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Revision of Neogene Mackerel Shark of Genus *Isurus* from Japan

By

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Abstract

Fossil so-called *Isurus* from various localities in Japan are studied taxonomically and paleoecologically. Five species, *Isurus desori*, *Isurus planus*, *Isurus hastalis*, *Isurus oxyrinchus* and *Isurus cf. paucus*, representative in Neogene of Japan, are described. New genus *Uyenoa* is proposed for *Isurus benedeni*.

Introduction

The fossil elasmobranchs have been studied mainly by the European and American students. The knowledge of Asian fossil sharks are still meager though the number of related reports is increasing after 1960's in Japan. In fact the widely developed marine sediments have yielded numerous detached teeth of the elasmobranchs in Japan. There are advantageous situations for studying fossil elasmobranchs for their sediments has often been studied geologically in high degrees of accuracy. Nevertheless the problems have remained in identification of fossil species. The subject tackled here is to attempt a critical revision to the genus *Isurus*. *Isurus* has been commonly found in the Neogene sediments together with other elasmobranchs, marine mammals and molluscs. For example, ISHIWARA (1921), HASEGAWA and UYENO (1967), GOTO (1972), UYENO *et al.* (1974), Hatai *et al.* (1974), ITOIGAWA and NISHIMOTO (1974), ITOIGAWA *et al.* (1975), KATTO *et al.* (1976), GOTO *et al.* (1978), NISHIMOTO and UJIHARA (1979), KUGA and NAKATA (1980), UYENO *et al.* (1980), UYENO and ONO (1982), UYENO and OSHIRO (1982) and UYENO *et al.* (1983) described fossil shark teeth including several species of *Isurus*. But their classification of this genus is confused at present.

Materials

Abbreviations:

GDSU — Department of Geology, Shimane University, Matsue.

HMH — Historical Museum of Hokkaido, Sapporo.

HT — Private Collection of Hiroyuki Taruno.

IGPS — Institute of Geology and Paleontology, Tohoku University, Sendai.

KU — Department of Geology and Mineralogy, Kyoto University, Kyoto.

MFM — Mizunami Fossil Museum, Mizunami.

MG — Private Collection of Masatoshi Goto.

NK — Private Collection of Naoyuki Kuga.

NSMT — National Science Museum, Tokyo.

OPM — Okinawa Prefectural Museum, Naha.

SHKM — Saito Ho-on Kai Museum of Natural History, Sendai.

Isurus desori

Upper anterior teeth: MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described by Itoigawa and Nishimoto, 1974 as *I. retroflexus*), NSMT-PV16867 (1st anterior), NSMT-PV16870 (2nd anterior) (Misato-mura, Mie Prefecture: Ichishi Group; Middle Miocene. described by UYENO *et al.* 1980 as *I. oxyrinchus*), GDSU-T 572 (Kimachi, Shinji-cho, Shimane Prefecture: Fujina Formation, Kimachi Sandstone Member; Late Miocene)

Lower anterior teeth: IGPS 6306 (1 specimen, Kintaichi, Ninohe City, Iwate Prefecture. described by Ishiwara, 1921 as *I. hastalis*), MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described by Itoigawa and Nishimoto, 1974 as *I. retroflexus*)

Upper and lower lateral teeth: MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described as *I. retroflexus*), NSMT-PV 16865, 16869 (Misato-mura, Mie Prefecture: Ichishi Group; Middle Miocene. described by UYENO *et al.*, 1980 as *Isurus oxyrinchus*)

Isurus planus

Upper anterior tooth: GDSU-T 582 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Upper and lower lateral teeth: SHKM collection (unnumbered 6 specimens, Kumanodo and Nihondaria, Sendai City, Miyagi Prefecture: Moniwa Formation; Middle Miocene. described by HATAI *et al.* 1974 as *I. hastalis*), IGPS 6298 (8 specimens, Hannoura, Notojima-cho, Ishikawa Prefecture: Hannoura Bed; Middle Miocene. described by ISHIWARA, 1921 as *I. hastalis*), NK 442, 675, 678-690 (Iwaya, Fujihashi-cho Nanao city, Ishikawa Prefecture: Iwaya Calcareous Sandstone Bed; Middle Miocene), GDSU-T 585, 589, 590, 591-593, 599, 603, 606, 607, 612 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Lower anterior teeth: GDSU-T 580 (Kagami, Shinji-cho, Shimane Prefecture: Fujina Formation; Late Miocene), GDSU-T 596, 603 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Isurus hastalis

Upper anterior teeth: MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described by ITOIGAWA and NISHIMOTO, 1974), HT collection (Misato-mura, Age-gun, Mie Prefecture: Ichishi Group; Middle Miocene), NK 423 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Upper anterior teeth?: HMH 44619-2 (Hatsune Mine, Kitahiyama-cho, Setana-gun, Hokkaido: Babagawa Formation; Middle Miocene. described KUGA and NAKATA, 1980), KU unnumbered specimen (Iwasaki-mura, Nishitsugaru-gun, Aomori Prefecture: Tanosawa Formation; Middle Miocene), DGSU T 577 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Upper lateral teeth; MFM collection (Mizunami City, Gifu Prefecture: late Early to early Middle Miocene. partly described by ITOIGAWA and NISHIMOTO, 1972), HMH 44615-5, 44615-7, 44615-8, 44615-9, 44615-10 (Ryubu Mine, Kitahiyama-cho, Setana-gun, Hokkaido: Samatagawa Formation; Middle Miocene, described by KUGA and NAKATA, 1980), HMH 44619-4, 44619-5, 44619-6, 44619-7, 44619-8, 44619-9 (Hatsune Mine, Kitahiyama-cho, Setana-gun, Hokkaido: Babagawa Formation; Middle Miocene. described by KUGA and NAKATA, 1980), MG collection (Hanawa-cho, Higashishirakawa-gun, Fukushima Prefecture: Higashitanagura Group; Middle Miocene), IGPS 6298 (6 specimens, Hannoura, Notojima, Ishikawa Prefecture: Hannoura Bed; Middle Miocene. described by Ishiwara, 1921), DGSU-T 573, 574, KU Pb-12 (Kimachi, Shinji-cho, Shimane Prefecture: Fujina Formation, Kimachi Sandstone Member; Late Miocene), DGSU-T 594, 600, NK 424 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene), DGSU-T 620 (Nogifukutomi-cho, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Lower anterior teeth: MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described by ITOIGAWA and NISHIMOTO, 1974), KU unnumbered specimens (2 specimen, Iwasaki-mura, Nishitsugaru-gun, Aomori Prefecture: Tanosawa Formation, Middle Miocene), NK441 (Iwaya, Nanao City, Ishikawa Prefecture: Iwaya Calcareous Sandstone Bed; Middle Miocene), DGSU-T 572, 611 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Lower lateral teeth: MFM collection (Mizunami City, Gifu Prefecture: Mizunami Group; late Early to early Middle Miocene. partly described by ITOIGAWA and NISHIMOTO, 1974), DGSU T578, 601, 602, 605 (Ichinotani, Matsue City, Shimane Prefecture: Fujina Formation; Late Miocene)

