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Habitat reconstruction of Oligocene elasmobranchs from Yamaga Formation, Ashiya Group, western Japan

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Abstract. Remains of 11 species of extinct elasmobranch were obtained from the Oligocene Yamaga Formation on Ainosima Island in northern Kitakyushu City, Japan. More than 360 gill rakers belonging to a basking shark (*Cetorhinus* sp.) individual were collected from a stratigraphic horizon in the northern part of the island. This report represents the highest concentration of basking shark gill rakers in the fossil record of Japan.

Based on sedimentary facies analysis combined with habitat data of extant sharks, habitats of Oligocene elasmobranchs were reconstructed. The result indicates that Oligocene sharks probably lived in an environment similar to that of extant sharks at the genus level. This does not support the previous hypotheses that some shark taxa (e.g., *Hexanchus*) existed within shallow environments during the Oligocene, and have since migrated into deeper water habitats. Analysis of other genera supports this hypothesis of stability in elasmobranch habitat preference, at least at the genus level, between the Oligocene and present day.

Key words: Ashiya Group, elasmobranchs, Oligocene, shark

Introduction

Shark fossils are probably the most common vertebrate remains in the world, because a shark sheds enormous number of teeth throughout its life. However, the ecological aspects of fossil shark taxa are still poorly understood. This is because the majority of extant sharks are represented only by their teeth, and as a consequence of a nektonic lifestyle, teeth can be preserved in sediments and environments other than those which represent the shark's original habitat. The habitats of extinct sharks were discussed in some previous studies (e.g., Uyeno *et al.*, 1984; Goto and JCFSTR, 2004; Takakuwa, 2006), and suggested that extant deep sea taxa originally lived in shallow water, and that the appearance of new shark taxa (particularly *Carcharhinus* spp.) drove original shallow-water genera into deep-sea habitats. For example, Uyeno *et al.* (1984) interpreted the Oligocene sixgill shark, *Hexanchus* sp., as inhabiting shallow waters, whereas its modern counterparts are now found in deeper habitats. However, interpretation of habitats in deep-sea fossil sharks is difficult (Kriwet and Benton, 2004), and there is still little evidence for this inferred habitat shift.

In previous studies, shark habitats have frequently been inferred from the nature of the sediments in which the fossils were found, or from palaeoecological analysis of co-

occurring invertebrate taxa (e.g., Uyeno *et al.*, 1984; Goto and JCFSTR, 2004). However, these methods have severe limitations. Most of the neritic and pelagic sharks are efficient swimmers, and thus can shed teeth in a wide range of sedimentary environments. There is therefore considerable difficulty in inferring a sedimentary environment in which isolated shark teeth have been discovered as the principal habitat of the species or genus in question. Estimations of shark habitat from coexisting fossils are also difficult, because the habitats of coexisting fossils are not clear in many cases.

This study attempts to reconstruct the habitats of Oligocene elasmobranchs based on relative abundance data and species composition of fossil tooth assemblages collected from a range of sedimentary environments. The main habitat of each species is then assigned to a particular environment, and compared with known habitat ranges of extant members of the same genera. This method provides a test for the hypothesis that the Miocene radiation of *Carcharhinus* in shallow water forced *Hexanchus* to inhabit deep waters.

Geologic setting

Ainosima Island lies 10 km north off the coastline of Kitakyushu City, northwestern Kyushu, Japan. The marine

