. These taxa probably coexisted, as they occupied different ecological niches. The characteristics of the Late Cretaceous shark fauna in Japan are similar to those of the contemporaneous Southern Hemisphere fauna (e.g. Angola, Australia, and Antarctica). This shows that the characteristic shark fauna (e.g. *Notidanodon*, *Chlamydoselachus*, *Sphenodus*) of the Southern Hemisphere had spread to the middle latitudes of the Northern Hemisphere by the Late Cretaceous.

Key words: habitat, Hinoshima Formation, Late Cretaceous, paleoecology, shark

Introduction

Paleoecological studies of Upper Cretaceous shark fauna have been based on the many fossil shark teeth deposited in tropical and warm temperate shallow-marine environments including the Western Interior Sea (e.g. Shimada *et al*., 2006), Europe (e.g. Vullo *et al*., 2007), the Middle East area (e.g. Davis, 1887), North Africa (e.g. Rage and Cappetta, 2002), Australia (e.g. Siverson, 1996), and Antarctica (e.g. Kriwet *et al*., 2006). Regionally, studies of the Upper Cretaceous shark fauna have concentrated on the Western Interior Sea, Europe, and Australia, and in geological terms the origin of these faunas was the late Early Cretaceous to early Late Cretaceous periods (Albian to Turonian: Siverson, 1996, 1997; Cumbaa *et al*., 2010), and the remainder of the Late Cretaceous (Campanian to Maastrichtian: Siverson, 1992; Case and Cappetta, 1997; Beavan and Russell, 1999). However, reports of shark faunas from the Santonian are rare, particularly from the North Pacific region, leaving this fauna less well understood. Records of Cretaceous fossil shark teeth from Japan (northwestern Pacific region) have been sporadic, and restricted mainly to descriptions of specimens. Consequently, there is insufficient information to assess the taxonomic composition and paleoecological significance of the Cretaceous shark fauna from Japan and worldwide. In the present study, the Japanese Cretaceous shark fauna was investigated, primarily using shark teeth from the Hinoshima Formation (Santonian Age), and features of the Upper Cretaceous shark fauna in the western Pacific Ocean (mid-latitudes in the Northern Hemisphere) were studied.

Stratigraphy and age of the Himenoura Group

The Hinoshima Formation belongs to the Upper Cretaceous Himenoura Group (named by Nagao, 1930) and is distributed primarily from the Uto Peninsula to the east coast of Amakusa Kamishima Island, and south of Amakusa Shimoshima in Kumamoto Prefecture and Koshikishima Islands in Kagoshima Prefecture, Japan. Tashiro and Noda (1973) separated the Himenoura Group into the Lower Himenoura Subgroup (Santonian to lower Campanian) and the Upper Himenoura Subgroup (Campanian to Maastrichtian), and separated the Lower Himenoura Subgroup, which is distributed on the east coast of Amakusa Kamishima Island, into the Hinoshima Formation (mainly Santonian Stage) and the Amura Formation (mainly Campanian Stage). They also subdivided the Hinoshima Formation into the lower, middle, and upper members, and the Amura Formation into the lower and upper members (Tashiro *et al*., 1986). Kojo *et al.* (2011) stated that the Upper and Lower Himenoura subgroups were deposited in almost the same period, and also revised the stratigraphic division of the Himenoura Group. The present study follows the framework of Kojo *et al.* (2011). The Himenoura Group, which is distributed on Amakusa Kamishima and Goshoura islands, unconformably overlies the Higo metamorphic rocks on Amakusa Kamishima Island, and is unconformably overlain by the Paleogene Miroku Group (e.g. Komatsu *et al.*, 2009; Kojo *et al*., 2011). Studies of the depositional environmental of the Himenoura Group on Kamiamakusa Island (Tashiro *et al*., 1986; Fujino, 2003; Sato *et al*., 2005) indicate a rapid transgression and a transition to a deep-sea setting. Numerous paleontological studies of mollusks in the Himenoura Group have been reported (e.g. Kobayashi and Amano, 1955; Amano, 1956; Tashiro, 1971, 1972, 1976). This study follows Kojo *et al*. (2011) with respect to the geological age of the Hinoshima Formation of the Himenoura Group, which is assigned to the Santonian based on the presence of *Inoceramus amakusensis.* Previous studies have reported on (e.g. Kitamura *et al*., 1995; Kitamura, 1997; Goto and the Japanese Club for Fossil Shark Tooth Research, 2004; Kitamura, 2013) and reviewed (Yabumoto and Uyeno, 1994; Goto *et al*., 1996; Kitamura, 2008) the fossil shark teeth in the Himenoura Group.

Material and methods

Fossil shark teeth (168 specimens) were collected from outcrops and float rocks near outcrops at five localities in Kamiamakusa City (Kumamoto, Japan): Himedo Park (64 specimens), Kugushima (38 specimens), Wadanohana (63 specimens), Higashiura (two specimens), and Kotorigoe (one specimen) (Table 1, Appendix 1). Some of these specimens had been studied by Kitamura *et al.* (1995) and Kitamura (1997, 2013), but private collections were excluded. The specimens are held in the Kumamoto City Museum (KCM) and the Goshoura Cretaceous Museum (GCM). The classification of specimens followed Cappetta (2012).

Shark teeth horizons and sedimentary facies of the Upper Cretaceous in the Hinoshima Formation

Himedo Park.—The lower part of the Hinoshima Formation is exposed at Himedo Park (Figure 1), and three fossil layers are evident: a bottom fine sandstone bed (105 cm thick) containing bivalves (*Nipponoectes tamurai tamurai*, *N. t. immodesta*, and oyster fragments), a medium–coarse sand bed (80 cm thick) containing an abundance of fossil shark teeth, and an upper fine sand bed (280 cm thick) containing ammonoids (*Polyptychoceras* sp. and *Protexanites* sp.). All the shark teeth in the coarse sand bed layer are small. The bivalves in the fine sandstone bed layer include articulated shells and oyster (*Crassostrea* sp.) fragments. Hummocky cross-stratified (HCS) sandstone beds occur in the southern part of Himedo Park (Figure 1).

Kugushima.—At Kugushima Island the two main beds that contain fossil shark teeth belong to the lower part of the Hinoshima Formation (Figure 1). The first of these (horizon *a*) is a black shale layer (70 cm thick) located 132–133 m above the boundary between the lower part of the Hinoshima Formation and the basal Higo metamorphic rocks. The fossil shark teeth are associated with bivalves including *Fenestricardita ezonuculana*, *Glycymeris* (*Glycymeris*) *amakusensis*, *Apiotrigonia* sp., and *Inoceramus* sp., and are scattered irregularly throughout the beds. The second bed (horizon *b*) is a fine sandstone layer (1 m thick) located 167–168 m above the boundary. The fossil shark teeth in this layer are associated with bivalves including *G.* (*G.*) *amakusensis*. Fossil shark teeth were also evident in three other horizons: a mudstone layer immediately below horizon *a*; a mudstone layer approximately 4 m above horizon *a*; and a sandstone bed layer containing gravel and *Apiotrigonia minor* and *G.* (*G.*) *amakusensis*, located ~4 m above horizon *b*. Fossil shark teeth were also obtained from float stones of mudstone to fine sandstone, which also contained *G.* (*G.*) *amakusensis*.

Wadanohana.—The shark teeth beds of Wadanohana belong to the lower part of the Hinoshima Formation. Many fossil shark teeth were obtained from the black shale layer (50 cm thick) located 38.5–38 m below the boundary between the lower and middle parts of the Hinoshima Formation (Figure 1). Here the fossil shark teeth are asso-

Table 1. The Hinoshima Formation fossil shark teeth: taxa and number of specimens. Him, Himedo Park; Kug, Kugushima; Wad, Wadanohana; Hig, Higashiura; Kot, Kotorigoe.

				Number of specimens at each locality				
Order	Family	Species	Number of specimens	Him	Kug	Wad	Hig	Kot
Hybodontiformes	Ptychodontidae	*Ptychodus mammillaris*	6	1	2	3		
		Ptychodus sp.	1		1			
Hexanchiformes	Chlamydoselachidae	*Chlamydoselachus* sp. A	1		1			
		Chlamydoselachus sp. B	1				1	
	Hexanchidae	*Hexanchus microdon*	5			5		
		Hexanchus sp.	2		1	1		
		gen. et sp. indet.	5		3	1	1	
		Notorynchus sp.	2	1	1			
		Notidanodon dentatus	1			1		
		Notidanodon sp.	3			3		
	Orthacodontidae	*Sphenodus* sp.	2		1	1		
Echinorhiniformes	Echinorhinidae	*Echinorhinus wadanohanaensis*	5		1	4		
Squaliformes	Squalidae	*Centrophoroides* cf. *latidens*	2		2			
Lamniformes	Mitsukurinidae	gen. et sp. indet.	1		1			
	Cretoxyrhinidae	*Cretalamna appendiculata*	116	62	20	34		
		Cretalamna sp.	1		1			
	Pseudoscapanorhynchidae	*Protolamna* sp.	1			1		
	Anacoracidae	*Squalicorax falcatus*	1		1			
		Squalicorax sp.	3			2		1
	incert. fam.	*Cretodus* sp.	1		1			
		Dwardius sp.	3		1	2		
		Paranomotodon sp.	2			2		
Synechodontiformes	Palaeospinacidae	*Synechodus* sp.	3			3		
		Total	168					

ciated with bivalves including *Nucula* (*Nucula*) *amanoi*, *Acila* (*Truncacila*) *hokkaidoensis*, and *Ezonuculana mactraeformis mactraeformis*. Gastropods (Buscyconidae) and ammonoids (*Eupachydiscus haradai*, *Eupachydiscus* sp., and *Polyptychoceras* sp.) are also present (Kitamura *et al*., 1995; Kitamura, 1997, 2008, 2013).

Higashiura.—The Higashiura region ranges from the head of Cape Matsugahana to southern Ryugatake, and consists of the Higo metamorphic rocks and the lower and middle parts of the Hinoshima Formation. The lower part is composed of fine sandstone overlying the basement Higo metamorphic rocks, and is conformably overlain by the middle part, which is composed of black mudstone (>100 m thick; Figure 1) containing ammonoids (*Polyptychoceras* sp., *Gaudryceras* sp., and *Eupachydiscus* sp. in nodules) and bivalves including *Inoceramus* (*Inoceramus*) *amakusensis* and *Parvamussium yubarense*. The sedimentary structures of the lower part are indeterminable. Fossil shark teeth have been obtained from 30 cm below a fossiliferous horizon (~20 cm thick) in the