Isurus oxyrinchus

Upper anterior teeth: MFM collection (3 specimens, Nagasakibana, Choshi City, Chiba Prefecture: Naarai Formation; Upper Pliocene. figured by ITOIGAWA *et al.* as *I. retroflexus*)

Lower anterior teeth: NK 21 (Hirono-cho, Fukushima Prefecture: Tomioka Formation; Pliocene), GDSU T641 (Sukegawa, Hitachi City, Ibaraki Prefecture: "Taga Group"), MFM collection (2 specimens, Nagasakibana, Choshi City, Chiba Prefecture: Naarai Formation; Upper Pliocene. figured by ITOIGAWA *et al.* as *I. retroflexus*)

Isurus cf. paucus

Upper anterior teeth: NK363 (Kamiyanagi, Saito City, Miyazaki Prefecture: Kawahara Formation, Miyazaki Group; Pliocene)

Uyenoa benedeni

Upper lateral teeth: SHKM unnumbered specimen (Akaishi, Sendai City, Miyagi Prefecture: Moniwa Formation; Middle Miocene. type specimen of *I. moniwaensis* described by Hatai *et al.* 1974), HMM unnumbered specimen (Iwamizawa City, Hokkaido: Takinoue Formation; Early to Middle Miocene)

Lower anterior teeth: MFM collection (1 specimen, Okuna, Mizunami City, Gifu Prefecture: Mizunami Group, Oidawara Formation, Nataki Conglomerate Member: early Middle Miocene.)

Lower lateral teeth: OPM-GF195 (Tomigusuku-mura, Okinawa Prefecture: Shimajiri Group; Late Miocene to Pliocene. described by Uyeno and Oshiro, 1982), MFM collection (1 specimen, Nagasakibana, Choshi City, Chiba Prefecture: Naarai Formation; Upper Pliocene. figured by Itoigawa *et al.* 1974 as *I. sp.*)

Methods

The dental terminology used in this study follows Kuga and Goto (1980) with slight modification. The directional and tooth terminology are shown in figures 1 and 2. The tooth kind nomenclature follows Leriche (1905) and Applegate (1965). But in *Isurus*, morphology of the upper post-intermediate teeth and the lower post-anterior teeth change gradually. So I do not adopt the posterior teeth in *Isurus* throughout of this study.

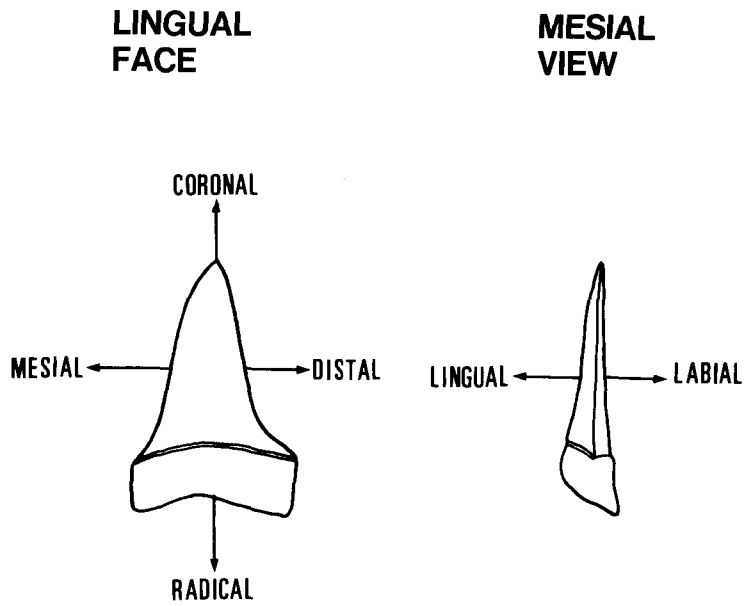


Fig. 1. Directional terminology.

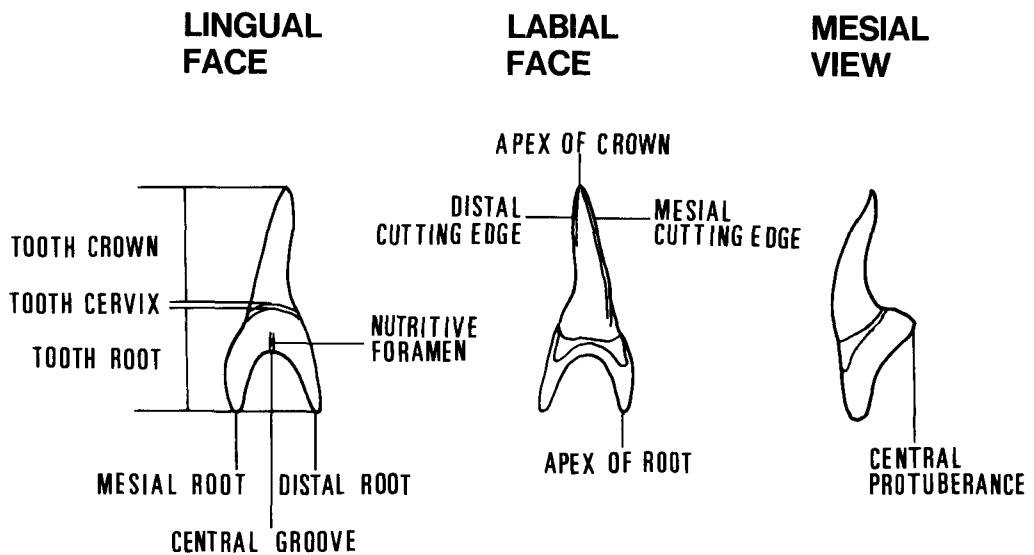


Fig. 2. Tooth terminology.

Systematic Description

Class Chondrichthyes
Subclass Elasmobranchii
Cohort Euselachii
Superorder Galeomorphii
Order Lamniformes

Family Lamnidae MÜLLER and HENLE, 1838

Diagnosis:

Two dorsal fins; the 1st much shorter at base than length of caudal, the posterior end of 1st dorsal base for advance of pelvic origin; 2nd dorsal and anal much smaller than 1st dorsal, caudal fin lunate in form; gill arches without rakers; both jaws with labial furrows at corners (Bigelow and Schroeder, 1948). Teeth large, absent of striations, differ in shape at mesiodistal positions and upper or lower jaws; composing with osteodentine.

Remarks:

Three genera, *Lamna*, *Isurus*, and *Carcharodon*, belong to Family Lamnidae in the recent sharks. These genera are separated by not only the body forms but the dental morphology. The teeth of *Lamna* possess one or more subcusps in mesial and distal side except in the very young specimen. And the cutting edge is smooth without serrations. In *Carcharodon*, the tooth is large and triangular and have coarsely serrations.

As to the body form, both *Lamna* and *Carcharodon* have the 1st dorsal fins origin anterior to the verticals through the posterior corner of pectorals. *Lamna*, but not *Carcharodon*, has a secondary lateral keel on the anterior part of the caudal fin (GARRICK, 1967)

Genus *Isurus* RAFINESQUE, 1810

Type Species: *Isurus oxyrinchus* RAFINESQUE, 1810

Diagnosis:

Origin of 1st dorsal fin definitely posterior to inner corner of pectoral when later is laid back; trunk slender; caudal fin without secondary caudal keels (BIGELOW and SCHROEDER, 1948). Teeth large without subcusps, cutting edge smooth without serrations.