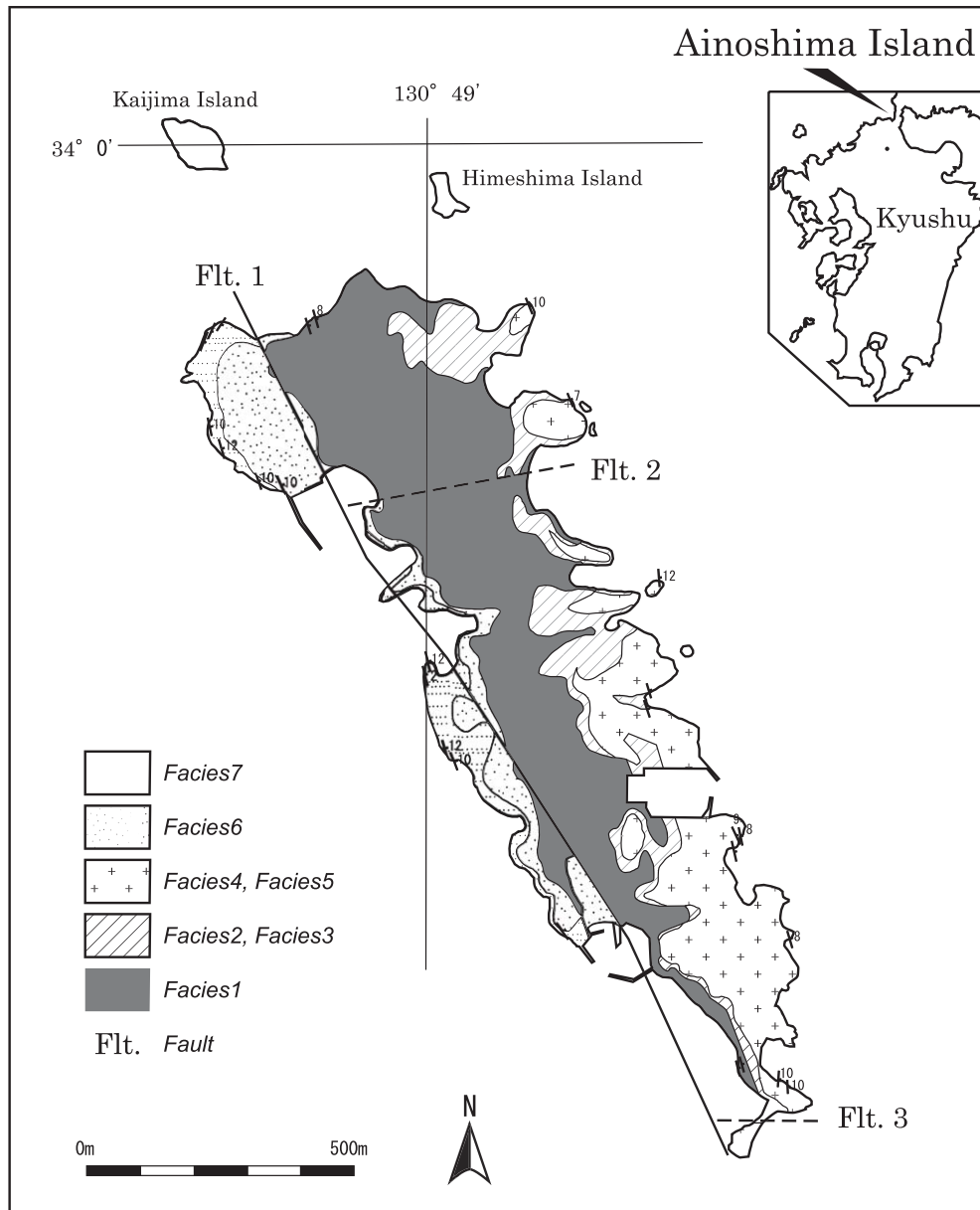


Figure 1. Geologic map of Ainoshima Island. Each facies is described in the text.

deposits of this island are correlated with the Yamaga Formation of the Ashiya Group, based on biostratigraphy (Murata, 1961) and sequence stratigraphy (Nakae *et al.*, 1998). The Ashiya Group is divided into five formations: Yamaga, Norimatsu, Ginnoharu, Honjyo, and Waita formations in ascending order. The Yamaga Formation is the lowest part of the Ashiya Group. The age of the Yamaga Formation in the Ashiya area was placed at 31.7 ± 2.3 Ma (upper Lower Oligocene) based on fission track dating (Ozaki and Hamasaki, 1991). This was supported by further fission track dating and biostratigraphic studies conducted in

the upper and lower formations (Tsuchi *et al.*, 1987; Ozaki and Hamasaki, 1991; Okada, 1992).

The structure of the Oligocene beds on Ainoshima Island (Figure 1) is simple. Beds dip east between 8 and 12 degrees, and in general strike N10W. The Yamaga Formation on the island is mainly composed of silt-grade to coarse-grained sandstones. Along the northwest and central-west coasts, several layers of rounded pebble to cobble conglomerates belonging to the lowermost horizons can be observed. Above these conglomerates, an approximately 100-m-thick sequence of shallow marine sediments is stacked and extends


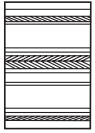





Facies	Typical log	Facies characteristics	Environments	Shark taxa
7		Interbedded fine to coarse sandstone and siltstone; bioturbation; parallel lamination; mud drape	Tide dominated environment	No shark tooth record
6		Medium to coarse sandstone; planar cross-stratification; herringbone cross-stratification	Tide dominated environment	? <i>Negaprion</i>
5		Amalgamated hummocky cross stratified fine sandstone; volcanic clastics; lags of big shells and volcanic clastics	Lower shoreface	<i>Carcharias</i> <i>Negaprion</i> <i>Myliobatis?</i> <i>Heterodontus</i> <i>Isurus</i> <i>Squalus</i> <i>Hexanchus</i>
4		Interbedded hummocky cross stratified sandstone and bioturbated sandstone; fine sandstone; long wavelength of HCS	Lower shoreface	<i>Carcharias</i> <i>Negaprion</i> <i>Myliobatis?</i> <i>Heterodontus</i> <i>Isurus</i> <i>Squalus</i> <i>Hexanchus</i> <i>Squatina</i> <i>Carcharhinus</i> <i>Cetorhinus</i>
3		Interbedded hummocky cross stratified coarse to fine sandstone and laminated very fine to fine sandstone;	Inner shelf	<i>Isurus</i>
2		Parallel laminated very fine to fine sandstone; bioturbation; poorly sorted	Outer shelf	<i>Squalus</i> <i>Hexanchus</i> <i>Isurus</i> <i>Carcharias</i> <i>Negaprion</i> <i>Squatina</i> <i>Heterodontus</i> <i>Cetorhinus</i>
1		Massive, very fine sandstone to siltstone	Outer shelf	<i>Isurus</i> <i>Cetorhinus</i>

Figure 2. Classification of sedimentary facies, interpreted environments, and shark species of Ainoshima Island.

eastwards.

Methods

Sedimentary structures, grain size and fossil occurrences were examined during our original fieldwork. The Yamaga Formation was divided into several subdivisions according to sedimentary facies, and used to reconstruct the depositional environments. Shark fossils from each sedimentary facies were identified (Appendix 2), and the number of teeth belonging to each species recorded. The principal, or main, habitat of each species is inferred using the relative abun-

dances of teeth collected from each facies.

Facies description and interpretation

The rocks of Ainoshima Island can be divided into seven sedimentary facies (Figure 2). Correspondingly seven estimated sedimentary environments are identified. More detailed characteristics and interpretations of these facies are documented in Appendix 1. Facies 1—Well bioturbated and massive very fine sandstone to siltstone. Estimated environment is outer shelf. Facies 2—Laminated very fine-grained to fine-grained sandstones. Estimated environment is