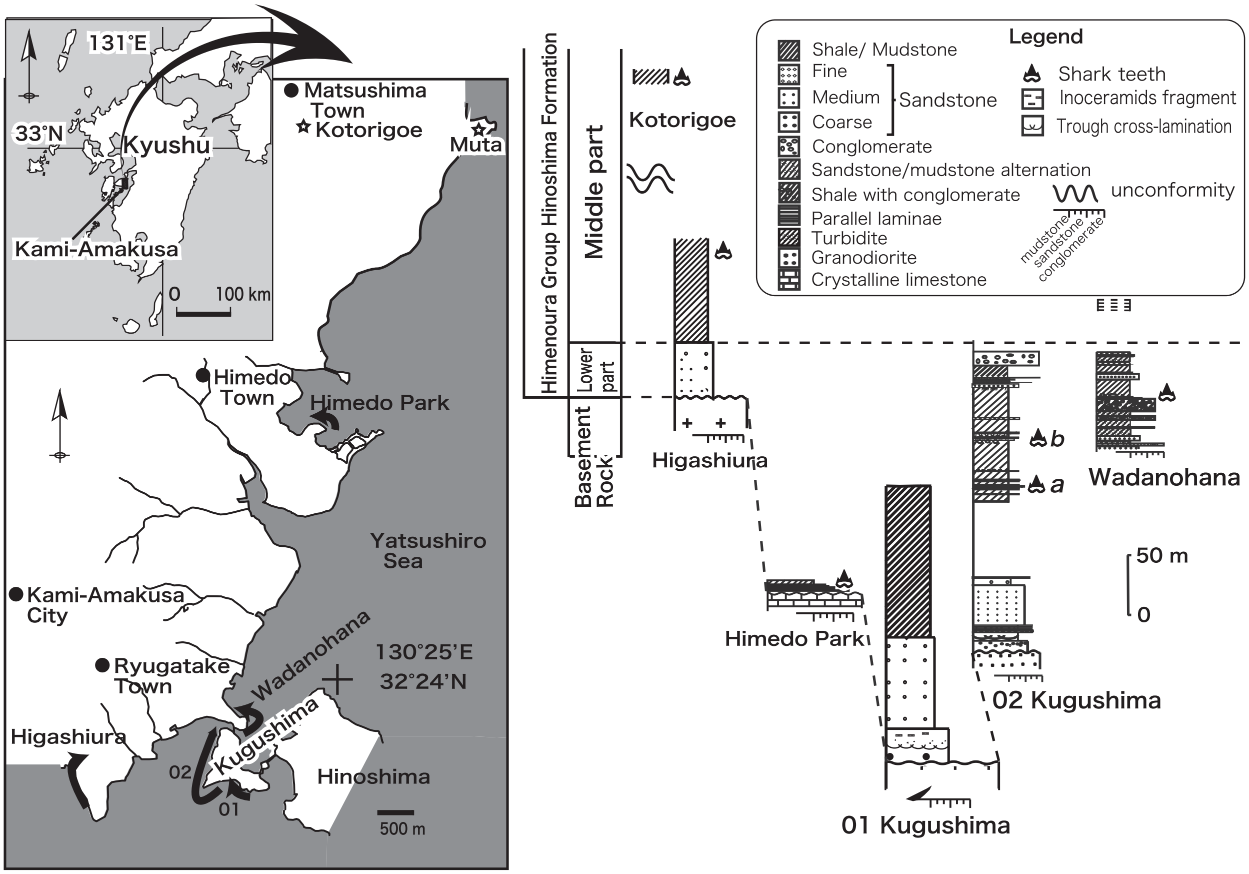

Figure 1. Study area (localities) and comparison of columnar sections containing horizons with fossil shark teeth.

middle part of this mudstone layer (Figure 1), where they are associated with the disarticulated bivalve *Acila* (*Truncacila*) sp. (Kitamura, 2008) (Table 1). The mudstone of the shark teeth horizon does not contain slump debris, but adult ammonoids and inoceramids are present in the horizons above and below.

Kotorigoe.—The shark teeth bed of Kotorigoe belongs to the middle part of the Hinoshima Formation and is composed of black mudstone (Figure 1). This mudstone has yielded fossil shark teeth and the ammonoid *Gaudryceras* sp. (Kitamura *et al*., 1995).

Features and paleoecological significance of the shark fauna from the Upper Cretaceous Himenoura Group of the Hinoshima Formation

Himedo Park.—*Crassostrea* sp. is known to inhabit tidal flats (Kumagae and Komatsu, 2004), and the presence of HCS indicates a shallow water (shoreface) depositional environment (Saito, 1989). These factors indicate the presence of a coastal shallow-water environment and the para-autochthonous occurrence of bivalves. Similar findings have been reported by Komatsu *et al*. (2008). The depositional environment of Himedo Park suggests a distributary channel and sand bar developed on a delta at the head of a bay. The coarse sand bed containing many shark teeth is considered to have formed the sand body at the bay mouth (Komatsu *et al*., 2008, 2009), as inferred from features including a coarse sand bed, HCS sandstone beds, and the presence of brackish water bivalves (*Crassostrea* sp.) and marine bivalves (e.g. *Nipponeonectes tamurai*). The fossil shark taxa include *Notorynchus* sp., *Ptychodus mammillaris*, and *Cretalamna appendiculata*, which appear to have inhabited the waters of inner coastal bays. The presence of highly worn fossil shark teeth (*C. appendiculata*), teeth having cusps, and the roots of shark teeth suggests deposition in fast-moving currents. This active circulation of marine water is thought to have resulted from the effects of the transgression (Komatsu *et al*., 2008).

Kugushima.—The presence of fossil shark teeth in horizon *a* is thought to be an autochthonous occurrence because sedimentary structures and gravels are not visible in the massive mudstone layer (Komatsu *et al*., 2008), which is intensively bioturbated. In contrast, the fossil shark teeth in horizon *b* are thought to be a result of gravity flow, perhaps a submarine debris flow, because the fine sandstone contains sandstone gravels, indicating an allochthonous occurrence. Horizon *a* contains shallow-water bivalves including *Apiotrigonia minor*, *Ezonuculana mactraeformis mactraeformis*, and *Glycymeris* (*Glycymeris*) *amakusensis*, while horizon *b* also contains *G.* (*G.*) *amakusensis* and non-articulated shells. As noted above, horizon *a* contains teeth of a number of shark species thought to have inhabited the bottom and surface layers offshore, while horizon *b* contains teeth of shark species thought to have inhabited shallow to offshore waters. These fossil shark teeth are better preserved than those from Himedo Park.

Wadanohana.—Fossil shark teeth were also obtained from a black massive mudstone bed containing slump debris and many bivalves. This bed is thought to have been formed by a gravity flow (i.e., a submarine debris flow) because the presence of mudstone containing bivalves, and non-articulated and irregularly scattered shells, indicates an allochthonous occurrence. The bivalves comprise shallow-water taxa including *Apiotrigonia minor*, *Ezonuculana mactraeformis mactraeformis*, *Glycymeris* (*Glycymeris*) *amakusensis*, and *Eriphyla* sp., as well as deep-water taxa including *Nucula* (*Nucula*) *amanoi*, *Nanonavis sachalinensis*, *Myrtea* (*Myrtea*) *ezoensis*, and *Thayasira* (*Thayasira*) *himedoensis* (Tashiro *et al*., 1986; Aberhan, 1994; Tashiro, 1994). This bed also contains offshore taxa including *E. mactraeformis mactraeformis* and *G.* (*G.*) *amakusensis*, and continental shelf taxa including *Inoceramus* sp. and *Nanonavis sachalinensis* (Kumagae and Komatsu, 2004). This assemblage indicates that shallow and continental shelf bivalves were deposited together in the deep sea by a submarine debris flow. It is thought that teeth from shallow-water to offshore shark species were also deposited there. These teeth are better preserved than those from Himedo Park. For example, multicuspid teeth (such as those from *Hexanchus*) and labio-lingually compressed teeth (such as those from *Echinorhinus*) are well preserved, indicating a shorter transport distance than the teeth at Himedo Park.

Higashiura.—Fossil shark teeth were obtained from <30 cm below a fossiliferous horizon (~20 cm thick) in the middle part of this mudstone layer (Figure 1). The fossil shark taxa detected were *Chlamydoselachus* sp. B and Hexanchidae gen. et sp. indet., associated with the disarticulated bivalve *Acila* (*Truncacila*) sp. The mudstone of the shark teeth horizon does not contain slump debris, but adult ammonoids and inoceramids are present in the horizons above and below. This indicates that the depositional facies were deeper-water than those of Kugushima or Wadanohana, and indicate an autochthonous occurrence.

Kotorigoe.—The mudstone yielded one fossil shark taxon (*Squalicorax* sp.) and ammonoids (*Gaudryceras* sp.). The depositional facies, which are similar to those of Higashiura, are thought to have been deeper than those of Kugushima or Wadanohana, and indicate an autochthonous occurrence.

Composition of the shark fauna from the Hinoshima Formation

The shark fauna from the Hinoshima Formation consists of 23 species, 15 genera, 11 families, and six orders (Table 1). In order of abundance the taxa include Lamniformes and Hexanchiformes (nine species), each comprising 39%; Hybodontiformes (two species: 9%); and Echinorhiniformes, Squaliformes, and Synechodontiformes (single species: each 4%). The number of specimens collected from the Hinoshima Formation included 129 Lamniformes, among which *Cretalamna appendiculata* (Cretoxyrhinidae) was the dominant species (116); 22 Hexanchiformes; seven Hybodontiformes; five Echinorhiniformes; two Squaliformes; and three Synechodontiformes. The Lamniformes included five families, six genera, and nine species (Figures 2–5). The teeth designated KCM 12-000378 and KCM 12-000272 were identified as *Notorynchus* sp. based on the following criteria. Cretaceous specimens of *Notorynchus* have been described as *Notorynchus aptiensis* (Pictet, 1865) or indeterminate species (Underwood *et al*., 2011; Cappetta, 2012). Underwood *et al*. (2011) erected the genus *Gladioserratus* based on Early and "Middle" Cretaceous specimens (including *N. aptiensis*), which were distinguished from *Notorynchus. Notorynchus* specimens (lower jaw teeth) obtained from the Hinoshima Formation (KCM 12-000378, Figure 3-22; KCM 12-000272, Figure 3-23) are distinguished from congeners of the genus *Gladioserratus* by having a rectangular root profile, gracile cusps, and a gradual increase in the size of the serrations on the mesial edge of the teeth.

The habitats of sharks from the Hinoshima Formation

Morphology and locomotion of sharks

Wilga and Lauder (2004) classified extant sharks in terms of four body types and four modes of locomotion (anguilliform, subcarangiform, carangiform, and thunniform) ranging from the slowest to the fastest swimming speeds. The swimming abilities of the sharks from the Hinoshima Formation were categorized based on the locomotion types described above. The genera *Chlamydoselachus* and *Echinorhinus* are comparable to anguilliform sharks (slim, with eel-like movement and generally

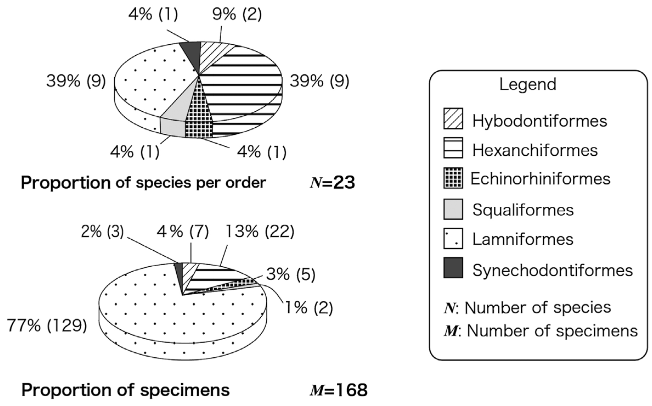

Figure 2. Proportion and total number of fossil shark tooth specimens from the Hinoshima Formation.

body type 4). The genera *Paranomotodon*, *Hexanchus*, *Notorynchus*, and *Notidanodon* are comparable to subcarangiform sharks (faster than anguilliform). *Paranomotodon* is considered to have had body type 2, and the others body type 3. The genera *Centrophoroides* and *Cretascymnus* were carangiform (undulating movement is limited to the back half of the body). The genera *Squalicorax*, *Dwardius*, *Cretodus*, *Cretalamna*, *Protolamna*, and Mitsukurinidae gen. et sp. indet. are comparable to thunniform sharks (rapid undulation of the tail or tail lobes), and generally had body type 1.

Behavior and habitat of shark groups

Hybodontiformes.—Members of the genus *Ptychodus* (Agassiz, 1835) are thought to have been sluggish swimmers using suction feeding, similar to that of extant Orectolobiformes (Shimada *et al*., 2009; Shimada, 2012). Its crushing type dentition is thought to have enabled *Ptychodus* to crush inoceramids and ammonoids (Niedźwiedzki and Kalina, 2003; Shimada, 2012).