Remarks:

Two living species, *Isurus oxyrinchus* Rafinesque, 1810 and *I. paucus* Guitart-

Manday, 1966 are known. *Isurus oxyrinchus* have the moderately long pectoral fins, always shorter than length of the head, and underside of the snout and around mouth white in color. On the contrary, *I. paucus* have the very long pectoral fins equal in length to the head, at some dusky coloration on underside of the snout and around the mouth (GARRICK, 1967). Also the two species can be divided by the dental forms (GARRICK, 1967; KUGA, 1980 MS)

Isurus oxyrinchus distributes in the Pacific, Atlantic, and Indian Oceans. In the North Pacific region, it lives from equator to N 35–43°, and occasionally appears around the Japanese Islands. Mainly *I. oxyrinchus* inhabits under the surface of open sea. Because it is named the epipelagic fish. However it sometimes makes an excursion to shallow sea region. For example many individuals are caught in the East China Sea in Autumn (TANIUCHI, 1979).

Isurus paucus was described recently, so the mode of life is scarcely enlightened. This species is found in every ocean. GARRICK (1967) pointed out that the larger eyes of it suggest the possibility that it lives rather deeper water than *I. oxyrinchus*. His view accords with allied one of *I. paucus* in Japan. The Japanese fishers call it "Sokomoro", which literally means submarine mackerel shark. It may well be that this species inhabits in the middle depth of the ocean.

GLÜCKMAN (1964) divided the living and fossil *Isurus* into five genera (*Cosmopolitodus*, *Isurus*, *Isuroopsis*, *Macrorhizodus* and *Lamiostoma*) based entirely on the morphology of the teeth. Recently, GARRICK (1967) summarized living *Isurus* as two species (*I. oxyrinchus* and *I. paucus*). According to Garrick, type species of genus *Isuroopsis*, *I. glaucus*, is conspecific with *I. oxyrinchus*. Glückman's *Lamiostoma belyavi* closely resembles to *I. paucus*. But GARRICK retained the evaluation of the status *Lamiostoma belyavi* until more information is available. If Glückman's *Lamiostoma belyavi* is not conspecific with *I. paucus*, it should be included in genus *Isurus*. I do not find Glückman's classification convincing, so I have chosen to retain older nomenclature of *Isurus* in this paper except one species (*Uyenoa benedeni* see p. 14)

The fossil species are reported after Paleocene. No more than the teeth and vertebral columns were discovered, so complete information of the soft parts is wanted.

Isurus desori (AGASSIZ)

pl. 1, figs. 1–3, pl. 2, figs. 1–7, pl. 3, figs. 1–8.

1843. *Oxyrhina desorii* AGASSIZ: Recherches sur Poissons fossiles, tome 3, pp. 282–283, atlas, tome 3, pl. 37, figs. 8–13.
1843. *Oxyrhina leptodon* AGASSIZ: ibid., p. 282, atlas ibid., pl. 37, figs. 3–5.
1888. *Oxyrhina ensii* DAVIS: *Sci. Trans. Roy. Dublin Soc.*, vol. 4, no. 2, pp. 28–29, figs. 17–20.
1888. *Oxyrhina grandis* DAVIS: ibid., p. 30, figs. 15–16.

1967. *Isurus* sp.: HASEGAWA and UYENO (in part). Anancho no Kaseki, p. 116, pl. 22, figs. 3.
1972. *Isurus oxyrinchus hastalis*: CARETTO (in part). *Boll. Soc. Paleont. Soc. Italiana*, vol. 11, n. 1, pp. 42–51, tav. 5, figs. 1, 10, tav. 7, figs. 2, 4, 5.
1974. *Isurus retroflexus*: ITOIGAWA and NISHIMOTO (in part). *Bull. Mizunami Fossil Mus.*, no. 1, pp. 247–248, pl. 81, figs. 1–3.
1980. *Isurus oxyrinchus*: UYENO, HASEGAWA and KAKUTA. *Bull. Nat. Sci. Mus.*, ser. C, vol. 6, no. 4, p. 127, pl. 2, figs. G, J, K.

Diagnosis:

Isurus with moderate size of teeth. Anterior teeth with slender elongate crowns, both cutting edges extend to cervix, Roots obviously bifurcated.

Description:

The upper anterior teeth have elongate, slender, slightly oblique crowns. The lingual faces are moderately convex. The labial faces are nearly flat. The cutting edges are sharp. The both margins always reach the tooth cervixes. The roots of the upper anteriors are bifurcated obviously, and more extended mesiodistally than those of the lower anteriors. The central protuberances are observed, but less developed than those of the lower anteriors.

The intermediate tooth is small and resembles to that of *I. oxyrinchus*. The crown is subtriangular and curved distally. The mesial cutting edge is slightly concave. The distal cutting edge consists of deeply concave radical half and nearly straight coronal half. The tooth apex extends coronodistally.

The lower anterior teeth have elongate, sharply pointed crowns. The crowns are straight or very slightly oblique distally. The degree of inclination is less than that of the upper anteriors. The lingual faces are more convex than those of the upper anteriors. Both cutting edges reach the tooth cervix (pl. 2, fig. 6) or do not reach them (pl. 2, figs. 5, 7). The roots are markedly bifurcated, reversed U shape and extended radically. The central protuberances are remarkably projecting as in recent *Isurus oxyrinchus*.

The upper and lower lateral teeth are not distinguishable each other in this study. The crowns of the lateral teeth are oblique subtriangles. They are more erect than those of *I. oxyrinchus*. The lingual faces are moderately convex. The labial faces are flat. The mesial cutting edges are nearly straight. The distal cutting edges consist of straight coronal halves and concave radical halves. The roots are slightly bifurcated and extended mesioradiacally and distoradically. The mesial and the distals roots are square.

The tooth morphology of *Isurus paucus*, one of the living species, closely resembles to that of this species. The information on *I. paucus* is not sufficient. Especially

data of large specimens are entirely lacked. I think that the two species are distinguishable following characters: the crowns of the anterior teeth of *I. desori* are thicker and narrower. The roots of the anteriors are thicker and the central protuberances are more developed.

Remarks:

ITOIGAWA and NISHIMOTO (1974) described two species of *Isurus*. One is *I. hastalis* and the other is *I. retroflexus*. I examined their specimens stored in the Mizunami Fossil Museum. Their *I. retroflexus* contained *I. desori* and probably *I. planus*.

The recent *Isurus* were considered to be originated from this species by LERICHE (1910). By the view point of tooth morphology, it is appropriate interpretation. Particularly *I. paucus* might be a descendant in the direct line.

Occurrence:

In the Miocene deposits of Japan, this species is not so common as *I. planus* and *I. hastalis*. But cooccurrence of these species, *I. hastalis* and *I. desori* are probably tropical-subtropical shallow sea dwellers, not pelagic fishes.

Horizon:

Isurus desori is known from Oligocene (Yamaga Formation, this paper) to Middle Miocene (Ichishi Group, Uyeno *et al.*, 1980. and this paper) of Japan.

Isurus planus (AGASSIZ)

pl. 4, figs. 1-5, pl. 5, fig. 1.