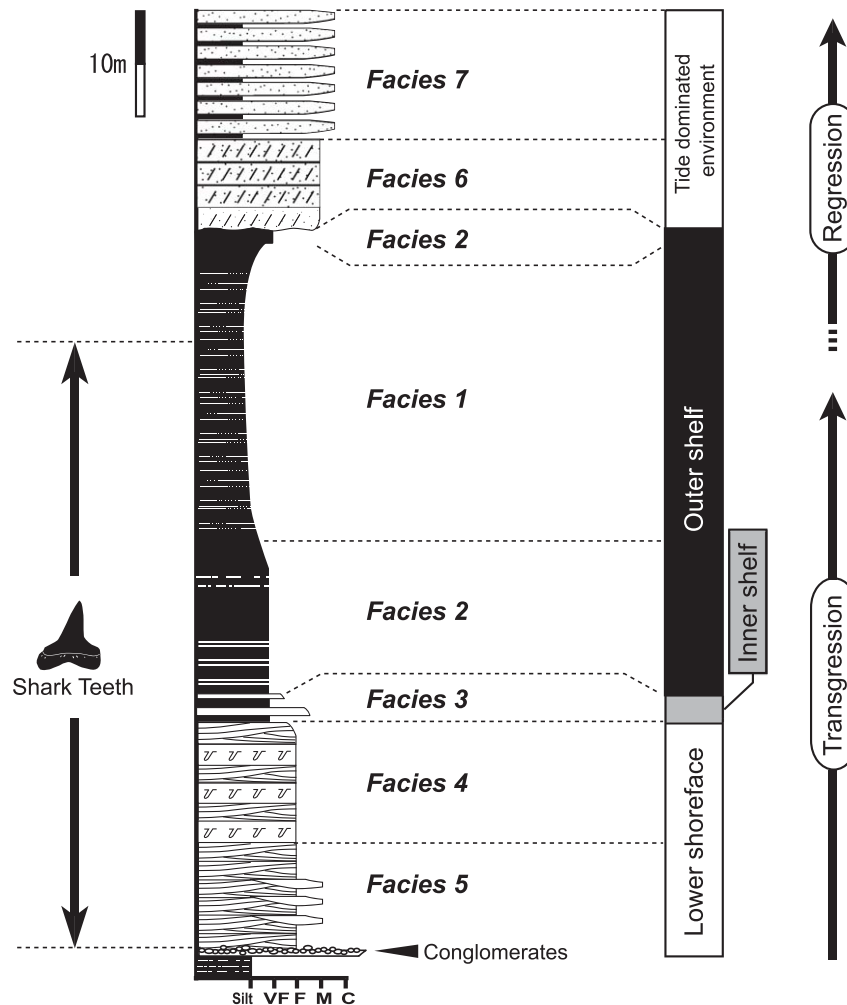


Figure 3. Columnar section of Ainosshima Island mainly based on data along its northern coast, and occurrence range of shark teeth. Right column shows inferred sedimentary environments.

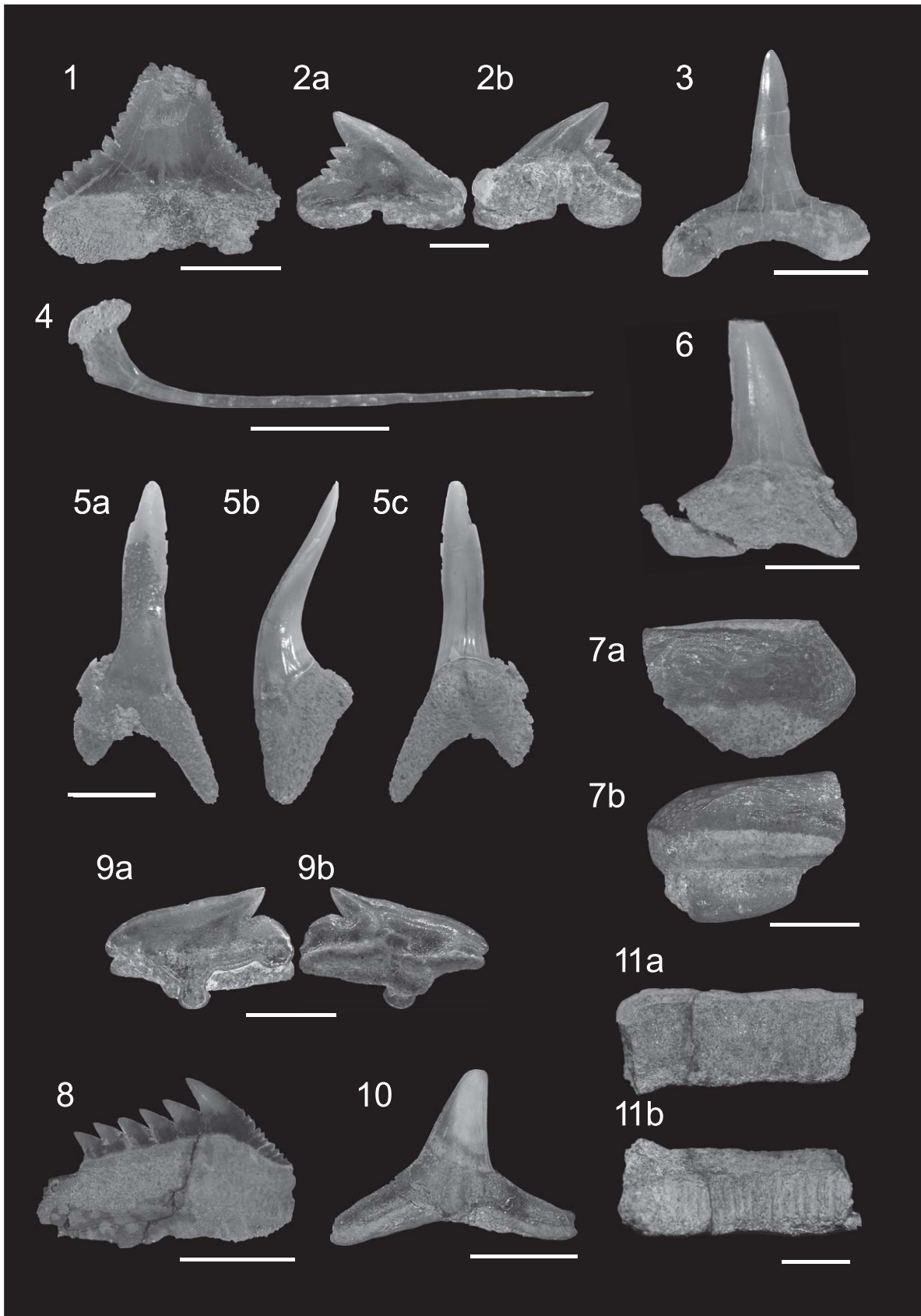
outer shelf (shallower than Facies 1). Facies 3—Interbedded medium- to coarse-grained hummocky cross-stratified (HCS) sandstone, and very fine-grained sandstone. Estimated environment is inner shelf. Facies 4—Alternating hummocky cross-stratified fine sandstones and bioturbated massive fine-grained sandstones. Estimated environment is lower shoreface. Facies 5—Amalgamated hummocky cross-stratified fine sandstone. Estimated environment is lower shoreface (shallower than Facies 4). Facies 6—Planar cross-bedded, or partly bidirectional planar cross-bedded (herring-

bone cross-stratification), medium-grained sandstones. Estimated environment is a tide dominated environment. Facies 7—Fine- to coarse-grained sandstone with intercalations of thin siltstones. Estimated environment is tide dominated environment.