Hexanchiformes.—Extant Hexanchiformes Buen, 1926 include Chlamydoselachidae and Hexanchidae, which live mainly in deep water and occur worldwide (Compagno, 1984). Chlamydoselachidae are primitive fish similar to the Paleozoic *Symmorium.* Extant species of Chlamydoselachidae live mainly in the deep sea around Japan, and their occurrence extends from the upper Turonian to the Coniacian (Goto and the Japanese Club for Fossil Shark Tooth Research, 2004). The chlamydoselachids from the Hinoshima Formation are divided into two classes: (i) *Chlamydoselachus* sp. A (Figure 3-8, "*Chlamydoselachus* sp. 3" in Goto and the Japanese Club for Fossil Shark Tooth Research, 2004), almost three times larger than the extant species *C. anguineus* and *C. africana*, and (ii) *Chlamydoselachus* sp. B (Figure 3-9), which is almost 1.5 times larger than the extant species. It is thought that members of the genus *Chlamydoselachus* lived in shallow waters during the Mesozoic and early Cenozoic, because of the associated presence of fossil inoceramids and ammonoids, and later moved to deep water (Richter and Ward, 1990; Goto and the Japanese Club for Fossil Shark Tooth Research, 2004). Hexanchid sharks from the Hinoshima Formation include *Hexanchus microdon*, *Hexanchus* sp., *Notorynchus* sp., and the extinct cow shark *Notidanodon dentatus*. Although extant *Notorynchus cepedianus* inhabit shallow water, most of the extant Hexanchidae species are deep-water inhabitants (Compagno, 1984). *Sphenodus* sp. (Orthacodontidae) from the Hinoshima Formation is thought to have been an active offshore predator (Rees, 2012).

Echinorhiniformes.—Cappetta (2012) removed the Family Echinorhinidae (including the genus *Echinorhinus*) from the Squaliformes of Compagno (1984). The extant genus *Echinorhinus* is a sluggish swimming predator inhabiting continental shelves and slopes in deep water (Compagno, 1984).

Squaliformes.—Squaliformes (dogfish sharks) include 130 species in seven families, and mainly inhabit deep waters (Compagno, 1984). Extant squaliforms are diverse and globally distributed, mainly inhabiting deep water from the Arctic to the Antarctic (Compagno, 1984). Studies of foraminifera in Sweden indicate that the squaliform sharks inhabited shallow water in the Late Cretaceous (Siverson, 1993; Siverson and Cappetta, 2001). Klug and Kriwet (2010) suggested that deep sea adaptations in Squaliformes developed in the early Late Cretaceous, based on the construction, dating, and analysis of a genus-level phylogeny of extinct and living dogfish sharks.

Lamniformes.—Based on their skeletons, it is thought that the genera *Squalicorax*, *Paranomotodon*, *Cretodus*, and most of the Mitsukurinidae sharks were fast swimmers and the top offshore predators on the continental shelf (Kriwet and Benton, 2004; Tomita and Kurihara, 2011). Furthermore, *Cretalamna appendiculata*, which is a dominant species in the Hinoshima Formation, is thought to be similar to the extant genus *Lamna* in terms of the size and morphology of the jaw and teeth (see Shimada, 2007). The genus *Squalicorax* has teeth similar in form to the extant *Galeocerdo cuvier* and is thought to have been an offshore shark (Antunes and Cappetta, 2002). It is thought that *Cretodus semiplicatus* inhabited shallow water, as fossil remains were found in shallow-water facies of the Mikasa Formation in Hokkaido (Tomita and Kurihara, 2011).

Synechodontiformes.—The genus *Synechodus* is thought to have been a sluggish benthic shark, as the dentition is similar to that of extant scyliorhinids (Compagno *et al*., 2005; Klug, 2009).

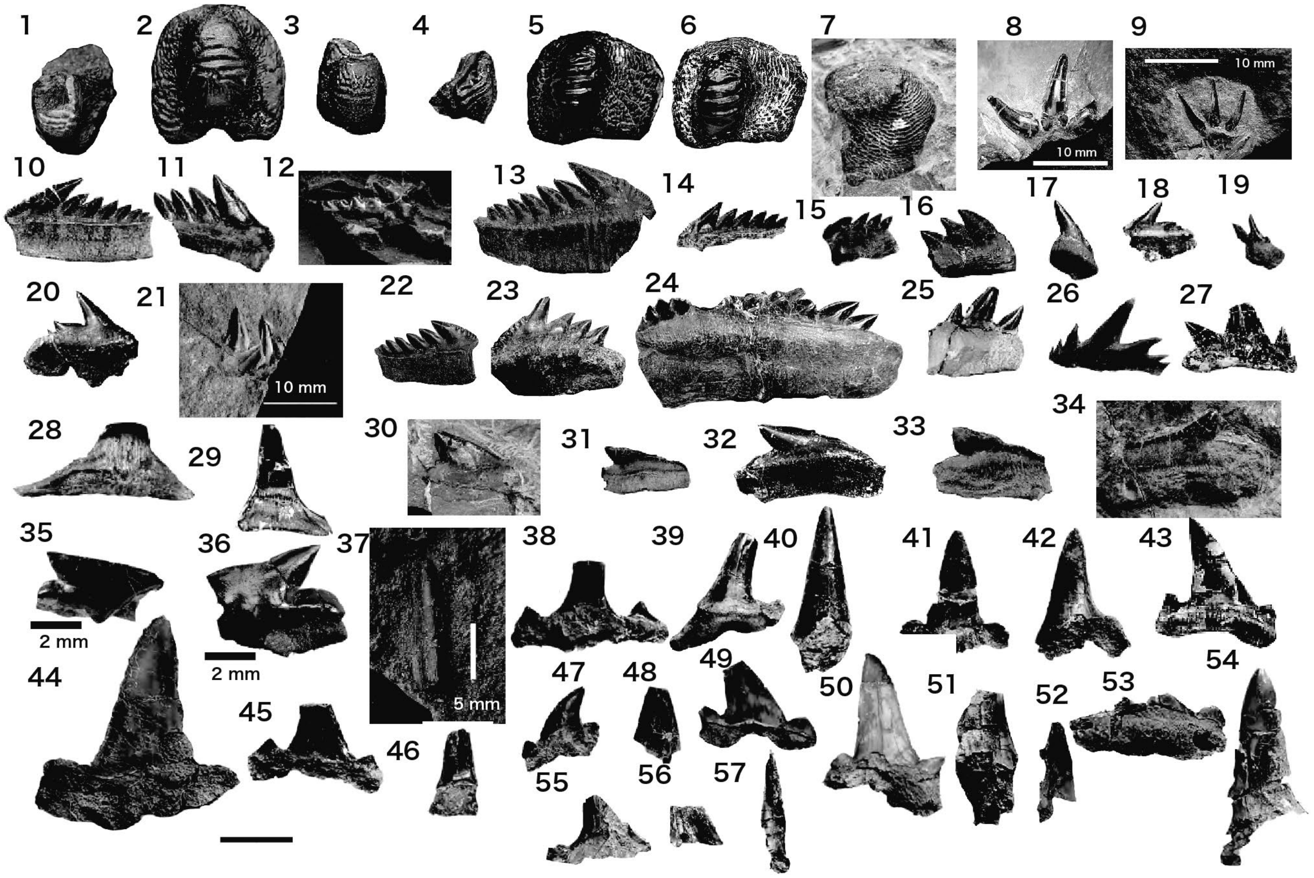

Figure 3. Shark fossils from the Hinoshima Formation. **1–6,** *Ptychodus mammillaris*; 1, KCM12-000061 (Himedo Park); 2, KCM12-000148 (replica, Kugushima); 3, KCM12-000149 (replica, Kugushima); 4, KCM12-00060 (Wadanohana); 5, KCM12-000144 (replica, Wadanohana); 6, KCM12-000257 (Wadanohana); **7,** *Ptychodus* sp., KCM12-000150 (Kugushima); **8,** *Chlamydoselachus* sp. A, GCM-VP400 (Kugushima); **9,** *Chlamydoselachus* sp. B, KCM12-000360 (Higashiura); **10–14,** *Hexanchus microdon*; 10, KCM 12-000039 (Wadanohana); 11, KCM 12-000042 (Wadanohana); 12, KCM 12-000044 (Wadanohana); 13, KCM 12-000263 (Wadanohana); 14, GCM-VP401 (Wadanohana); **15, 16,** *Hexanchus* sp.; 15, KCM 12-000346 (Kugushima); 16, KCM 12-000040 (Wadanohana); **17–21,** Hexanchidae gen. et sp. indet.; 17, KCM 12-000413 (Kugushima); 18, GCM-VP402 (Kugushima); 19, KCM 12-000043 (Wadanohana); 20, GCM-VP403 (Kugushima); 21, GCM-VP407 (Higashiura); **22, 23,** *Notorynchus* sp.; 22, KCM 12-000378 (Himedo Park); 23, KCM 12-000272 (Kugushima); **24,** *Notidanodon dentatus*; KCM 12-000365 (Wadanohana); **25–27,** *Notidanodon* sp.; 25, GCM-VP404 (Wadanohana); 26, GCM-VP405 (replica, Wadanohana); 27, GCM-VP406 (Wadanohana); **28, 29,** *Sphenodus* sp.; 28, GCM-VP411 (Kugushima); 29, KCM 12-000359 (Wadanohana); **30–34,** *Echinorhinus wadanohanaensis*; 30, KCM 12-000429 (Kugushima); 31, KCM12-000064 (Wadanohana); 32, KCM 12-000266 (Wadanohana); 33, KCM12-000267 (Wadanohana); 34, KCM12-000362 (Wadanohana); **35, 36,** *Centrophoroides* cf. *latidens*; 35, KCM12-000361 (Kugushima); 36, KCM12-000419 (Kugushima). **37,** Mistukurinidae gen. et sp. indet.; KCM 12-000424 (Kugushima). **38–57,** *Cretalamna appendiculata* (Himedo Park); 38, lateral tooth (KCM 12-000031); 39, lateral tooth (KCM 12-000032); 40, anterior tooth (KCM12- 000033); 41, anterior tooth (KCM 12-000034); 42, KCM 12-000035; 43, lateral tooth (KCM 12-000036); 44, lateral tooth (KCM 12-000045); 45, lateral tooth (KCM 12-000153); 46, KCM 12-000156; 47, lateral tooth (KCM 12-000180); 48, KCM 12-000211; 49, lateral tooth (KCM 12-000261); 50, anterior tooth (KCM 12-000262); 51, KCM 12-000302; 52, KCM 12-000305; 53, KCM 12-000306; 54, anterior tooth (KCM 12-000307); 55, KCM 12-000308; 56, KCM 12-000309; 57, KCM 12-000310. Scale bars are 10 mm unless labelled otherwise.

Habitat at each locality

The habitats for the Hinoshima Formation shark fauna can be separated into three types (Figure 6).