1856. *Oxyrhina plana* AGASSIZ, *Am. Jour. Sci. Arts*, 1856, p. 275.
 1907. *Isurus planus*: JORDAN, *Univ. Calif. Pub., Bull. Dept. Geol.*, vol. 5, no. 7, pp. 107-109, fig. 9 (except upper right figure)
 1921. *Isurus hastalis*: ISHIWARA (in part), *Sci. Rep. Tohoku Imp. Univ.*, ser. 2, vol. 5, no. 3, pp. 62-65, pl. 10, figs. 1-14.
 1974. *Isurus hastalis*: HATAI, MASUDA and NODA, *Saito Ho-on Kai Mus. Res. Bull.*, no. 43, pp. 16-19, pl. 2, figs. 3-5, 8, 13, 14, 16; 23.

Diagnosis:

An *Isurus* with moderate to large size of tooth: Crowns of lateral teeth slightly to strongly curved for distal. Root apexes of laterals round.

Description:

The crown of the upper anterior tooth is elongate and slender. The lingual face of the crown is moderately convex. The labial face is nearly flat. The cutting

edge is sharp. The both edges reach the tooth cervix. The root of the upper anterior is bifurcated, but not so obviously than those of other *Isurus* except *Isurus hastalis*.

The intermediate tooth is not included in the materials examined.

The lower anterior teeth have elongate, slender crowns. They are narrower than that of the upper anterior. The lingual faces of the crowns are more convex than that of the upper anterior. The labial faces are nearly flat. The both cutting edges reach the tooth cervixes, but in DGSU-T 572 (pl. 4, fig. 2), they do not reach it. The roots of the anteriors are bifurcated as in *Isurus hastalis*.

The upper lateral and lower lateral teeth are not distinguishable clearly. The crowns of the lateral teeth are compressed labiolingually and narrow, oblique triangles. The degree of obliquity is variable according to the tooth position. The mesial cutting edges are concave. The distal cutting edges consist of slightly concave to nearly straight coronal halves and slightly to deeply concave radical halves. The root apexes of the lateral teeth are round.

Remarks:

The fossil records of *Isurus planus* are geographically limited in the circum Pacific region (California of USA, AGASSIZ, 1856 and JORDAN, 1907; Australia, Kemp, 1983—no description; Japan, this paper). Especially in Europe, many fossil *Isurus* were described, but there is no record of this species. It is very comprehensive for me because all species of *Isurus* except this species were world-wide in distribution. There are two possibilities for this problem. First, *Isurus planus* was speciated in the Pacific Ocean and did not enter into the Atlantic. The other is misidentification by European students. But no data exist to determine which one is correct at present.

Occurrence:

This species is one of the commonest fossil elasmobranchs in Middle to Late Miocene age in Japan.

Horizon:

Isurus planus is known from Middle Miocene (Moniwa Formation) to Late Miocene (Fujina Formation).

Isurus hastalis (AGASSIZ)

pl. 5, fig. 2, 3, pl. 6, figs. 1–4, pl. 7, figs. 1–3, pl. 8, figs. 1–6,
pl. 9, figs. 1–8.

1843. *Oxrhina hastalis* AGASSIZ (in part): Recherches sur les Poissons fossiles, tome 3, pp. 277–278, atlas, tome 3, pl. 34, figs. 3–17.
1843. *Oxyrhina xiphodon* AGASSIZ: ibid. pp. 287–279, atlas ibid., pl. 33, figs. 11–17.
1843. *Oxyrhina plicatilis* AGASSIZ: ibid. pp. 279–280, atlas ibid., pl. 37, figs. 14–15.

1843. *Oxyrhina trigonodon* AGASSIZ: *ibid.*, p. 279, atlas, *ibid.*, pl. 37, figs. 17–18.
1843. *Oxyrhina crassa* AGASSIZ: *ibid.*, p. 282, atlas, *ibid.*, pl. 37, fig. 16.
1889. *Oxyrhina hastalis*: WOODWARD. Catalogue of the Fossil Fishes in the British Museum. part. 1, pp. 385–389.
1907. *Isurus tumulus* JORDAN (in part): *Univ. California Pub. Bull. Dep. Geol.*, vol. 5, no. 7, pp. 109–111, fig. 10 (in part, excluding upper central figure).
1907. *Isurus smithii* JORDAN: *ibid.*, pp. 111–112, fig. 12.
1921. *Isurus hastalis*: ISHIWARA (in part). *Sci. Rep. Tohoku Imp. Univ.*, ser. 2, vol. 5, pp. 62–65, pl. 10. figs. 19–26.
1967. *Cosmopolitodus hastalis*: GLÜCKMAN. *Fundamentals of Paleontology*, vol. 11, p. 340, pl. 5, fig. 5.
1967. *Cosmopolitodus trigonodon*: GLÜCKMAN. *ibid.*, pl. 5, figs. 6–7.
1967. *Isurus* sp.: HASEGAWA and UYENO (in part). *Anancho no Kaseki*, p. 116, pl. 22, fig. 7a.
1972. *Isurus oxyrinchus hastalis*: CARETTO (in part). *Bol. Soc. paleont. Italiana*, vol. 11, n. 1, pp. 42–51, tav. 7, fig. 1.
1982. *Isurus hastalis*: UYENO and ONO. *Mem. Nat. Sci. Mus.*, no. 15, pp. 64–65, pl. 3, fig. E–K.
1983. *Isurus hastalis*: UYENO *et al.* *Bull. Saitama Mus. Nat. Hist.*, no. 1, p. 29, pl. 3, fig. A, B.

Diagnosis:

An *Isurus* which have large teeth. Crowns thin, triangular, broad bases except lower anterior teeth; roots thin, square except lower anteriors.

Description:

The upper anterior and lateral teeth are large and resemble to each other. The crowns are thin, broad, nearly isosceles triangles. Small specimen (pl. 5, fig. 3, pl. 6, fig. 1) has narrower crown and more radically extended root than that of full adult (pl. 5, g. 2) as in *Carcharodon carcharias*. Especially the morphological change of the root in ontogeny can be observed in the lateral tooth of this species. They stand erect or slightly oblique in position. In some anterior teeth, the tips of the crowns slightly flexuous lingually (HT collection, pl. 5, fig.3). The lingual faces are moderately convex and the labial faces are nearly flat. The cutting edges are sharp and nearly straight or slightly curved, and reach the tooth cervixes. The tooth cervixes are narrow grooves on the lingual faces while indistinct on the labial faces. The roots are thin square, short and not extended radically.

The lower anterior teeth are elongate. The crowns are slender isosceles triangles. They stand erect ly or very slightly oblique. The lingual faces are strongly convex. The labial faces are very slightly convex. The cutting edges are

nearly straight or slightly curved and extended to the tooth cervixes. The roots are clearly bifurcated and elongated radically. The central protuberances on the lingual faces are recognized but not remarkably.

The lower lateral teeth resemble to the upper lateral teeth. The crowns of the lower laterals are thicker than those of the upper laterals. The cutting edges are composed of moderately or deeply concave radical halves and nearly straight of coronal halves. The roots of the lower lateral teeth resemble to those of the upper laterals. In comparison with those of the upper laterals, they are thicker and more remarkably bifurcated. The nutritive foramens open clearly but the central grooves are not observed.