Temporal change of sedimentary environments

One cycle of transgression and regression can be recognized in the compiled columnar section made along the

► **Figure 4.** 1. *Carcharhinus* sp., UMUT CV 30210 (Facies 4) in labial view; 2. *Galeorhinus* sp., UMUT CV 30245 (Facies 2) in labial (a) and lingual (b) views; 3. *Negaprion* sp., UMUT CV 30224 (Facies 4) in labial view; 4. A gill raker of *Cetorhinus* sp., UMUT CV 30334 (Facies 2); 5. *Carcharias* sp., UMUT CV 30246 (Facies 2) in labial (a), lateral (b) and lingual (c) views; 6. *Isurus* sp., UMUT CV 30276 (Facies 2) in lingual view; 7. *Heterodontus* sp., UMUT CV 30288 (Facies 2) in occlusal (a) and labial (b) views; 8. *Hexanchus* sp., UMUT CV 30301 (Facies 4) in lingual view; 9. *Squalus* sp., UMUT CV 30305 (Facies 2) in labial (a) and lingual (b) views; 10. *Squatina* sp., UMUT CV 30322 (Facies 2) in labial view; 11. *Myliobatis?* sp., UMUT CV 30328 (Facies 4) in occlusal (a) and basal (b) views. Scale bar=20 mm (2, 7, 9, 11), 50 mm (1, 3–6, 8, 10)



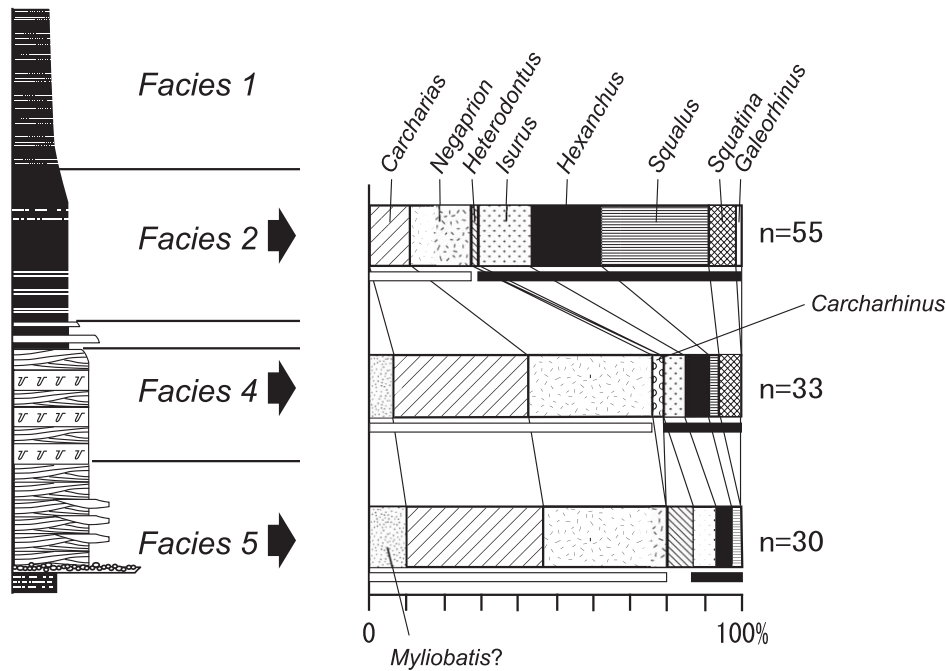


Figure 5. Thick columns: Occurrence of shark teeth in Facies 2, 4 and 5. Thin bars below the thick columns indicate proportion of extant relative species expected to drop their teeth into foreshore to lower shoreface (white bars) and outer shelf to continental slope (black bars). Numbers to right of the columns show the numbers of shark teeth from each facies.

northern coast of Ainosshima Island (Figure 3). The sedimentary facies change in upward sequence from Facies 4, 3, 2, 1, 3, and 5, to Facies 6 and 7. The first sequence (from Facies 4 to Facies 1), suggests that the sedimentary environment deepened from lower shoreface to outer shelf. Sedimentary structural change in Facies 3 suggesting a deepening upward is consistent with this interpretation. The second sequence (Facies 1 to Facies 7) suggests a prograding shallow marine environment that gradually shallows from an outer-shelf setting, towards tidally dominated facies at the top. During this regression, outer shelf deposits (Facies 2) are overlain by tidal sediments (Facies 6), further suggesting that the intermediate inner shelf and shoreface deposits are missing in this latter transgressive sequence.

Composition of fossil shark occurrence

We collected 118 shark teeth and 374 *Cetorhinus* gill rakers (Figure 4). Elasmobranch fossils from Ainosshima Island were previously reported by Uyeno *et al.* (1984), comprising *Carcharhinus* sp., *Negaprion* sp., *Galeorhinus* sp., *Carcharias* sp., *Cetorhinus* sp., *Isurus* sp., *Heterodontus* sp., *Hexanchus* sp., *Squalus* sp., *Squatina* sp. and *Myliobatis?* sp.

The relative abundance of each species within three of the facies is shown in Figure 5. Shark fossil were recovered from

Facies 1, 2, 4, and 5, in half of the Ainosshima section. However, because the extant basking shark *C. maximus* possesses over 10,000 gill rakers on each side of the body, gill rakers of basking sharks were not treated the same as other shark teeth for the purposes of this study. Proportions of *Cetorhinus* gill rakers (number of gill rakers of *Cetorhinus* ÷ number of elasmobranch fossils (=number of shark teeth + number of gill rakers of *Cetorhinus*)), however, were recorded and are shown in Figure 6.