The first habitat type includes the coastal zone, which is evident at Himedo Park. A number of mostly small fossil teeth of *Cretalamna appendiculata* (62 specimens) and the genera *Ptychodus* (one specimen) and *Notorynchus* (one specimen) were found at Himedo Park (Table 1). The absence of evidence of the presence of *Carcharias* and *Hybodus*, and the abundant presence of *C. appendiculata*, *Ptychodus*, and *Notorynchus*, is a feature of the Hinoshima fauna. In addition, the fossil shark teeth from Kugushima and Wadanohana are much larger than those from Himedo Park. It is thought that larger sharks

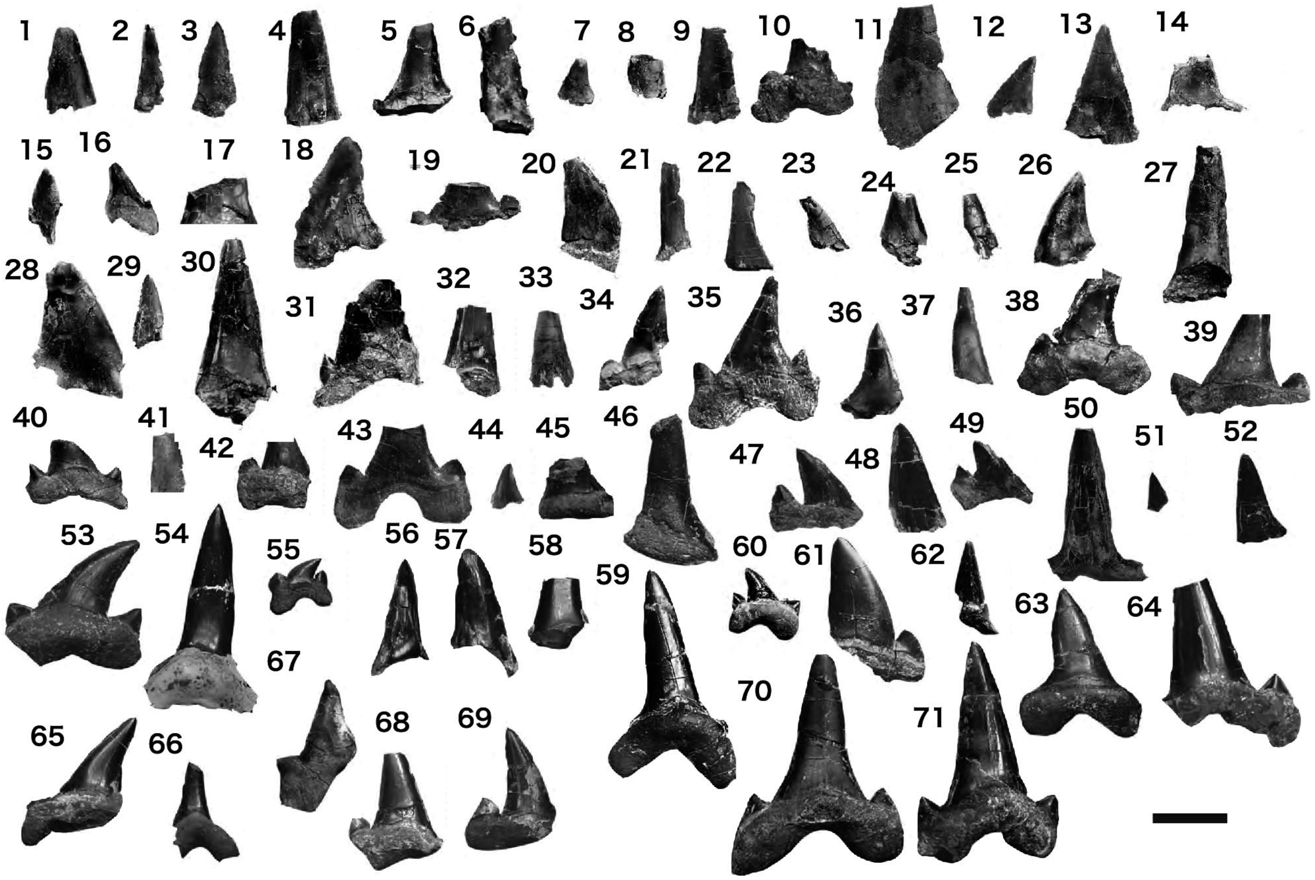

Figure 4. Shark fossils from the Hinoshima Formation, continued. **1–42,** *Cretalamna appendiculata* (Himedo Park); 1, KCM 12-000311; 2, KCM 12-000312; 3, KCM 12-000313; 4, KCM 12-000314; 5, KCM 12-000315; 6, KCM 12-000316; 7, KCM 12-000317; 8, KCM 12-000318; 9, KCM 12-000319; 10, KCM 12-000320; 11, KCM 12-000321; 12, KCM 12-000322; 13, KCM 12-000324; 14, KCM 12-000325; 15, KCM 12-000326; 16, KCM 12-000327; 17, KCM 12-000328; 18, KCM 12-000329; 19, KCM 12-000330; 20, KCM 12-000331; 21, KCM 12-000332; 22, KCM 12-000333; 23, KCM 12-000334; 24, KCM 12-000335; 25, KCM 12-000336; 26, KCM 12-000337; 27, anterior tooth (KCM 12-000338); 28, lateral tooth (KCM 12-000339); 29, KCM 12-000340; 30, anterior tooth (KCM 12-000341); 31, KCM 12-000342; 32, KCM 12-000343; 33, KCM 12-0000344; 34, KCM 12-000357; 35, lateral tooth (KCM 12-000364); 36, KCM 12-000376; 37, KCM 12-000377; 38, lateral tooth (KCM 12-000383); 39, lateral tooth (KCM 12-000384); 40, lateral tooth (KCM 12-000394); 41, KCM 12-000412; 42, lateral tooth (KCM 12-000415); **43–62,** *Cretalamna appendiculata* (Kugushima); 43, anterior tooth (KCM 12-000010); 44, anterior tooth (KCM 12-000047); 45, KCM 12-000196; 46, KCM 12-000269; 47, lateral tooth (KCM 12-000270); 48, KCM 12-000271; 49, lateral tooth (KCM 12-000279); 50, anterior tooth (KCM 12-000280); 51, KCM 12-000281; 52, KCM 12-000282; 53, lateral tooth (KCM 12-000289); 54, anterior tooth (KCM 12-000290); 55, posterior tooth (KCM 12-000345); 56, KCM 12-000347; 57, KCM 12-000350; 58, KCM 12-000358; 59, anterior tooth (KCM12- 000416); 60, posterior tooth (KCM 12-000417); 61, lateral tooth (KCM 12-000420); 62, KCM 12-000421; **63–71,** *Cretalamna appendiculata* (Wadanohana); 63, lateral tooth (KCM 12-000003); 64, KCM 12-000004; 65, lateral tooth (KCM 12-000005); 66, anterior tooth (KCM 12-000006); 67, KCM 12-000007; 68, KCM 12-000008; 69, lateral tooth (KCM 12-000011); 70, anterior tooth (KCM 12-000012); 71, anterior tooth (KCM 12-000013). Scale bar is 10 mm.

inhabited offshore waters, whereas smaller sharks used coastal zones as their breeding area. Similar habitat isolation is known for the extant species *Sphyrna lewini*, with adult individuals inhabiting offshore waters and smaller individuals inhabiting shallow inner waters (Compagno, 1984; Holland *et al*., 1993). Yamaguchi (2007) noted that the breeding zone for extant *S. lewini* is the back of Ariake Bay (Kyushu, Japan). Coastal areas provide important breeding grounds for extant shark taxa including *Hexanchus griseus* and *Notorynchus cepedianus*, and extinct taxa including *Scapanorhynchus puercoensis* (e.g. Yamaguchi, 2007; Quigley, 2010; Bourdon *et al*., 2011). Himedo Park may have been a breeding area, based on the examination of each taxon (described below).

Shimada *et al.* (2010) used teeth size to estimate the length of *Cretalamna appendiculata* from the Futaba Group. Shimada (2005) had previously shown that the crown height of shark teeth can be used to predict the

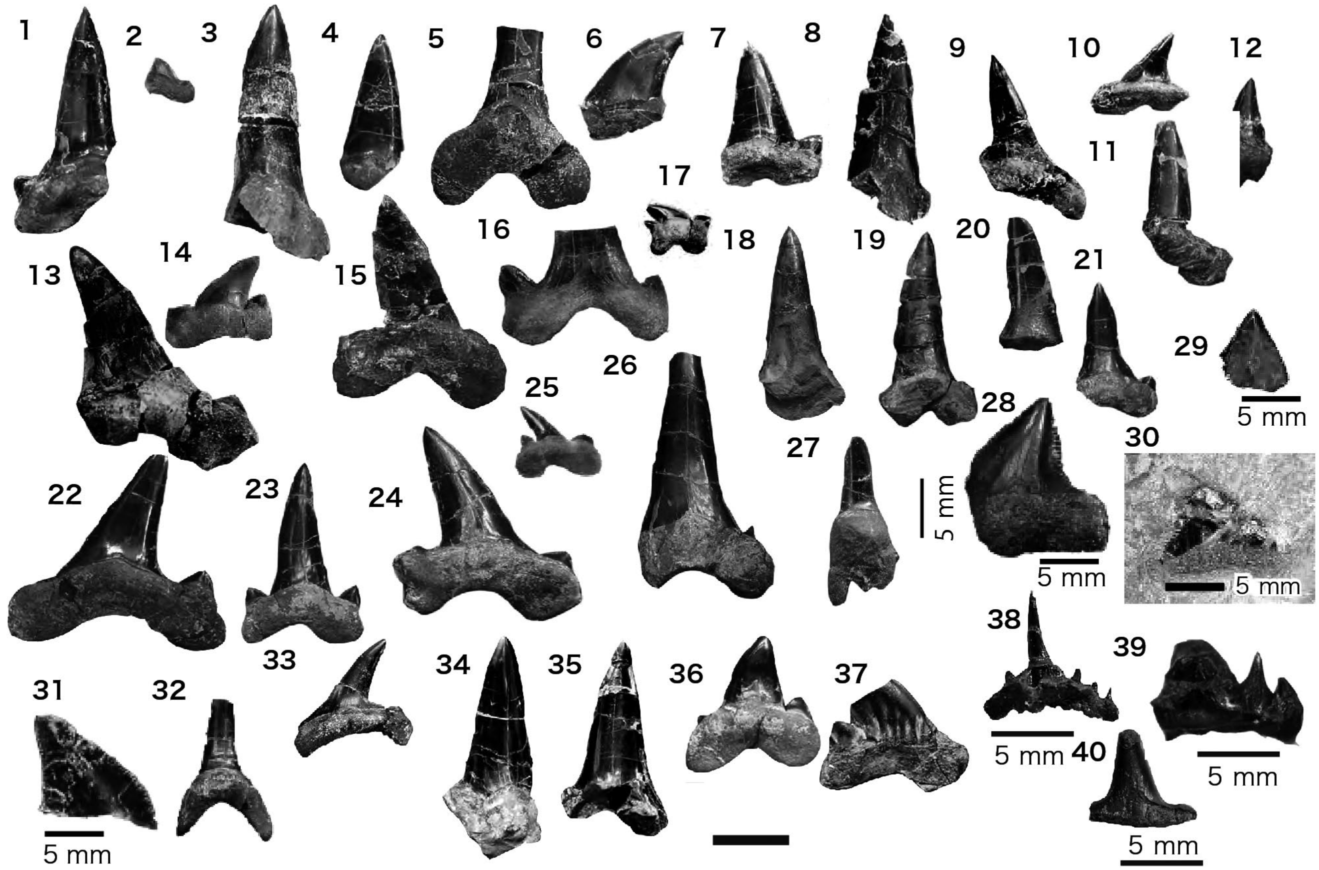

Figure 5. Shark fossils from the Hinoshima Formation, continued. **1–25,** *Cretalamna appendiculata* (Wadanohana); 1, anterior tooth (KCM 12-000014); 2, KCM 12-000015; 3, anterior tooth (KCM 12-000016); 4, anterior tooth (KCM 12-000017); 5, anterior tooth (KCM 12-000018); 6, lateral tooth (KCM 12-000019); 7, KCM 12-000020; 8, KCM 12-000021; 9, lateral tooth (KCM 12-000022); 10, lateral tooth (KCM 12-000023); 11, KCM 12-000024; 12, KCM 12-000025; 13, lateral tooth (KCM 12-000026); 14, lateral tooth (KCM 12-000027); 15, lateral tooth (KCM 12-000028); 16, anterior tooth (KCM 12-000029); 17, posterior tooth (KCM 12-000030); 18, anterior tooth (KCM 12-000046); 19, anterior tooth (KCM 12-000048); 20, KCM 12-000049; 21, KCM 12-000050; 22, lateral tooth (KCM 12-000258); 23, anterior tooth (KCM 12-000259); 24, lateral tooth (KCM 12-000260); 25, lateral tooth (GCM-VP409); **26,** *Cretalamna* sp.; KCM 12-000047 (Kugushima); **27,** *Protolamna* sp., GCM-VP410 (Wadanohana); **28,** *Squalicorax falcatus*, KCM 12-000352 (Kugushima); **29–31,** *Squalicorax* sp.; 29, KCM 12-000052 (Wadanohana); 30, GCM-VP413 (Wadanohana); 31, KCM 12-000265 (Kotorigoe); **32, 33,** *Paranomotodon* sp.; 32, KCM 12-000051 (Wadanohana); 33, GCM-VP408 (Wadanohana); **34–36,** *Dwardius* sp.; 34, KCM 12-000002 (Kugushima); 35, KCM 12-000001(Wadanohana); 36, KCM 12-000009 (Wadanohana); **37,** *Cretodus* sp., KCM 12-000278 (Kugushima); **38–40,** *Synechodus* sp.; 38, KCM 12-000264 (Wadanohana); 39, KCM 12-000363 (Wadanohana); 40, GCM-VP412 (Wadanohana). Scale bar at bottom center is 10 mm and applies to all photographs unless stated otherwise.

length of lamniform sharks because there is a positive correlation between tooth size and body size in these sharks. Thus, Shimada (2007) estimated the total length of an individual of *C. appendiculata* from the Niobrara Chalk (Kansas, USA) to be 2.3–3.0 m, based on an average crown height of 15.5 mm for the anterior teeth, and a maximum crown height of 13.5 mm for lateral teeth. Shimada *et al*. (2010) estimated the length range for the *C. appendiculata* population from the Futaba Group to be 1.5–4.2 m, by comparing the crown height of anterior teeth and the tallest lateral teeth of a *C. appendiculata* individual from the Niobrara Chalk with those of *C. appendiculata* from the Futaba Group.