Remarks:

ISHIWARA (1917) identified *Isurus* with a strongly curved tooth to the upper lateral tooth of *I. hastalis*, indistinctly curved tooth to the lower lateral, and long slender tooth to the anterior. He followed LERICHE (1908) and JORDAN and BEAL (1913). Since then, Japanese paleontologists (for example, HATAI *et al.*, 1974) accepted his opinion. Consequently the Japanese so-called *I. hastalis* shows a great variety in form. I examined the same specimens described by ISHIWARA. The results are as follows. The Ishiwara's upper lateral teeth of *I. hastalis* should be the upper lateral teeth of *I. planus*. His lower lateral teeth are composed the upper anterior, upper lateral, and lower lateral teeth of *I. hastalis*. His anterior teeth should be the lower anterior teeth.

GOTO (1972) listed 27 localities of this species in Japan, but most of them are undescribed. There is a large possibility that *I. hastalis* by GOTO contains 2 or more species. The so-called *I. hastalis* reported from Japan should be reexamined.

Occurrence:

Isurus hastalis is one of the common species in the Japanese fossil sharks. It occurs with many species of the fossil mollusks, sharks' teeth and mammals. Especially in the fossil mammals, the desmostilia and Cetacea are often associated with this species. I have confirmed the cooccurrence relationships based on the specimens from the Pirika and Meppu Mines in the Hokkaido (KUGA and NAKATA, 1980). The concordance of the transgression indicated by the lithofaces and benthonic fossil remains, ITOIGAWA and NISHIMOTO (1974) considered this species as a subtropical epipelagic fish. But it is the fact that *I. hastalis* is often found with the shallow sea molluscan fossils and desmostilids which might live on the sea coast (IJIRI and KAMEI, 1961; SHIKAMA, 1966). Furthermore I cannot recognize *I. hastalis* in the South Pacific Sea bottom fossils which are considered to be of the pelagic shark fauna (KUGA and USUI, 1982). By these reasons, it is thought to be a shallow sea dweller in the view point of paleoecology.

Horizon:

Isurus hastalis lived in Miocene concentrately. It is not discovered in the Pliocene strata of Japan.

Isurus oxyrinchus Rafinesque

pl. 10, fig. 1.

Diagnosis:

An *Isurus* have moderate size of teeth: anterior teeth on upper and lower jaws have slender, elongate crown, obviously bifurcated root: distal cutting edges of both 1st anterior teeth extended from apex to midway of crown.

Description:

The upper and lower anterior teeth have slender and pointed crowns. The crowns of the upper anteriors are more labiolingually compressed than those of the lower anteriors. The distal cutting edges of the upper and lower anteriors do not reach the tooth cervixes. The morphology of the fossil specimens of this species completely agree with the recent specimens (KUGA, 1980 MS).

Remarks:

CARRETTO (1972) compared fossil shark teeth from the Miocene sediments of Monferrato, Italia with living shark teeth. He concluded that some fossil sharks are closely similar to recent species and they are intraspecific variations. Consequently he regarded certain fossil species to subspecies of recent taxa. For example, *Isurus hastalis* was determined *Isurus oxyrinchus hastalis* by him. Moreover his *Isurus oxyrinchus* contained three species in this paper. He attached much importance of the variation and ignore difference of the specific morphological feature. The intraspecific variation of the fossil shark teeth from Monferrato in CARRETTO (1972) is beyond the limit of difference of the tooth morphology of the living two species (KUGA, 1980MS). CARRETTO's *Isurus oxyrinchus hataalis* should be revised *I. hastalis*.

Isurus cf. *paucus* Guitart-Monday

pl. 10, fig. 2.

Description:

The specimen obtained is the right lower second anterior tooth only. The crown is elongated, very slightly oblique and flexuous. The both cutting edges reach the tooth cervix. The plications are observed on central base of the labial face. The tooth cervix, colored in dark brown, is obviously. The root is bifurcated and extended radially. The mesial root is longer than the distal one. The central protuberance is recognized distinctly. The central groove and nutritive foramen are observed.

Comparing this specimen with living *Isurus paucus*, fossil teeth have relatively

shorter and thicker root. It is possible to consider that their difference is ontogenetic change.

Remarks:

UYENO *et al.* (1974) made a description of *I. cf. paucus* from Tamagusuku-mura, Okinawa Island. The specimens have more robust crown, and the central protuberance is more projecting than *I. oxyrinchus*. The latter character contradicts my observation of young specimens of *I. paucus* (KUGA, 1980MS).

Horizon:

This specimen is obtained from the Pliocene bed. There is no sufficient information about the occurrence and range of this species.

Genus *Uyenoa*, n. gen.

Etymology:

Named in honor of Dr. Teruya UYENO, eminent ichthyologist.

Diagnosis:

Crowns of laterals very thick, broad bases and absent of sub-cusps and serrations; tooth cervix wide and chevron in shape; roots thick, extended radically.

Type species: *Oxyrhina benedeni* LE HON

Remarks:

The dental morphology of this species differs from *Isurus* by having wide, chevron shaped tooth cervix and much radically extended root. Judging from its tooth cervix morphology, this species does not belong to the *Lamna-Isurus* lineage, but includes the *Cretolamna-Procarcharodon* lineage of Casier (1960).

Uyenoa benedeni (LE HON)

pl. 10, fig. 3, pl. 11, figs. 1, 2.

1871. *Oxyrhina benedeni* LE HON: Preliminaire d'un Memoire sur les poissons tertiaires de Belgique, p. 6.
1888. *Oxyrhina vonhaastii* DAVIS: *Sci. Trans. Royal Dublin soc.*, vol. 4, no. 2, pp. 26–27, pl. 4, figs. 1–3.
1894. *Oxyrhina crassa*: WOODWARD. *Geol. Mag.* dec. IV, vol. 1, pp. 75–76.
1910. *Oxyrhina benedeni*: LERICHE. *Mus. Roy. D'Hist. Nat. Belgique*, Tome 5, pp. 281–283.
1959. *Oxyrhina benedeni*: DARTVILLE and CASIER. *Ann. Mus. Roy. Congo. Belge.*, A, Ser. III, tome III, Fas. 3., pp. 300–301, pl. 28, fig. 2.
1964. *Isurus benedictus* DAVIS: *African Assoc. Mar. Biol. Res. Oceanogr. Res. Inst.*,

- Rep.*, no. 10, pp. 11–12, text-fig. 11.
1972. *Isurus oxyrinchus hastalis*: CARETTO (in part). *Boll. Soc. Paleont. Italiana*, vol. 11, n. 1, pp. 42–51, tav. 7, figs. 3, 6–7.
1974. *Isurus moniwaensis* HATAI, MASUDA, and NODA: *Saito Ho-on Kai Mus. Res. Bull.*, no. 43, 10–20, pl. 2, figs. 20, 22.
1975. *Isurus* sp.: ITOIGAWA *et al.* *Bull. Mizunami Fossil Mus.*, no. 2, p. 92, p. 22, fig. 11.
1977. *Isurus moniwaensis*: KATTO, SAKO and HATAI. *Res. Rep. Kochi Univ.*, vol. 25, no. 12, p. 103, pl. 1, figs. 10–11.