Special remarks on *Cetorhinus* gill rakers

In this research, more than 360 gill raker fragments belonging to the basking shark *Cetorhinus* sp. were collected. This is the first report of such a high-order concentration of basking shark gill rakers from the Oligocene of the Pacific area. The extant *Cetorhinus* is a planktonic feeder and distributed in boreal to temperate water in the world (Compagno *et al.*, 2002). Fossil *Cetorhinus* gill rakers have been recovered from the Miocene of France, Belgium, Austria, Netherlands, Switzerland, Japan and United States; the Pliocene of Belgium, Italy, Japan and Chile; and the Pleistocene of Japan (Uyeno and Matsushita, 1974; Herman, 1975, 1979; Kikuchi and Takaoka, 1979; Bosh, 1984; Itoigawa *et al.*, 1985; Cione and Reguero, 1998). This indicates that *Cetorhinus* was distributed in high latitudes of both the Atlantic and Pacific

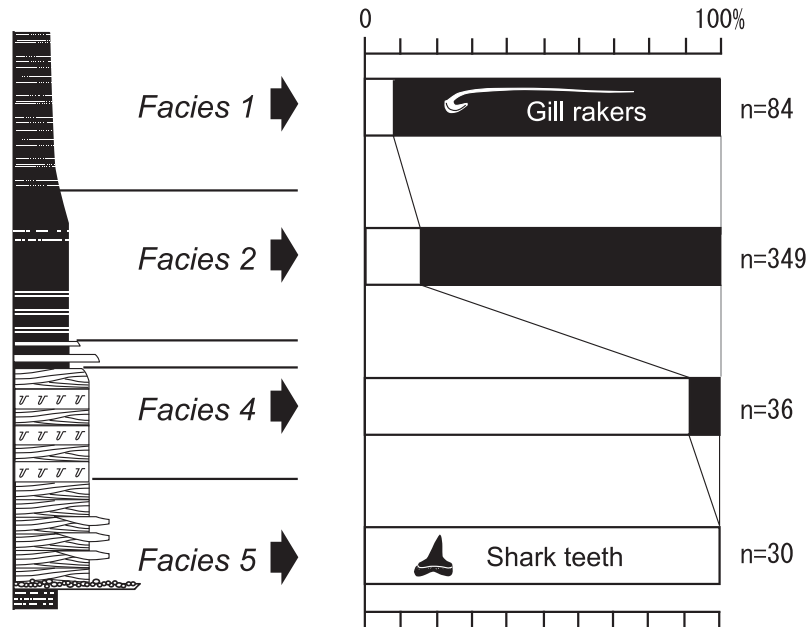


Figure 6. Occurrence of *Cetorhinus* gill rakers and shark teeth for Facies 1, 2, 4 and 5. Numbers to right of the columns show the number of shark remains (shark teeth + *Cetorhinus* gill rakers) from each facies.

oceans after the Miocene. On the other hand, the occurrence of *Cetorhinus* in the Oligocene is remarkably confined to the Atlantic area having been found in the Netherlands, Germany and Belgium (Bosch, 1984) and, Romania and France (Cione and Reguero, 1998). Only a single specimen of *Cetorhinus* from the Pacific during the Oligocene has been reported from Japan up to now (Uyeno and Yabumoto, 1984). More than 360 additional specimens obtained in this study support previous interpretations that the world-wide distribution of *Cetorhinus* extends back to the Oligocene at the latest. In order to confirm this hypothesis, additional fossil records from the Oligocene from eastern Pacific area were needed.

Discussion

The habitats of extant elasmobranchs

In order to compare the habitats of Oligocene elasmobranchs with those of extant ones, habitats of extant elasmobranchs were compiled (Table 1) and the sedimentary environments from where their teeth are most expected to be found were reconstructed. Some biotelemetric data were used to reconstruct both main and potential habitats (detailed data for each species are shown in Table 1).

Based on the main inferred habitats for demersal and pelagic species of modern sharks, three patterns of habitat have been recognized, namely, coastal fauna, deep sea fauna, and epipelagic fauna. Members of the coastal faunas are present in the nearshore zone between 0 and 20 m depth and comprise *Myliobatis*, *Carcharias*, and *Negaprion*.

Elasmobranchs of deep sea faunas mainly inhabit environments deeper than 50 m on or near the sea floor, and include *Squalus*, *Hexanchus*, and *Squatina*. Elasmobranchs of epipelagic faunas mainly inhabit near-surface environments (0–20 m depth) in offshore waters between 20 and 1,000 m in depth, and consist of *Isurus* and *Cetorhinus* (although *Cetorhinus* also inhabits the mesopelagic zone).

Based on main inferred habitats, each extant genus is expected to shed teeth in the following sedimentary environments: *Negaprion*—foreshore to lower shoreface; *Carcharias*—foreshore to lower shoreface; *Cetorhinus*—outer shelf; *Isurus*—outer shelf to continental slope; *Hexanchus*—outer shelf to continental slope; *Squalus*—outer shelf to continental slope; *Squatina*—outer shelf; and *Myliobatis*—foreshore to lower shoreface. In general, the coastal fauna is expected to shed their teeth within foreshore to shoreface settings, deep sea fauna within outer shelf to slope settings, and the epipelagic fauna within outer shelf to slope settings. According to Saito (1989), the boundary between shoreface and inner shelf (storm wave base) is 20 m deep, and the boundary between inner shelf and outer shelf (fair weather wave base) is between 50 m and 80 m.

Interpretation of fossil shark ratios

In order to compare the habitats of extant and Oligocene elasmobranchs, we calculated the proportion of shark genera in which teeth of the cogenetic genera are expected to be found within a sedimentary environment (foreshore to lower shoreface environment or outer shelf to slope environ-

Table 1. Compiled habitats of extant elasmobranchs.