The length of *Cretalamna appendiculata* from the Hinoshima Formation was estimated based on the method of Shimada *et al.* (2010). Figure 7 shows the relationship between tooth crown height (*CH*) and the total length (*TL*) of *C. appendiculata* at each locality (Himedo Park, Kugushima, and Wadanohana) in the study area. For the Himedo Park specimen KCM 12-000262 (Figure 3-50), the crown height for the anterior tooth is 16.0 mm, which is 107.7% of the average crown height (15.5 mm) for anterior teeth of *C. appendiculata* from the Niobrara Chalk. Based on this relationship the total length of the

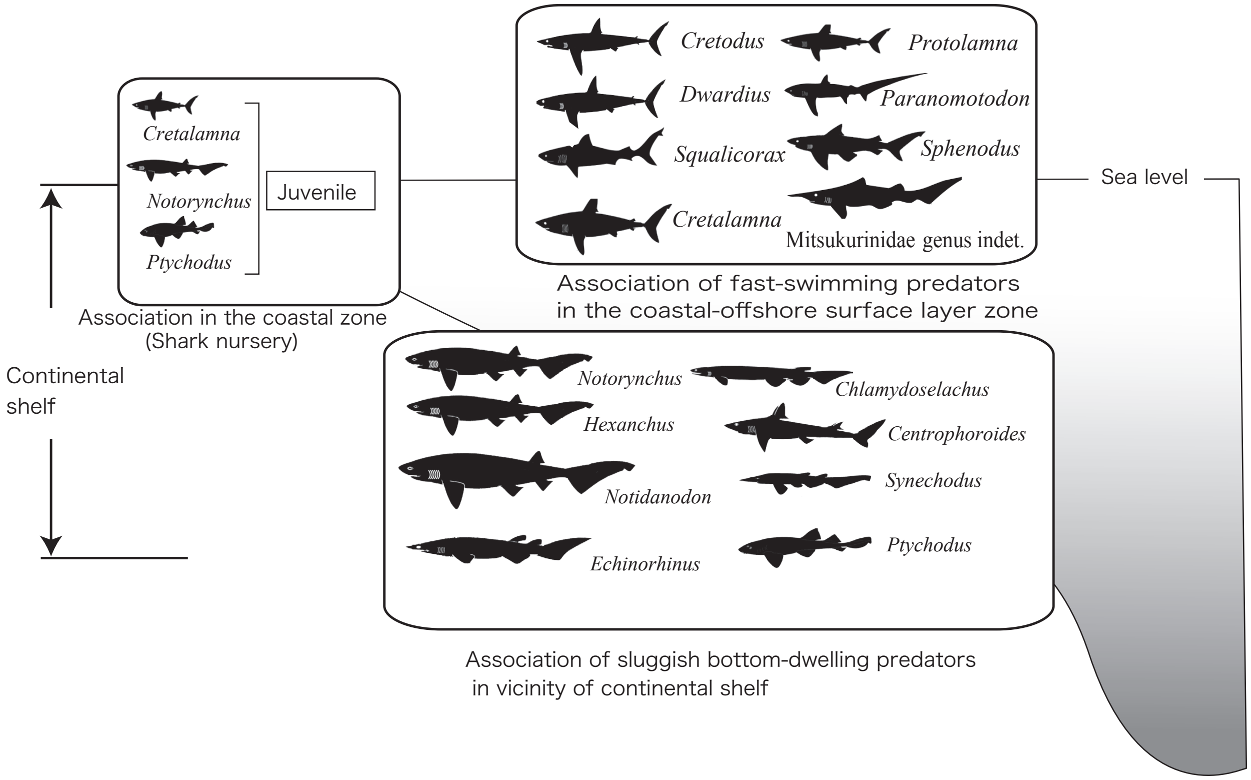

Figure 6. Habitats of the Hinoshima Formation shark fauna.

KCM 12-000262 specimen was estimated to be 2.4–3.2 m. The estimated total length of *C. appendiculata* from Himedo Park was 1.1–3.4 m, based on measurements of anterior teeth (2 specimens) and lateral teeth (6 specimens). For *C. appendiculata* from Kugushima the length range is 2.3–4.5 m, based on measurements of anterior teeth (1 specimen) and lateral teeth (2 specimens), and for *C. appendiculata* from Wadanohana the length range is 1.2–5.0 m, based on measurements of anterior teeth (4 specimens) and lateral teeth (5 specimens). The smallest tooth of *C. appendiculata* was found for a juvenile specimen from Himedo Park, and the specimens from this location were generally smaller than those from Kugushima and Wadanohana.

The *Notorynchus* sp. (KCM 12-000378; Figure 3-22) from Himedo Park is represented by a small lower tooth. Adnet (2006) calculated the length of extant hexanchid sharks from the strong relationship between shark length and the width of lower teeth, as described by the following equation: length (in m) = [111 × width of tooth (in cm) + 3.9 ($R = 0.97, p < 0.001; N = 243$)]/100. Based on this equation, the length of the Himedo Park *Notorynchus* sp. specimen (KCM 12-000378; tooth width = 14.6 mm) is estimated to have been ~1.66 m. Similarly, the length of the *Notorynchus* sp. (KCM 12-000272; Figure 3-23; tooth width = 18.8 mm) from Kugushima is estimated to have been ~2.13 m. The length range for the extant *N. cepedianus* is 2.0–2.9 m (possibly 3–4 m) (Compagno *et al*., 2005). Consequently, the *Notorynchus* sp. (KCM 12-000378) from Himedo Park was probably a juvenile.

The dentition (upper and lower) of the Ptychodontidae exhibits monognathic heterodonty and forms a crushing pavement similar to that of extant Heterodontidae (e.g. Welton and Farish, 1993; Shimada, 2012). In terms of crown width, the specimens of *Ptychodus mammillaris* (KCM12-000061; Figure 3-1; mesial–distal crown width: 12.1 +mm) from Himedo Park are similar to the specimens of *P. mammillaris* KCM12-000257 (Figure 3-6; mesial–distal crown width: 15.5 mm) and KCM12-000144 (Figure 3-5; mesial–distal crown width: 15.0 mm) from Wadanohana, although slightly smaller. Consequently, the *P. mammillaris* (KCM12-000061) specimen from Himedo Park was probably a juvenile. As noted above, although a large specimen (maximum length 3.4 m) of *Cretalamna appendiculata* was found at Himedo Park, most of the individuals were relatively small and were probably juveniles, suggesting that this was a breeding area. The presence of the large specimen of *C. appen-*

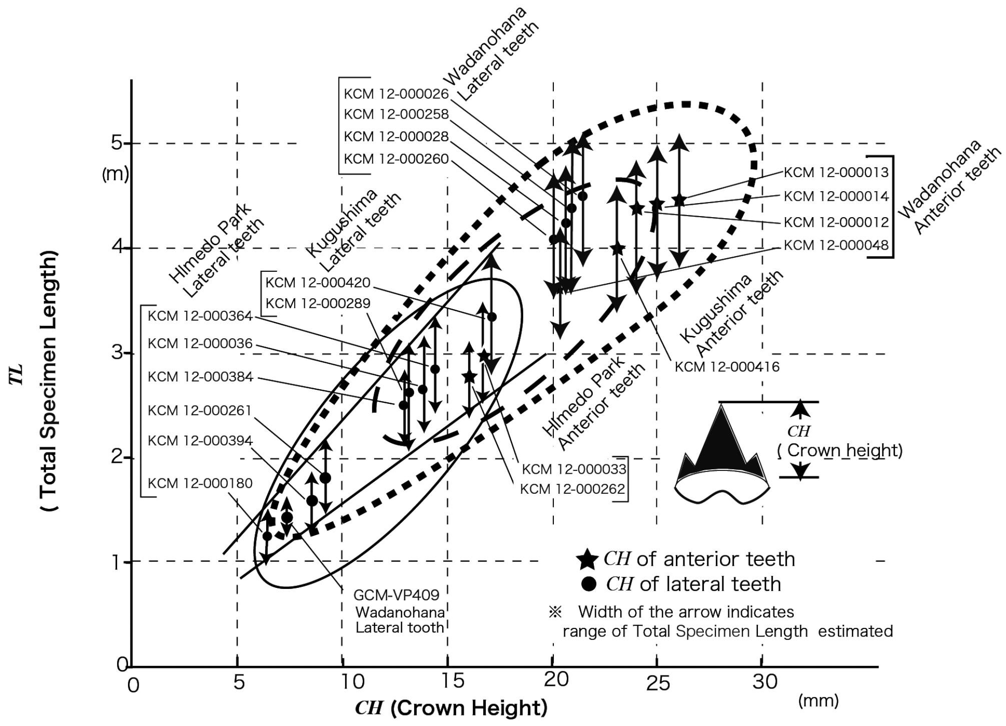

Figure 7. Relationship between tooth crown height and the total length of *Cretalamna appendiculata* at each locality (Himedo Park, Kugushima, Wadanohana). Specimen numbers reflect those in Figures 3–5. The method for estimating total length (*TL*) followed Shimada (2007) and Shimada *et al*. (2010).

diculata at Himedo Park probably indicates that adult sharks entered the breeding area to deliver pups, as occurs with extant sharks. For example, adult hammerhead sharks (*Sphyrna lewini*) enter Ariake Bay in southwestern Japan (Yamaguchi, 2007) and bays in Hawaii (Clarke, 1971) to give birth and deliver pups.

The second habitat type is the coastal–offshore surface layer zone, which is the habitat of fast-swimming predators, as inferred for Kugushima, Wadanohana, and Kotorigoe. The genera *Cretodus*, *Dwardius*, *Squalicorax*, *Cretalamna*, and *Protolamna* (Lamniformes), and the genus *Sphenodus* (Synechodontiformes) are associated with this habitat.

The third habitat type is that in the vicinity of the continental shelf, and is characterized by the occurrence of sluggish bottom-dwelling predators. This habitat type can be seen at Kugushima, Wadanohana, Higashiura, and Kotorigoe, where it is associated with the genera *Hexanchus*, *Notorynchus*, *Notidanodon*, *Chlamydoselachus*, *Echinorhinus*, *Centrophoroides*, and *Ptychodus*. The shark teeth fossils associated with this habitat are thought to have been deposited on the continental shelf, as they lack signs of abrasion and are associated with well preserved ammonoid fossils.