Diagnosis: as for genus

Description:

The upper anterior and intermediate teeth are not discovered in my materials.

The crown of the lower anterior tooth is elongate and thick. The lingual face is very strongly convex. The labial face is slightly convex. The tooth cervix is wide groove on lingual face and chevron in shape as in *Otodus* and *Procarcharodon*. The root is robust, thick, bifurcated and extended radically. The central protuberance is markedly developed. The lower anterior tooth of this species is similar to those of *Isurus hastalis*, but distinguished by having more thicker crowns, wider tooth cervix and more developed central protuberance of the root.

The crown of the upper lateral tooth is very thick, wide, and remarkably curved distally. The lingual face of the crown is very strongly convex. The labial face is very slightly convex. The mesial cutting edges of the crown strongly convex. The distal edge is deeply concave. The plications are recognized on cervical base of the labial face. The tooth cervix on lingual face is wide groove and chevron as in the lower anterior tooth. The root is thick, wide and obviously bifurcated. The apex of the root is round.

The lower lateral teeth are subangular. The crowns of the lower laterals are narrower and thicker than that of the upper lateral tooth. Other characters agree with that of the upper lateral tooth.

Remarks:

HATAI *et al.* (1974) described *I. moniwaensis* from the Miocene Moniwa Formation. I examined the type specimen stored in Saito Ho-on Kai Museum. The characters of *I. moniwaensis* completely agree with the upper lateral tooth of *I. benedeni*. Therefore, *I. moniwaensis* is synonymous to *I. benedeni*.

Fossils of *I. sp.* reported by GOTO *et al.* (1978) include 44 teeth and numerous dermal denticles. They appear to belong to single individual on the basis of their condition of occurrence. One of these teeth has triangular, very thick crown and

its width is approximately as broad as high. In consequence, they are considered to be *U. benedeni*. It is possible to reconstruct the tooth row of this species. Further study on the specimens is desirable.

Occurrence:

This species is seldom found in the Japanese Tertiary deposits. But in the Central Pacific Sea bottom, many fossil *Uyenoa* were discovered with manganese nodule (Kuga and Usui, 1982). KUGA and USUI (1982) discussed that it might be a epipelagic shark as recent *Isurus oxyrinchus* because of their abundant occurrence in the Central Pacific Sea bottom.

Horizon:

Except above-mentioned localities, two strata are known. One is the Pliocene Tomioka Formation in Hirono-cho, Fukushima Prefecture (HASHIMOTO and KOUHA, 1979). Another is the late Early-early Middle Miocene Kumano Group in Kushimoto-cho, Wakayama Prefecture. (KATTO *et al.*, 1975). In consequence geological distribution of this species is from late early Eearly Middle Miocene (KATTO *et al.*, 1975) to Upper Pliocene (Naarai Formation, this paper) in Japan.

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Explanations of Plates

Plate 1

Isurus desori (Agassiz)

- Fig. 1. Upper 1st anterior tooth, NSMT-PV 16867, Misato-mura, Age-gun, Mie Prefecture Ichishi Group (Middle Miocene).
- Figs. 2 and 3. Upper 1st anterior teeth. MFM collection, Mizunami City, Gifu Prefecture Mizunami Group (late Early to early Middle Miocene).
- Fig. 4. Upper 2nd anterior tooth, NSMT-PV 16870, Misato-mura, Age-gun, Mie Prefecture Ichishi Group (Middle Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 2

Isurus desori (Agassiz)

- Figs. 1–3. Upper 2nd anterior teeth.
- Fig. 4. Intermediate tooth.
- Figs. 5–7. Lower anterior teeth.
MFM collection, Mizunami City, Gifu Prefecture, Mizunami Group (late Early to early Middle Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 3

Isurus desori (Agassiz)

- Figs. 1, 2. Lateral teeth, NSMT-PV 16865 (Fig. 1) and NSMT-PV 16869 (Fig. 2), Misato-mura, Age-gun, Mie Prefecture, Ichishi Group (Middle Miocene).
- Figs. 3–8. Lateral teeth, MFM collection, Mizunami City, Gifu Prefecture, Mizunami Group (late Early to early Middle Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 4*Isurus planus* (Agassiz)

- Fig. 1. Upper anterior tooth, DGSU-T 582, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).
 Fig. 2. Lower anterior tooth, DGSU-T 580, Kagami, Shinji-cho, Shimane Prefecture, Fujina Formation (Late Miocene).
 Fig. 3. Lower anterior tooth, DGSU-T 603, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).
 Figs. 4, 5. Lateral teeth, DGSU-T598 (Fig. 4), DGSU unnumbered specimen (Fig. 5), Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 5*Isurus planus* (Agassiz)

- Fig. 1. Lateral tooth, DGSU unnumbered specimen, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).

Isurus hastalis (Agassiz)

- Fig. 2. Upper anterior tooth, NK 423, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).
 Fig. 3. Upper anterior tooth, HT collection, Misato-mura, Age-gun, Mie Prefecture, Ichishi Group (Middle Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 6*Isurus hastalis* (Agassiz)

- Fig. 1. Upper anterior tooth, MFM collection, Mizunami City, Gifu Prefecture, Mizunami Group (late Early to early Middle Miocene).
 Fig. 2. Upper anterior tooth?, DGSU-T 577, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).
 Fig. 3. Upper anterior tooth?, KU unnumbered specimen, Iwasaki-mura, Nishitsugaru-gun, Aomori Prefecture, Tanosawa Formation (Middle Miocene).
 Fig. 4. Upper anterior tooth?, HMH 44619-2, Hatsune Mine, Kitahiyama-cho, Setana-gun, Hokkaido, Babagawa Formation (Middle Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 7*Isurus hastalis* (Agassiz)

- Fig. 1. Upper lateral tooth, MG collection, Hanawa-cho, Higashishirakawa-gun, Fukushima Prefecture, Higashitanagura Group (Middle Miocene).
 Figs. 2, 3. Upper lateral teeth, DGSU-T 573 (Fig. 2), DGSU-T574 (Fig. 3), Fujina Formation, Kimachi Member (Late Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 8*Isurus hastalis* (Agassiz)

- Figs. 1-4. Upper lateral teeth, MFM collection, Mizunami City, Gifu Prefecture, Mizunami Group (late early to early Middle Miocene).
 Fig. 5. Upper lateral tooth, DGSU-T 620, Nogifukutomi-cho, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).
 Fig. 6. Lower anterior tooth, DGSU-T 576, Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 9*Isurus hastalis* (Agassiz)

- Fig. 1. Lower anterior tooth, KU unnumbered specimen, Iwasaki-mura, Nishitsugaru-gun, Aomori Prefecture, Tanosawa Formation (Middle Miocene).
 Fig. 3. Lower lateral tooth, MG collection, Nishikatsura-cho, Tsuru-gun, Yamanashi Prefecture, Nishikatsura Group (Middle Miocene).
 Figs. 4, 5, 7. Lower lateral teeth, MFM collection, Mizunami City, Gifu Prefecture, Mizunami Group (late Early to Middle Miocene).
 Figs. 6, 8. Lower lateral teeth, DGSU-T 601 (Fig. 6), DGSU-T 602 (fig. 8), Ichinotani, Matsue City, Shimane Prefecture, Fujina Formation (Late Miocene).

a: labial face, b: lingual face, c: mesial view

Plate 10*Isurus oxyrinchus* (Agassiz)

- Fig. 1. Lower anterior tooth, NK 21, Hirono-cho, Futaba-gun, Fukushima Prefecture, Tomioka Formation (Pliocene).