Genus	Species	Possible habitat (Main habitat)	Depth of seafloor	Habitat group	Sources	
<i>Isurus</i>	<i>I. oxyrinchus</i>	0–201 m (0–20 m)	n. a.	Epipelagic	Sepulveda <i>et al.</i> , 2004 Klimley <i>et al.</i> , 2002 Holts and Bedford, 1993 Compagno <i>et al.</i> , 2005	
		0–60 m (0–20 m)	20–1200 m			
		0–35 m (0–20 m)	n. a.			
		0–500 m (0–20 m)	n. a.			
<i>Cetorhinus</i>	<i>C. maximus</i>	0–1000 m (0–10 m) in summer	0–2000 m (100–500 m)	Epipelagic	Sim <i>et al.</i> , 2003 Sims <i>et al.</i> , 2005 Southall <i>et al.</i> , 2005, fig 2(A)	
		0–1000 m (50–350 m) in autumn and winter	n. a.			
		0–130 m in summer	n. a.			
		n. a.	0–2000 m (50–100 m)			
<i>Carcharias</i>	<i>C. taurus</i>	1–191 m (15–25 m)	n. a.	Coastal	Compagno <i>et al.</i> , 2005 Smale, 2002 Ferrari and Ferrari, 2000	
		0–100 m (2–20 m)	n. a.			
		0–190 m	n. a.			
<i>Myliobatis</i>	<i>M. californica</i>	2–12 m	2–12 m		Martin and Caira, 2002 Klimley <i>et al.</i> , 2005	
		0–20 m	0–20 m			
<i>Negaprion</i>	<i>N. acutidens</i>	0–30 m	n. a.		Compagno <i>et al.</i> , 2005 Edren and Gruber, 2005	
		n. a.	0 ≤ 30 m (0–10 m)			
<i>Hexanchus</i>	<i>H. griseus</i>	600–1500 m (600–1100 m)	n. a.	Deep sea	Carey and Clark, 1995 Compagno <i>et al.</i> , 2005 Dunbrack and Zielinski, 2003 Kanesawa and Tanaka, 2002 Compagno <i>et al.</i> , 2005	
		0–1875 m (500–1100 m)	n. a.			
		20–40 m	n. a.			
		<90 m	n. a.			
		0–621 m (90–621 m)	n. a.			
<i>Squatina</i>	<i>S. aculeata</i>	30–500 m	30–500 m	Deep sea	Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005 Compagno <i>et al.</i> , 2005	
		<i>S. argentina</i>	51–320 m (120–320 m)			51–320 m (120–320 m)
		<i>S. australis</i>	0–130 m			0–130 m
		<i>S. californica</i>	1–200 m			1–200 m
		<i>S. dumeril</i>	inshore-1290 m (40–250 m)			inshore-1290 m (40–250 m)
		<i>S. formosa</i>	183–385 m			183–385 m
		<i>S. guggenheim</i>	35–115 m (35–93 m)			35–115 m (35–93 m)
		<i>S. nebulosa</i>	inshore-330 m			inshore-330 m
		<i>S. oculata</i>	20–500 m (50–100 m)			20–500 m (50–100 m)
		<i>S. punctata</i>	10–80 m			10–80 m
		<i>S. squatina</i>	5 ≥ 150 m			5 ≥ 150 m
		<i>S. tergocellata</i>	130–400 m (most 300 m)			130–400 m (most 300 m)
		<i>Squalus</i>	<i>S. mitsukurii</i>			50–740 m
4–954 m (100–500 m)	n. a.					
<i>S. megalops</i>	50–732 m			n. a.		
59–494 m	n. a.					
<i>S. acanthias</i>	0–600 m			n. a.		

ment). The proportion was calculated as number of shark teeth whose congeneric genera inhabits foreshore to lower shoreface (or outershelf to slope) ÷ total number of shark teeth found within each facies × 100.

The proportion of shark genera in which teeth are expected to be found within foreshore to lower shoreface environments (*Carcharias*, *Negaprion*, and *Myliobatis*) is 80.0% for Facies 5, 75.8% for Facies 4, and 27.3% for Facies 2 (Figure 5). The proportion of genera whose teeth are mostly expected to be found in the outer shelf to slope environments (*Isurus*, *Hexanchus*, *Squalus*, and *Squatina*) is 20.0% for Facies

5, 21.2% for Facies 4, and 69.1% for Facies 2. Considering that the sedimentary environment of Facies 4 and 5 are lower shoreface (Facies 4 is deeper than Facies 5), and that of Facies 2 represents an outer shelf, the sedimentary environments reconstructed through facies analyses and hence main habitats agree with those inferred from extant congeneric sharks.

Equally, when *Cetorhinus* gill rakers are added to the composition of shark teeth discussed above, the ratio of the extant species whose teeth are mostly expected to be distributed in the foreshore to lower shoreface environments is 80.0% for

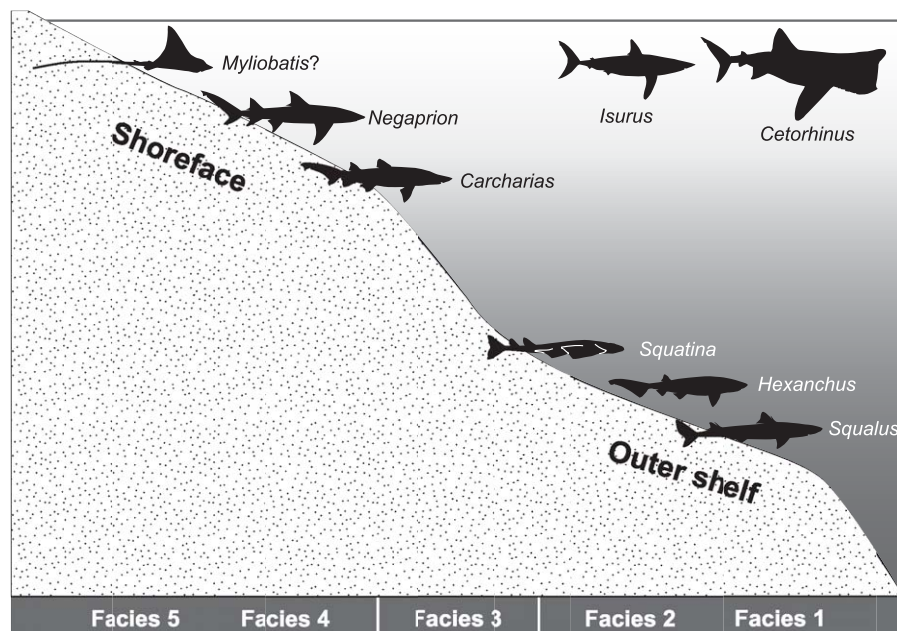


Figure 7. Reconstruction of habitats of Oligocene elasmobranchs based on sedimentary environments of shark remains inferred from sedimentary facies analyses. *Carcharias*, *Negaprion*, and *Myliobatis* belong to the coastal fauna, *Hexanchus*, *Squalus*, and *Squatina* are members of the deep sea fauna, and *Isurus* and *Cetorhinus* are epipelagic faunal elements.