Habitat shift in the genera *Chlamydoselachus* and *Echinorhinus*

Extant *Chlamydoselachus anguineus* and *Echinorhinus brucus* primarily inhabit the deep sea and prey on Cephalopoda and bottom-dwelling fishes (Compagno, 1984). Two types of fossil teeth of the genus *Chlamydoselachus* from the Hinoshima Formation were reported by Goto and the Japanese Club for Fossil Shark Tooth Research (2004). The first type (*Chlamydoselachus* sp. 3) is three times larger than those of extant species, and the second type (*Chlamydoselachus* sp. 2) is similar in size to those of extant species. In this study, *Chlamydoselachus* sp. A (GCM-VP400; Figure 3-8) is similar to the first type described above, and *Chlamydoselachus* sp. B (KCM12-000360; Figure 3-9) is similar to the second type. The first type, comprising large and robust teeth, has also been found in Upper Cretaceous deposits of the Izumi Group in Osaka, in Antarctica, and in Angola. They are thought to have belonged to species inhabiting shallow water (Richter and Ward, 1990; Antunes and Cappetta, 2002; Goto and the Japanese Club for Fossil Shark Tooth Research, 2004). Consoli (2008) noted that following the extinction of cephalopods having a shell (such as ammonoids) after the Cretaceous-Paleogene (K-Pg) boundary, the rise

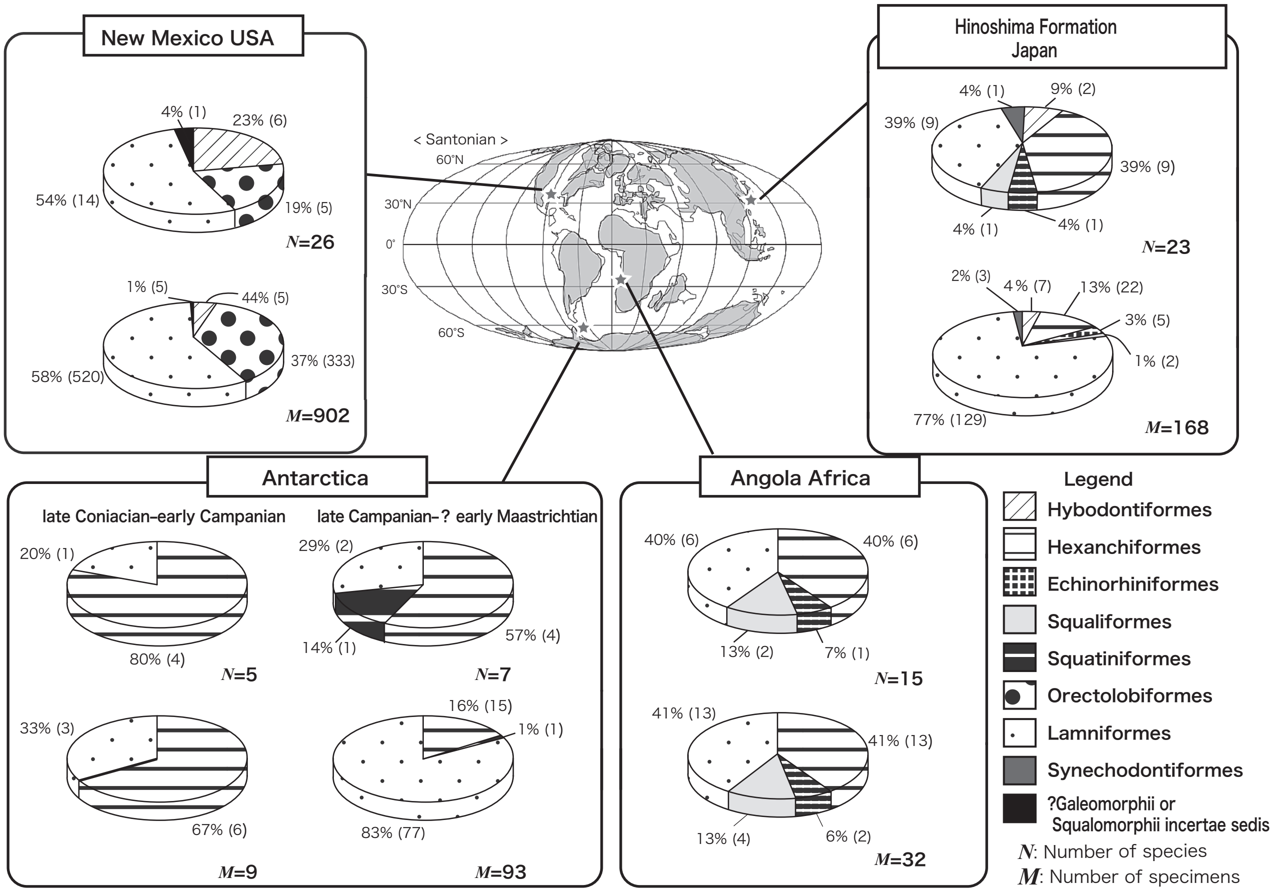

Figure 8. Numbers of species and total number of specimens (by order) in the Hinoshima Formation and other areas. Paleomap from Smith *et al.* (2004). New Mexico, USA (Santonian); Bourdon *et al*. (2011). Antarctica, Santa Marta Formation, late Coniacian–early Campanian, late Campanian?–early Maastrichtian; Kriwet *et al*. (2006). Angola (Campanian–Maastrichtian); Antunes and Cappetta (2002). Hinoshima Formation (present study), Santonian. For each locality, the upper circles show the numbers of species by order, and the lower circles are the total numbers of specimens.

of modern soft-bodied taxa resulted in a change in tooth structure. Thus, shark dentition evolved from that well suited to eating hard-shelled cephalopods to gracile cusps, and the sharks migrated into deep-sea areas. Large robust (*Chlamydoselachus* sp. A) and small (*Chlamydoselachus* sp. B) shark teeth types were found in Kugushima horizon *b* and from Wadanohana; these depositional environments appear to have been allochthonous. *Chlamydoselachus* sp. B was also found at Higashiura, which was a deeper depositional environment than those of Kugushima and Wadanohana, and is also indicative of an autochthonous occurrence. Thus, it is likely that *Chlamydoselachus* sp. A and B inhabited similar environments, or that *Chlamydoselachus* sp. B occurred in deeper waters than did *Chlamydoselachus* sp. A. Large and robust (*C. goliath*) and small (*C. gracilis*) shark teeth have been found associated with the ammonoid genus *Eupachydiscus* in Upper Cretaceous deposits (upper Campanian–Maastrichtian) in Africa (Angola), and in deep-sea environments (Antunes and Cappetta, 2002; p. 137). Tanabe (1979) also raised the possibility that desmoceratid ammonoids, including *Eupachydiscus*, inhabited deeper offshore environments than did collignoniceratids and heteromorphic ammonites, suggesting that the two types of *Chlamydoselachus* in the Hinoshima Formation also inhabited deeper offshore environments, along with *Eupachydiscus.* The fossil bramble shark (*Echinorhinus wadanohanaensis*) teeth from the Himenoura Group in the Hinoshima Formation are much larger than those of extant *Echinorhinus cookei* (almost double the tooth width ratio) (Kitamura, 2013). Similarly, large fossil bramble shark teeth have been found associated with the Upper Cretaceous (Santonian) Yezo Group (Kaneko *et al*., 2012). In addition, it has been suggested that fossil bramble shark (*E. eyrensis*) teeth were deposited in shallow coastal environments (Pledge, 1992). However, fossil evidence of the genus *Echinorhi-*

Table 2. Comparison of Late Cretaceous (mainly Santonian) shark taxa from the Hinoshima Formation and other areas worldwide.

	Fossil shark locality	Hinoshima Formation, Kumamoto Prefecture, Japan	Upper Yezo Group, Hokkaido, Japan	Futaba Group, Iwaki, Fukushima Precture, Japan	Austin Group, Texas, USA	Crevasse Canyon Formation, New Mexico, USA	"Upper Cretaceous deposits", Bassin d'Aquitaine, France	"Unités du Crétacé d'Angola", Benguela, Angola, Africa
	Reference	This study	Reseach Group for Mesozoic Fossil Shark (1977), Goto and Japanese Club for Fossil Shark Tooth Reseach (2004); Kaneko *et al* . (2012)	Uyeno and Suzuki (1995); Nabana (1990, 1991, 1992)	Welton and Farish (1993)	Bourdon *et al.* (2011)	Cahuzac *et al.* (2007)	Antunes and Cappetta (2002)
Shark Taxa	Age	Santonian	Santonian	Coniacian	Santonian	Santonian	Santonian	Campanian–Maastrichitian
Hybodontiformes	Hybodontidae					*Egertonodus* sp.(?) *Meristodonoides* cf. *montanensis* *M.* aff. *montanensis* *Planohybodus* sp.		
	Lonchididae					*Lonchidion* sp.		
	Ptychodontidae	*Ptychodus mammillaris* *Ptychodus* sp.	*Ptychodus mammillaris*			*Ptychodus mortoni* *Ptychodus* sp.		
Hexanchiformes	Chlamydoselachidae	*Chlamydoselachus* sp. A *Chlamydoselachus* sp. B	*Chlamydoselachus* sp. 1					*Chlamydoselachus gracilis* *C. goliath* *Chlamydoselachus* sp.
	Hexanchidae	*Hexanchus microdon* *Hexanchus* sp. gen. et sp. indet. *Notorynchus* sp. *Notidanodon dentatus* *Notidanodon* sp.		*Hexanchus microdon*				*Hexanchus microdon* (?) *Notidanodon dentatus*
	Orthacodontidae	*Sphenodus* sp.	*Sphenodus longidens*	*Sphenodus* sp.				*Sphenodus* sp.
	Paraorthacodontidae							*Paraorthacodus* sp.
Echinorhiniformes	Echinorhinidae	*Echinorhinus wadanohanaensis*	*Echinorhinus* sp.					*Echinorhinus lapaoi*
Squaliformes	Squalidae	*Centrophoroides* cf. *latidens* *Cretascymnus* sp.						*Centrophoroides* sp. Squaliformes indet.
Squatiniformes	Squatinidae			*Squatina* sp.				
Heterodontiformes	Heterodontidae							
Orectolobiformes	Hemiscyllidae					*Chiloscyllium* sp. *Cederstroemia ziaensis* *Columbusia* cf. *fragilis*		
	Orectolobidae							
	Parascylliidae							
	Ginglymostomatidae					*Cantioscyllium* aff. *decipiens* *Cantioscyllium* sp.		
Lamniformes	Mitsukurinidae	gen. et sp. indet.		*Scapanorhynchus* sp.		*Scapanorhynchus puercoensis* *S.* (?) *puercoensis* *S.* cf. *tenuis* *S.* cf. *texanus*		*Scapanorhynchus* cf. *lewisii*
	Odontaspididae			*Odontaspis* sp.		*"Carcharias"* sp. *Eostriatolamia* sp. (?) *Pueblocarcharias kawaikensis*		Odontaspididae indet.
	Cardabiodontidae							
	Cretoxyrhinidae	*Cretalamna appendiculata* *Cretalamna* sp.	*Cretalamna appendiculata lata*	*Cretalamna appendiculata* *Cretoxyrhina mantelli*	*Cretalamna appendiculata*	*Cretalamna* sp. *Cretoxyrhina mantelli*		*Cretalamna biauriculata*
	Paraisuridae							
	Pseudoscapanorhynchidae	*Protolamna* sp.				gen. et sp. indet.		
	Anacoracidae	*Squalicorax falcatus* *Squalicorax* sp.		*Squalicorax falcatus*	*Squalicorax falcatus*	*Scindocorax novimexicanus* *S.* aff. *novimexicamus* *S.* cf. *lindstromi* *S.* aff. *yangaensis*	*Squalicorax* sp. or *Ptychocorax* sp.	*Squalicorax pristodontus* *Squalicorax* cf. *kaupi* *Pseudocorax affinis*
	Pseudocoracidae							
	Serratolamnidae							
	incertae fam.	*Cretodus* sp. *Dwardius* sp. *Paranomotodon* sp.			*Paranomotodon* sp.			
	incertae sedis							
Carcharhiniformes	Scyliorhinidae							
	Triakidae							
Synechodontiformes	Palaeospinacidae	*Synechodus* sp.						
Galeomorphii(?) or Squalomorphii incertae sedis						*Parasquatina* sp.(?)		