Isurus cf. paucus

- Fig. 2. Upper anterior tooth, NK 363, Saito City, Miyazaki Prefecture, Miyazaki Group (Pliocene).

Uyenoa benedeni (Le Hon)

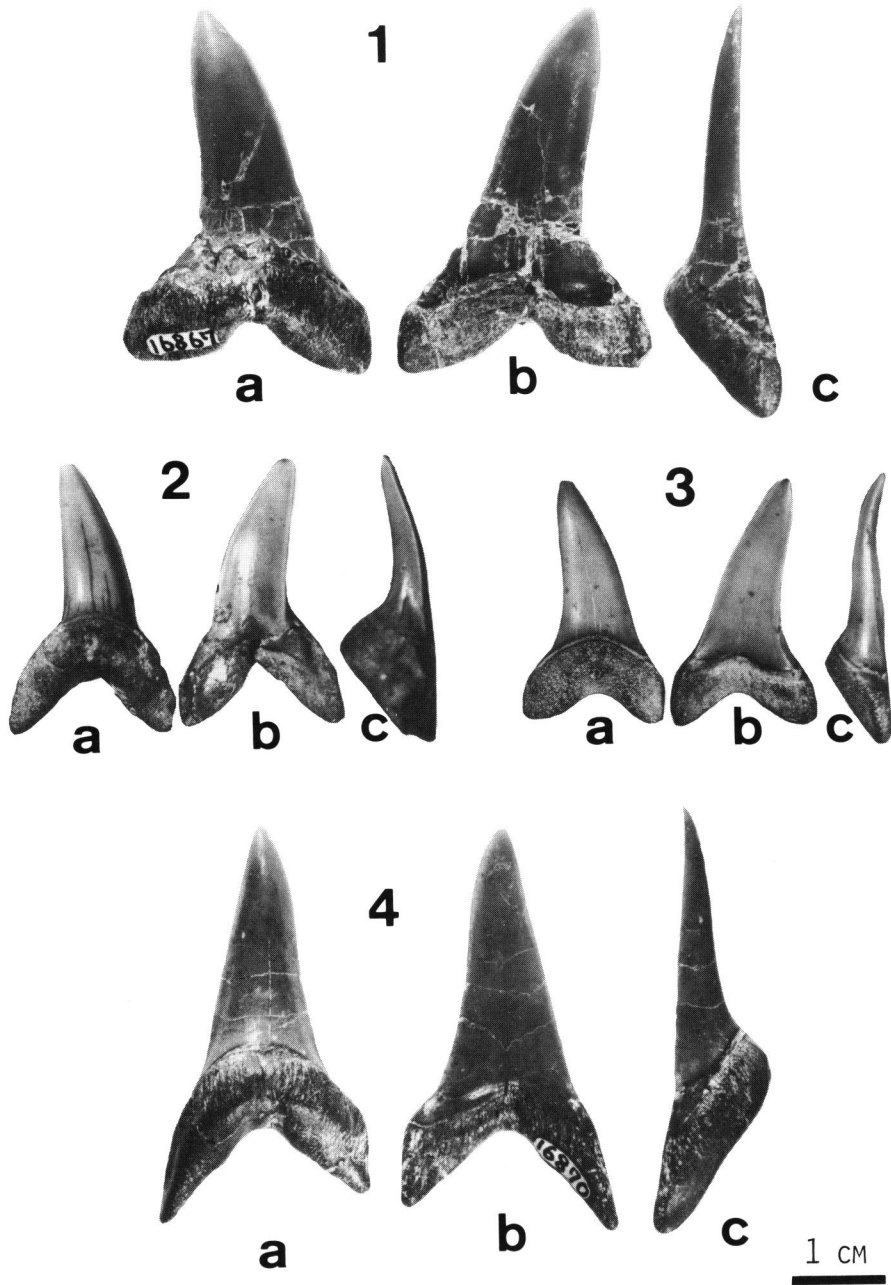
- Fig. 3. Lower anterior tooth, MFM collection, Okuna, Mizunami City, Gifu Prefecture, Mizunami Group Oidawara Formation, (early Middle Miocene).

a: labial face, b: lingual face, c: mesial view

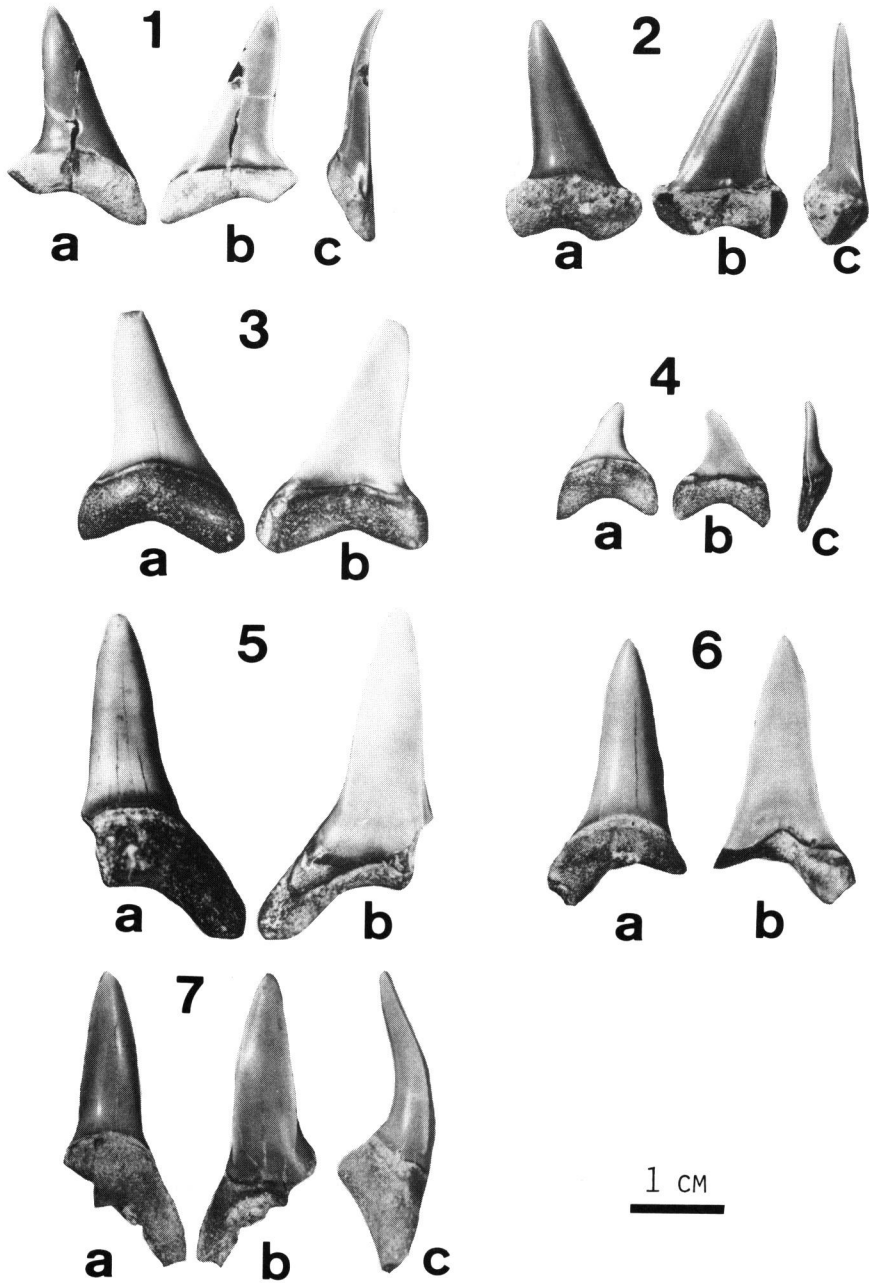
Plate 11*Uyenoa benedeni* (Le Hon)