Facies 5, 69.4% for Facies 4, 4.30% for Facies 2, and less than 8.3% for Facies 1. The proportions of the extant genera whose teeth are mostly expected to be shed in outer shelf to slope settings (*Hexanchus*, *Squalus*, *Squatina* and *Isurus*) is 20% for Facies 5, 27.8% for Facies 4, 95.1% for Facies 2, and more than 91.7% for Facies 1. These modern genera are reported to live in epipelagic and mesopelagic zones within outer shelf to slope settings, and thus the inferred habitats of these fossil genera fit well with the reported environments of extant congeneric sharks.

The proportions of extant coastal genera (*Myliobatis*, *Carcharias*, and *Negaprion*) gradually decrease from Facies 5 to Facies 2. In contrast, extant deep sea genera (*Squalus*, *Hexanchus*, and *Squatina*) and extant epipelagic genera (*Isurus*, and *Cetorhinus*) become more abundant from Facies 5 to Facies 2. This indicates that Oligocene shark habitats, at least at the genus level, were similar to those occupied by extant sharks to date (Figure 7).

Conclusions

The ratio of fossil shark species to the total number of species is different among the four lithofacies, and the estimated habitats of 11 Oligocene fossil sharks can be favorably compared to the current habitats of related extant species. Extant coastal shark taxa occur mainly in lower shoreface habitats, and extant deep marine shark taxa and extant epipelagic species mainly in outer shelf habitats. This

suggests that Oligocene shark habitats were similar to those of extant sharks, at the genus level. The results obtained by this study tend to contradict previous interpretations which suggested that the extant deep sea elasmobranch *Hexanchus* inhabited shallow environments during the Oligocene, and subsequently migrated into deep sea habitats during the Miocene.

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Appendix 1

Detailed description and interpretation of each sedimentary facies are as follows.

Facies 1

Description.—This facies is characterized by well bioturbated and massive (unlaminated) very fine sandstone to siltstone that is occasionally interbedded with about 10 cm thick medium- to coarse-grained sandstone layers containing volcanoclastics and shell remains. Onion structures are well developed, and articulated bivalve shells retaining living position and spatangoid echinoids are common. From a part of this facies, *Turritella* with barnacles adhered only on the upper surface of the shells is observed, indicating that barnacles are autochthonous. In this facies, shark teeth are uncommon but mainly occur in fine- to medium-grained sediments

which sometimes contain plant fragments or articulated but allochthonous bivalve shells.

Interpretation.—Abundant bioturbation indicates an only minor influence of storm wave on the substrate. Therefore, Facies 1 was likely deposited within an outer shelf environment. Autochthonous *Turritella* shells with barnacles indicate a stable environment with low sedimentation rates.

Facies 2

Description.—This facies is characterized by very fine-grained to fine-grained laminated sandstones. Laminae are often disturbed or completely destroyed by bioturbation. Sorting is relatively poor when compared to the sandstones of Facies 3 and 4. Gray calcareous nodules, 10 to 30 cm in diameter often occur in this facies with abundant burrows obscuring original sedimentary structures. Where mud layers are preserved, these layers show burrows infilled with mud or very fine sandstone. Other burrows in this nodule are also filled with mud or very fine sand and sometimes contain bivalve shells, such as *Glycymeris cisshuensis*, *Turritella* sp., and *Chlamys ashियाensis*, and vertebrate remains. Some shells are articulated and in life position, but the majority of bivalves are disarticulated and preserved with their convex exterior sides downward. Several shark teeth and centra were obtained from this facies. These shark fossils occurred within heavily bioturbated horizons along with molluscan debris, suggesting that the concentration of these fossils is caused by a decreased sedimentation rate.

Interpretation.—Mud layers and mud-filled burrows indicate that the environment was low-energetic. Extensive bioturbation has destroyed much of the original sedimentary structure, but the original lithology is thought to have been laminated very fine- to fine-grained sandstones, intercalated with thin mud layers. This facies is interpreted as having been accumulated in an outer shelf environment. The taphonomy of bivalves supports interpretation as a low-energy environment. Larger mean grain size and the extensive bioturbation suggests a slightly shallower depositional environment in Facies 2 than Facies 1, following the interpretation by Dott and Bourgeois (1982) for similar rocks.

Facies 3

Description.—This facies is characterized by interbedded medium- to coarse-grained, hummocky cross-stratified (HCS) sandstones, and very fine-grained sandstones. This facies is observed only within a limited interval and can be separated into lower and upper parts. HCS sandstone layers thin upwards. The lower part is characterized by alternating HCS sandstones and very fine-grained sandstone, although it is largely dominated by the coarser cross-stratified sediments. HCS sandstones are about 20 cm thick, composed of coarse- to medium-grained sand, and often contain sand clasts and shells as HCS lags. The majority of bivalves are buried with

their convex side upwards. Sand clasts are 3–5 mm in diameter, composed of very fine subangular sand and mixed with articulated bivalve shells. Complete Dott and Bourgeois (1982) sequences are recognized within the HCS beds. Thin (2–3 cm) intercalated layers of fine-grained sandstone occur in the lower part. These layers are laminated and are partly cut by overlying HCS sandstone layers. Very fine-grained sandstones pinch out laterally, and overlying HCS sandstone layers are in contact with lower HCS sandstones where they disappear.

The upper part of Facies 3 is characterized by alternating medium- to fine-grained sandstones (ca. 10 cm thick) and thicker (10–30 cm) horizons of very fine-grained sandstone. Medium- to fine-grained sandstones are HCS or contain wavy or parallel laminations, and are normally graded. The upper surfaces of these sandstone layers contain wave ripples and correspond to the HCS sandstone beds in the lower part of Facies 3. Layers of very fine-grained sandstone are intercalated between the medium- to fine-grained sandstones, and contain parallel laminations and plant fragments. The bottom surface of the sandstone is often wavy and sometimes cuts into very fine-grained sandstone layers below, like the lower part of Facies 3. In general, the grain size fines upward and sedimentary structures change from M-cutout type amalgamated HCS (Dott and Bourgeois, 1982) to parallel-laminated or wavy structures.