Table 2. *Continued.*

	Fossil shark locality	Santa Marta Formation, James Ross Island, Antarctica		Gearle Siltstone, Southern Carnarvon Basin, Western Australia	Alinga Formation and Beedagong Craystone, Western Australia	Lincoln Limestone Member of the Greenhorn Limestone, Russell County, Kansas, USA	Limestone (mainly), Kristianstad Basin, southern Sweden
	Reference	Kriwet *et al.* (2006)	Kriwet *et al*. (2006)	Siverson (1997)	Siverson (1996)	Cumbaa *et al.* (2010), Cook *et al.* (2010)	Sørensen *et al*. (2013)
Shark Taxa	Age	late Coniacian–early Campanian	late Campanian–?early Maastrichtian	late early Albian–early Cenomanian	early Cenomanian and/or middle Cenomanian	ealy late Cenomanian	late early Campanian
Hybodontiformes	Hybodontidae						*Hybodus* sp. *Polyacrodus siversoni* *Polyacrodus* sp.
	Lonchididae						
	Ptychodontidae					*Ptychodus anonymus* *Ptychodus decurrens* *Ptychodus occidentalis*	
Hexanchiformes	Chlamydoselachidae	*Chlamydoselachus thomsoni*	*Chlamydoselachus thomsoni*				
	Hexanchidae	*Notidanodon dentatus*	*Notidanodon dentatus*	*Notorynchus aptiensis*			
	Orthacodontidae	*Sphenodus* sp.	*Sphenodus* sp.				
	Paraorthacodontidae	*Paraorthacodus* sp.	*Paraorthacodus* sp.	*Paraorthacodus* sp.			*Paraorthacodus andersoni* *Paraothacodus conicus*
Echinorhiniformes	Echinorhinidae						
Squaliformes	Squalidae						Sualidae spp.
Squatiniformes	Squatinidae		*Squatina* sp.				*Squatina* spp.
Heterodontiformes	Heterodontidae						*Heterodontus* sp. 1 *Heterodontus* sp. 2
Orectolobiformes	Hemiscyllidae						*Chiloscyllium gaemersi* *Chiloscyllium* sp. *Hemiscyllidae* sp. *Hemiscyllium hermani*
	Orectolobidae						*Cederstroemia nilsi* *Cretorectolobus* sp.
	Parascylliidae						*Pararhincodon* spp.
	Ginglymostomatidae						
				Family incertae sedis			
Lamniformes	Mitsukurinidae		*Scapanorhynchus* sp.		'*Anomotodon*' sp.		*Anomotodon hermani* *Scapanorhynchus perssoni*
	Odontaspididae			*Carcharias striatula*	*Carcharias* sp. A *Carcharias* sp. B *Johnlongia allocotodon*	*Carcharias amonensis* *Carcharias saskatchewanensis*	*Carcharias aasenensis* *Carcharias latus* *Carcharias tenuis*
	Cardabiodontidae				*Pseudoisurus tomosus* *Pseudoisurus* sp.(?)	*Cardabiodon venator* *Cardabiodon* sp.	
	Cretoxyrhinidae			*Cretolamna* (= *Cretalamna*) sp.	*Cretolamna* (=*Cretalamna*) *appendiculata* *Cretolamna* (=*Cretalamna*) *gunsoni*	*Cretalamna appendiculata*	*Cretalamna appendiculata*
					Cretoxyrhina mantelli	*Cretoxyrhina mantelli*	*Cretoxyrhina mantelli*
				Archaeolamna sp.	*Archaeolamna* aff. *kopingensis* *Archaeolamna haigi*	*Archaeolamna kopingensis*	*Archaeolamna kopingensis*
	Paraisuridae			*Paraisurus* aff. *compressus*			
	Pseudoscapanorhynchidae			gen. et sp. indet. *Leptostyrax* sp.	*Leptostyrax* sp.		
	Anacoracidae			*Squalicorax primaevus*	*Squalicorax* ex gr. *curvatus* *Squalicorax volgensis*	*Squalicorax falcatus* *Squalicorax curvatus* *Palaeoanacorax* aff. *P. pawpawensis* *Squalicorax* sp.	*Squalicorax kaupi*
	Pseudocoracidae						*Pseudocorax laevis*
	Serratolamnidae						*Serratolamna* sp.
	incertae fam.			*Cretodus semiplicatus*			*Cretodus borodini*
						Eostriatolamia tenuiplicatus	
					Paranomotodon sp.		*Paranomotodon* sp.
	incertae sedis	Lamniformes indet.	Lamniformes indet.				
Carcharhiniformes	Scyliorhinidae						Scyliorhinidae sp. 1 Scyliorhinidae sp. 2 ‘*Scyliorhinus*’ *germanicus*
	Triakidae						*Galeorhinus* sp. *Palaeogaleus* sp. *Paratriakis* ? sp.
Synechodontiformes	Palaeospinacidae						*Synechodus* sp. 1 *Synechodus* sp. 2
Galeomorphii(?) or Squalomorphii incertae sedis							

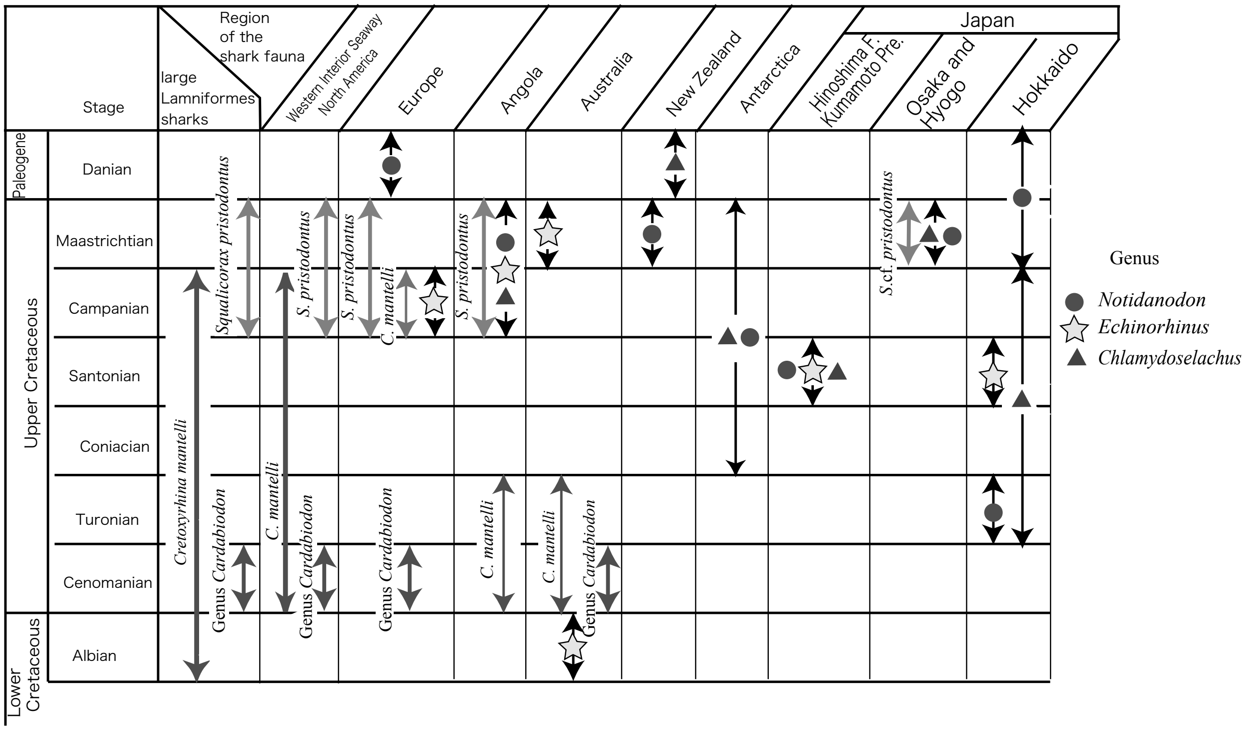

Figure 9. Coexistence relationships of large lamniform sharks, hexanchiform genera (*Notidanodon* and *Chlamydoselachus*), and the echinorhiniform genus *Echinorhinus* in world regions, primarily in the Late Cretaceous. North America: Cumbaa *et al*., 2010. Europe: Siverson, 1995; Jagt *et al*., 2006; Cook *et al*., 2010; Adnet *et al*., 2012; Sørensen *et al*., 2013. Angola: Antunes and Cappetta, 2002. Australia: Chapman, 1908; Kemp, 1991; Pledge, 1992; Siverson, 1996, 1999. New Zealand: Consoli, 2008. Antarctica: Kriwet *et al*., 2006. Japan: Hinoshima Formation, Kumamoto Prefecture (Kitamura, 1997, 2013; Goto and The Japanese Club for Fossil Shark Tooth Research, 2004), Osaka and Hyogo (Tanimoto *et al*., 2001a, 2001b; Goto and The Japanese Club for Fossil Shark Tooth Research, 2004), Hokkaido (Research Group for Mesozoic Fossil Shark, 1977; Uyeno and Matsui, 1993; Kaneko *et al*., 2012).

nus from the Hinoshima Formation indicates a similar habitat to *Chlamydoselachus* in Wadanohana, suggesting that in the Late Cretaceous *Echinorhinus* inhabited the same deeper offshore environments as the frilled shark *Chlamydoselachus*.

Comparisons with other fauna

Although many studies have reported the Upper Cretaceous shark fauna of the late Early and early Late Cretaceous (e.g. Siverson, 1996; Case, 2001; Vullo *et al*., 2007; Cumbaa *et al*., 2010), and the “last Cretaceous” (e.g. Case, 1987; Case *et al*., 2001; Becker *et al*., 2004), there have been few studies of the Santonian period (sometimes referred to as the “Santonian gap”; Welton and Farish, 1993).

Table 2 compares the Late Cretaceous shark fauna from the Hinoshima Formation with that from Hokkaido, the Futaba Group (Iwaki, Fukushima Prefecture), North America (Texas and New Mexico), Europe (France), Africa (Angola), and Antarctica. Figure 8 also shows the occurrence and number of species (by order) found in the Hinoshima Formation, North America (Texas and New Mexico), Africa (Angola), and Antarctica. Three faunae from Western Australia (Albian and middle Cenomanian), Kansas (USA; Cenomanian), and Sweden (Campanian) are included for further comparison (Table 2).

Hokkaido (Santonian) and Iwaki City Fukushima Prefecture (Coniacian), Japan.—Active highly motile predators of the coast and offshore zones, including *Cretalamna* and *Sphenodus*, and slow-swimming bottom and shelf-dwelling genera, including *Ptychodus*, *Chlamydoselachus*, and *Echinorhinus* are observed, as in the Hinoshima Formation (Table 2; Nabana, 1990, 1991, 1992; Uyeno and Suzuki, 1995; Goto and the Japanese Club for Fossil Shark Tooth Research, 2004; Kaneko *et al*., 2012). Far more diverse Late Cretaceous shark taxa are evident in the Hinoshima Formation than at Hokkaido and Iwaki, but the Upper Cretaceous shark fauna at Hokkaido and in the Futaba Group consist of fast-swimming predators and sluggish bottom-dwelling predators similar to those of the Hinoshima Formation.

Texas, USA (Santonian).—The Texas fauna contains no shallow-water (<150 m depth) or slow-swimming bottom- or shelf-dwelling shark species (Table 2; Welton and Farish, 1993). As shown in Table 2, only Lamniformes are evident in Texas (the Santonian gap) (Welton and Farish, 1993).

New Mexico, USA (Santonian).—The New Mexico fauna includes shallow-water hybodontiforms and odontaspidids, and includes the active highly motile predator genus *Cretoxyrhina* and slow-swimming bottom-dwelling squatiniforms and orectolobiforms of coastal to offshore waters. The orectolobiforms, hybodontiforms, squatiniforms, and the dominant species *Scapanorhynchus puercoensis* are evident in New Mexico, but not in the Hinoshima Formation (Table 2; Bourdon *et al*., 2011).

France (Santonian).—Only the genus *Squalicorax* is common to France and the Hinoshima Formation (Table 2; Cahuzac *et al*., 2007).

Angola (Africa) (Campanian–Maastrichtian).—The active predator genera *Cretodus* and *Dwardius*, slow-swimming bottom- or shelf-inhabiting members of the family Ptychodontidae, and the shallow-water shark fauna have not been found amongst the Angolan fauna. As shown in Figure 8, the numbers of species by order and specimen abundance are similar to those of the Hinoshima Formation. The hexanchiforms (genera *Chlamydoselachus* and *Notidanodon*), echinorhiniforms (genus *Echinorhinus*), squaliforms (genus *Centrophoroides*), and synechodontiforms (genus *Sphenodus*) in the Angolan shark fauna are similar to those in the Hinoshima Formation (Table 2; Antunes and Cappetta, 2002).

Antarctica (Santa Marta Formation) (late Coniacian–early Campanian).—Although the lamniform taxa, slow-swimming hexanchiform sharks, and echinorhiniform, squaliform, squatiniform, orectolobiform, and synechodontiform sharks are absent from the Antarctic fauna, other hexanchiform sharks in the Antarctic shark fauna are similar to those in the Hinoshima Formation (Figure 8; Table 2; Kriwet *et al*., 2006).

Antarctica (Santa Marta Formation) (late Campanian–? early Maastrichtian).—The Antarctica fauna has many elements in common with the Hinoshima Formation including the slow-swimming genera *Chlamydoselachus* and *Notidanodon*, and active predators including indeterminate Lamniformes and the genera *Scapanorhynchus* and *Sphenodus*. The genus *Squatina* is present in this fauna, but ptychodontids, the genus *Hexanchus*, echinorhinids, squaliforms, synechodontiforms, and a number of active predator lamniform sharks are absent (Table 2; Kriwet *et al*., 2006). The composition of hexanchiforms (genera *Chlamydoselachus* and *Notidanodon*) and synechodontiforms (genus *Sphenodus*) in the Antarctic shark fauna is similar to that in the Hinoshima Formation.

Western Australia (Albian, middle Cenomanian), Kansas, USA (Cenomanian).—Many lamniform genera found in the Hinoshima Formation fauna, including the genus *Cretalamna*, are evident in the Western Australian (Albian, middle Cenomanian) and Kansas, USA (Cenomanian) faunae, but the shallow-water genera *Carcharias* and *Hybodus* are not amongst the Hinoshima Formation taxa, and the slow-swimming genera are rare in the Western Australia and Kansas fauna (Table 2; Siverson, 1996, 1997; Cook *et al*., 2010; Cumbaa *et al*., 2010). In contrast with the shark fauna of the Hinoshima Formation, the dominant lamniform sharks and many slow-swimming taxa co-occur in Western Australia and Kansas.

Sweden (late early Campanian).—Comparison of the shark fauna from Kristianstad Basin (Sweden) (Table 2; Sørensen *et al.*, 2013) and the Hinoshima Formation shows that the fauna of the Kristianstad Basin was dominated by lamniform sharks similar to those in the Hinoshima Formation. Lamniform genera including *Cretalamna*, *Squalicorax*, *Cretodus*, *Paranomotodon*, and the synechodontiform genus *Synechodus* have also been found in the Hinoshima Formation. However, there are a number of differences between the two faunae. Sluggish bottom-dwelling sharks including squatiniform, heterodontiform, orectolobiform, and carcharhiniform (Scyliorhinidae, Triakidae) sharks only occur among the shark fauna from the Kristianstad Basin (Compagno, 1984). *Cretoxyrhina mantelli* and *Squalicorax kaupi*, which are thought to have been top predators (Shimada and Cicimurri, 2005), are present in the Kristianstad Basin fauna. The hexanchiform genus *Chlamydoselachus* and the echinorhiniform genus *Echinorhinus* have not been reported in the shark fauna of Kristianstad Basin.

Explaining the occurrence of large hexanchiform sharks in the Upper Cretaceous shark fauna of Japan, including the Hinoshima Formation

The Late Cretaceous genus *Notidanodon* is distributed in Antarctica (Grande and Chatterjee, 1987; Kriwet *et al.*, 2006), New Zealand (Woodward, 1886a, b), Angola (Antunes and Cappetta, 2002), South India (Underwood *et al*., 2011), Southern Patagonia (Bogan *et al.*, 2016), and Japan (e.g. Goto *et al*., 1996; the present study), but has not been recorded from low latitudes (Cione, 1996). Siverson (1995) noted that the absence of *Notidanodon* from the Late Cretaceous neritic zones may have been because of competitive pressures from large cosmopolitan lamniform sharks. The only areas where *Notidanodon* has been reported from Campanian/Maastrichtian neritic deposits are New Zealand and Antarctica (see Figure 9). Large Late Cretaceous lamniform sharks including *Cretoxyrhina mantelli*, *Squalicorax pristodontus*, and the genus *Cardabiodon* have been reported (Shimada, 1997, 2008; Siverson, 1999; Siverson and Lindgren, 2005; Shimada *et al*., 2006; Cook *et al*., 2010), particularly from the Western Interior Seaway, Europe, and Australia (Figure 9). However, Figure 9 shows that there are instances of the coexistence of these large lamniform sharks and the genus *Notidanodon* in the Late Cretaceous, including the coexistence of the genus *Notidanodon* and *Squalicorax pristodontus* in Angola and Japan. Underwood *et al.* (2011) also reported the coexistence of the genus *Notidanodon*(?) and the lamniform sharks *Cretalamna appendiculata* and *Dwardius sudindicus* in India. The Late Cretaceous lamnoids *Squalicorax* and *Cretoxyrhina mantelli* are thought to have been active pelagic sharks (e.g. Shimada, 1997, 2008) that lived in middle to low paleolatitudes, mainly inhabiting warm waters (e.g. Underwood *et al*., 2011). On the other hand, the Late Cretaceous *Notidanodon* are thought to have been bentho-pelagic sharks (Underwood *et al*., 2011) inhabiting cold waters in high-paleolatitude areas (e.g. Cione, 1996; Underwood *et al*., 2011). Furthermore, the depositional environments have been interpreted as offshore habitats with respect to reports of *Notidanodon* shark teeth from South India (early Cenomanian; Underwood *et al*., 2011), Angola (Campanian–Maastrichtian; Antunes and Cappetta, 2002), and Japan (e.g. Santonian, the present study). The records of Late Cretaceous *Notidanodon* from mid-paleolatitude areas including Angola, South India, and Japan thus expand its range to low paleolatitudes. Explanations for the coexistence of these taxa may be ecological; for example, *Squalicorax* and *Cretoxyrhina mantelli* were active pelagic predators while *Notidanodon* was a bentho-pelagic predator. Kriwet *et al.* (2006) investigated the selachian fauna from the Late Cretaceous in Antarctica, and noted that the shark fauna of the Late Cretaceous Weddelian Province (Antarctica-Patagonia-New Zealand; Zinsmeister, 1979) was characterized by high-latitude selachian taxa (e.g. *Notidanodon*, *Chlamydoselachus*, *Sphenodus*), as also noted by Bogan *et al*. (2016) and Cione (1996). Thus, the diversity of the Late Cretaceous shark fauna (e.g. *Notidanodon*, *Chlamydoselachus*, *Sphenodus*) in East Asia including Japan (e.g. Goto *et al*., 1996; the present study) is similar to that of the Weddelian Province and surrounding regions during the Late Cretaceous. The characteristics of the Upper Cretaceous shark fauna in Japan (including the Hinoshima Formation) are similar to those of the contemporaneous Southern Hemisphere fauna (e.g. Angola, Australia, and Antarctica). This shows that the characteristic shark fauna in the Southern Hemisphere had spread to the middle latitudes of the Northern Hemisphere by the Late Cretaceous.

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Appendix 1. List of the study materials in stratigraphic order and by study area. (1) Himedo Park, Himedo town, Kami-Amakusa City, Kumamoto Prefecture; (2) Kugushima, Ryugatake town, Kami-Amakusa City; (3) Wadanohana, Ryugatake town, Kami-Amakusa City; (4) Higashiura, Ryugatake town, Kami-Amakusa City; (5) Kotorigoe, Matsushima town, Kami-Amakusa City.

Himedo Park	
Ptychodus mammillaris	KCM12-000061
Notorynchus sp.	KCM 12-000378
Cretalamna appendiculata	KCM 12-000031-000036, KCM 12-000045, KCM 12-000153, KCM 12-000156, KCM 12-000180, KCM 12-000211, KCM 12-000261, KCM 12-000262, KCM 12-000302, KCM 12-000305, KCM 12-000306-000322, KCM 12-000324-0000344, KCM 12-000357, KCM 12-000364, KCM 12-000376, KCM 12-000377, KCM 12-000383, KCM 12-000384, KCM 12-000394, KCM 12-000412, KCM 12-000415
Kugushima	
Ptychodus mammillaris	KCM12-000148, KCM12-000149
Ptychodus sp.	KCM12-000150
Chlamydoselachus sp. A	GCM-VP400
Hexanchus sp.	KCM 12-000346
Hexanchidae gen. et sp. indet.	KCM 12-000413, GCM-VP402, GCM-VP403
Notorynchus sp.	KCM 12-000272
Sphenodus sp.	GCM-VP411
Echinorhinus wadanohanaensis	KCM 12-000429
Centrophoroides cf. *latidens*	KCM12-000361, KCM12-000419
Mitsukurinidae gen. et sp. indet.	KCM 12-000424
Cretalamna appendiculata	KCM 12-000010, KCM 12-000047, KCM 12-000196, KCM 12-000269-000271, KCM 12-000279-000282, KCM 12-000289, KCM 12-000290, KCM 12-000345, KCM 12-000347, KCM 12-000350, KCM 12-000358, KCM12-000416, KCM 12-000417, KCM 12-000420, KCM 12-000421
Cretalamna sp.	KCM 12-000047
Squalicorax falcatus	KCM 12-000352
Dwardius sp.	KCM 12-000002
Cretodus sp.	KCM 12-000278
Wadanohana	
Ptychodus mammillaris	KCM12-00060, KCM12-000144, KCM12-000257
Hexanchus microdon	KCM 12-000039, KCM 12-000042, KCM 12-000044, KCM 12-000263, GCM-VP401
Hexanchus sp.	KCM 12-000040
Hexanchidae gen. et sp. indet.	KCM 12-000043
Notidanodon dentatus	KCM 12-000365
Notidanodon sp.	GCM-VP404, GCM-VP405, GCM-VP406
Sphenodus sp.	KCM 12-000359
Echinorhinus wadanohanaensis	KCM12-000064, KCM 12-000266, KCM12-000267, KCM12-000362
Cretalamna appendiculata	KCM 12-000003-000008, KCM 12-000011, KCM 12-000012-000030, KCM 12-000046, KCM 12-000048-000050, KCM 12-000258, KCM 12-000259, KCM 12-000260, GCM-VP409
Protolamna sp.	GCM-VP410
Squalicorax sp.	KCM 12-000052 , GCM-VP413
Paranomotodon sp.	KCM 12-000051, GCM-VP408
Dwardius sp.	KCM 12-000001, KCM 12-000009
Synechodus sp.;	KCM 12-000264, KCM 12-000363, GCM-VP412
Higashiura	
Chlamydoselachus sp. B	KCM12-000360
Hexanchidae gen. et sp. indet.	GCM-VP407
Kotorigoe	
Squalicorax sp.	KCM 12-000265