Interpretation.—Alternating beds of coarse- to fine-grained HCS sandstones and very fine-grained laminated sandstones are interpreted as alternating fair-weather and storm-derived sediments. These characteristics suggest that Facies 3 was deposited in an inner shelf setting (see Walker and Plint, 1992). According to the interpretation offered by Dott and Bourgeois (1982), full sequence HCS sandstones in the lower part of Facies 3 and medium- to fine-grained sandstones in the upper part of Facies 3 are interpreted as being deposited during, and just after, stormy weather conditions. Laminated very fine grained sandstone layers are interpreted as having been formed under fair-weather conditions. Sand clasts in HCS sandstones within the lower part were possibly supplied by denudation, as they contain the very fine sandstones and articulated bivalve shells characteristic for fair-weather sediments. Bed thinning and fining-upwards of the HCS sandstone layers into beds containing wavy or parallel laminae (and converse thickening upward of finer-grained sandstone layers) are interpreted as representing a shift from proximal to distal depositional environment (Dott and Bourgeois, 1982). Facies 3 is overlapped by Facies 2 (interpreted as an outer shelf deposit), and thus is consistent with interpretation as representing a deepening sequence.

Facies 4

Description.—This facies is characterized by alternating hummocky cross-stratified fine and bioturbated fine-grained

sandstones. Hummocky cross-stratification is of the amalgamated type, and sometimes includes shell or pebble lags. Wavelengths of some hummocky cross stratification are 1–2 m. Bioturbated sandstone layers are 2–4 m thick. Shark teeth from this facies commonly occur in the lags of granule or pumice-rich layers, and are only rarely associated with bivalve shells.

Interpretation.—The HCS sandstone and bioturbated sandstone interbeds have identical grain sizes, and so are interpreted as representing periodic storm activity which mixed originally bioturbated sediments and redeposited them as HCS sandstone. This facies is similar to that reported by Bourgeois (1980) as ‘upper hummock-bedded and burrowed facies.

Facies 5

Description.—This facies is composed of amalgamated hummocky cross-stratified fine sandstones, and often includes thick lags of shells and pebbles. HCS lags are present and maybe well developed to more than 10 cm thick and 1 m wide. The lags are often composed almost exclusively of large (ca. 5 cm), disarticulated *Glycymeris cisshuensis* bivalves, almost all of which have surface abrasion. Facies 4 is similar to Facies 5 in containing HCS sandstones, but is distinguishable by the abundance of HCS lags and poorly developed bioturbated layers. Mode of occurrence of shark teeth is similar to that of Facies 4 where teeth occasionally occur in HCS lags with a possible control in weight or size selectivity in the process of sedimentation.

Interpretation.—Amalgamated hummocky cross-stratification and rare bioturbation allow this facies to be interpreted as representing a lower shoreface setting (e.g., Saito, 1989). In contrast to Facies 4, bioturbated layers are poorly developed, the wavelength of hummocky cross-stratification is short, and HCS beds contain abundant thick lags. These characteristics suggest that the sedimentary environment of Facies 5 was shallower and more storm-dominant than that of Facies 4 (Bourgeois, 1980).

Facies 6

Description.—This facies is characterized by planar cross-bedded or partly bidirectional planar cross-bedded (herringbone cross-stratification), medium-grained sandstones. Laminae are sometimes disturbed or completely destroyed by bioturbation. Sand grains are invariably well sorted.

Interpretation.—Herringbone cross-stratification is thought to be formed as a result of reversing currents within tidal inlet settings (e.g., Barwis and Makurath, 1987; Yagishita, 1997). Sandstones within Facies 6 are well sorted and grain size is medium-grained, suggesting the presence of a strong current at the time of deposition and supporting interpretation of Facies 6 as having formed within a tidal inlet (Yagishita, 1997).

Facies 7

Description.—This facies is characterized by fine- to coarse-grained, well sorted sandstones with intercalations of thin siltstones. Rapid alternations between coarse and fine grained size sections were observed in the field. Parallel laminae are common. Between sandstone layers, thin (1 mm–6 cm) siltstone layers are intercalated. These layers are sometimes wavy and are horizontally continuous. Only one shark tooth belonging to *Negaprion* sp. was collected from this facies.

Interpretation.—Intercalated mud layers and well sorted fine- to coarse-grained layers suggest deposition under alternately strong and weak currents. Alternation of fine to coarse sand layers and mud layers suggests repeated stagnation of currents, such as occur in tidal environments where current directions periodically reverse, creating lower-energy conditions under which thin mud layers are deposited between coarser layers.

Appendix 2

Specimen list. All specimens are housed in The University Museum, The University of Tokyo (UMUT).

Appendix 2. List of used specimens in this study.

Taxa	Facies	Specimen no.
<i>Carcharhinus</i> sp.	4	UMUT CV 30210
<i>Negaprion</i> sp.	1	UMUT CV 30211-30213
	2	UMUT CV 30214-30223
	4	UMUT CV 30224-30234
	5	UMUT CV 30235-30244
<i>Galeorhinus</i> sp.	2	UMUT CV 30245
<i>Carcharias</i> sp.	2	UMUT CV 30246-30251
	4	UMUT CV 30252-30262
	5	UMUT CV 30263-30273
<i>Cetorhinus</i> sp. (gill rakers)	1	UMUT CV 30333
	2	UMUT CV 30334
	4	UMUT CV 30335
<i>Isurus</i> sp.	1	UMUT CV 30275, UMUT CV 30276
	2	UMUT CV 30276-30283
	4	UMUT CV 30284, UMUT CV 30285
	5	UMUT CV 30286, UMUT CV 30287
<i>Heterodontus</i> sp.	2	UMUT CV 30288
<i>Hexanchus</i> sp.	2	UMUT CV 30291-30300
	4	UMUT CV 30301-30303
	5	UMUT CV 30304
<i>Squalus</i> sp.	2	UMUT CV 30305-30319
	4	UMUT CV 30320
	5	UMUT CV 30221
<i>Squatina</i> sp.	2	UMUT CV 30322-30325
	4	UMUT CV 30226, UMUT CV 30227
<i>Myliobatis</i> sp.	4	UMUT CV 30328, UMUT CV 30329
	5	UMUT CV 30330-30332