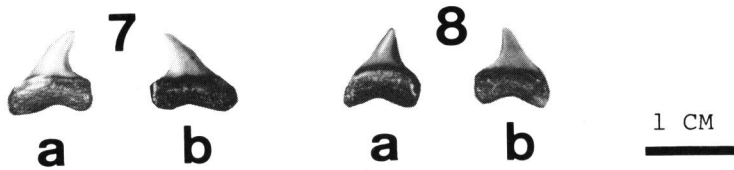
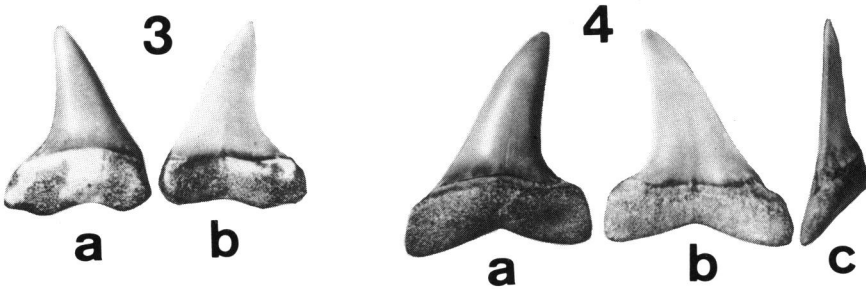
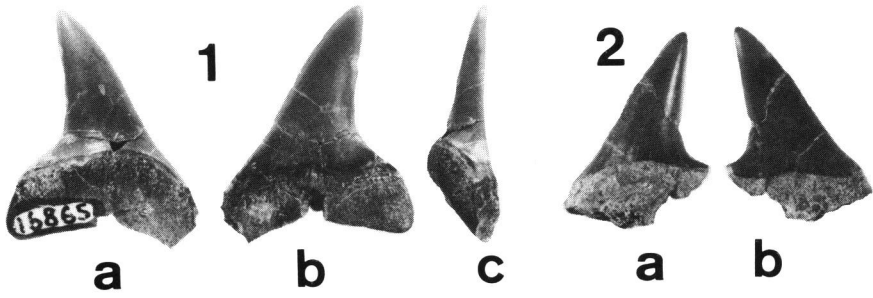
- Fig. 1. Lower lateral tooth, OPM-GF195, Tomigusuku-mura, Okinawa Prefecture, Shimajiri Group (Late Miocene to Pliocene).
 Fig. 2. Upper lateral tooth, SHKM unnumbered specimen, Akaishi, Sendai City, Miyagi Prefecture, Moniwa Formation (Middle Miocene).

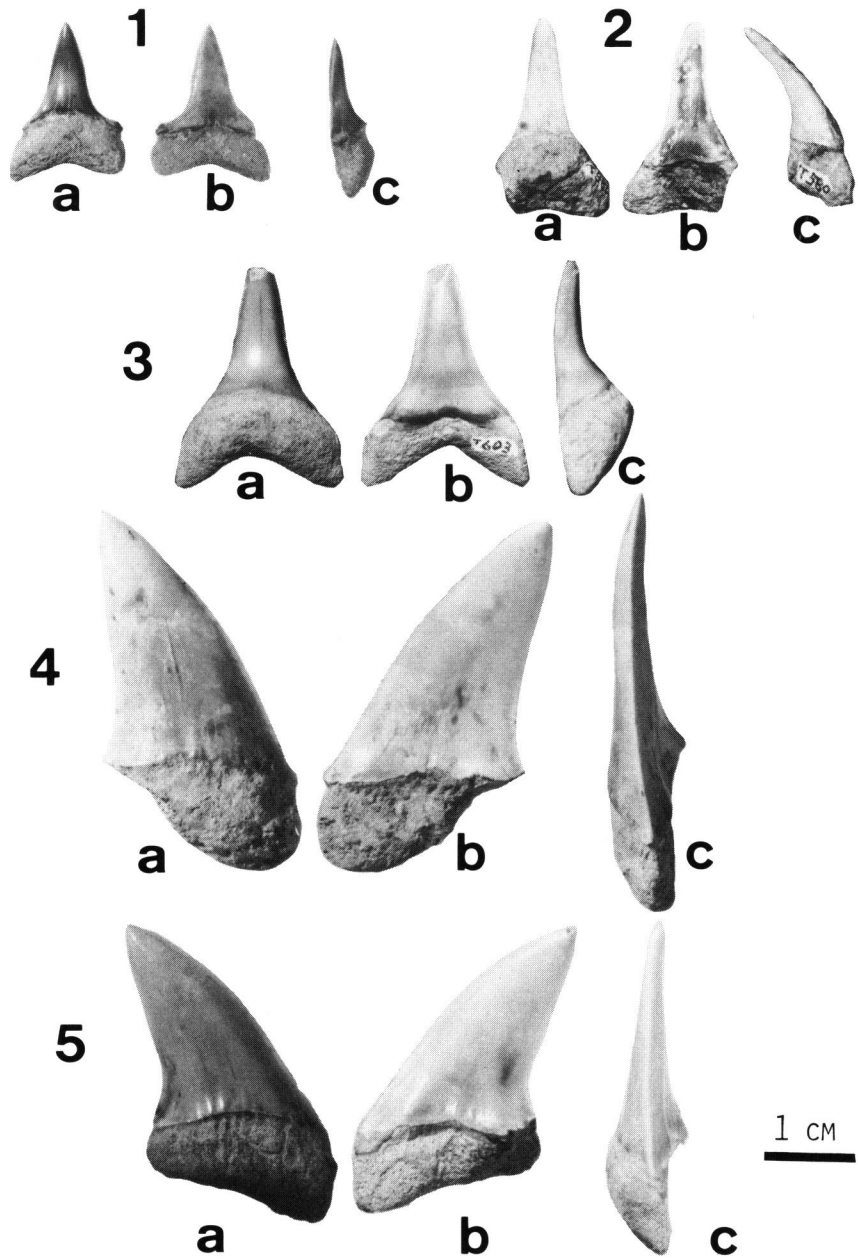
a: labial face, b: lingual face, c: mesial view

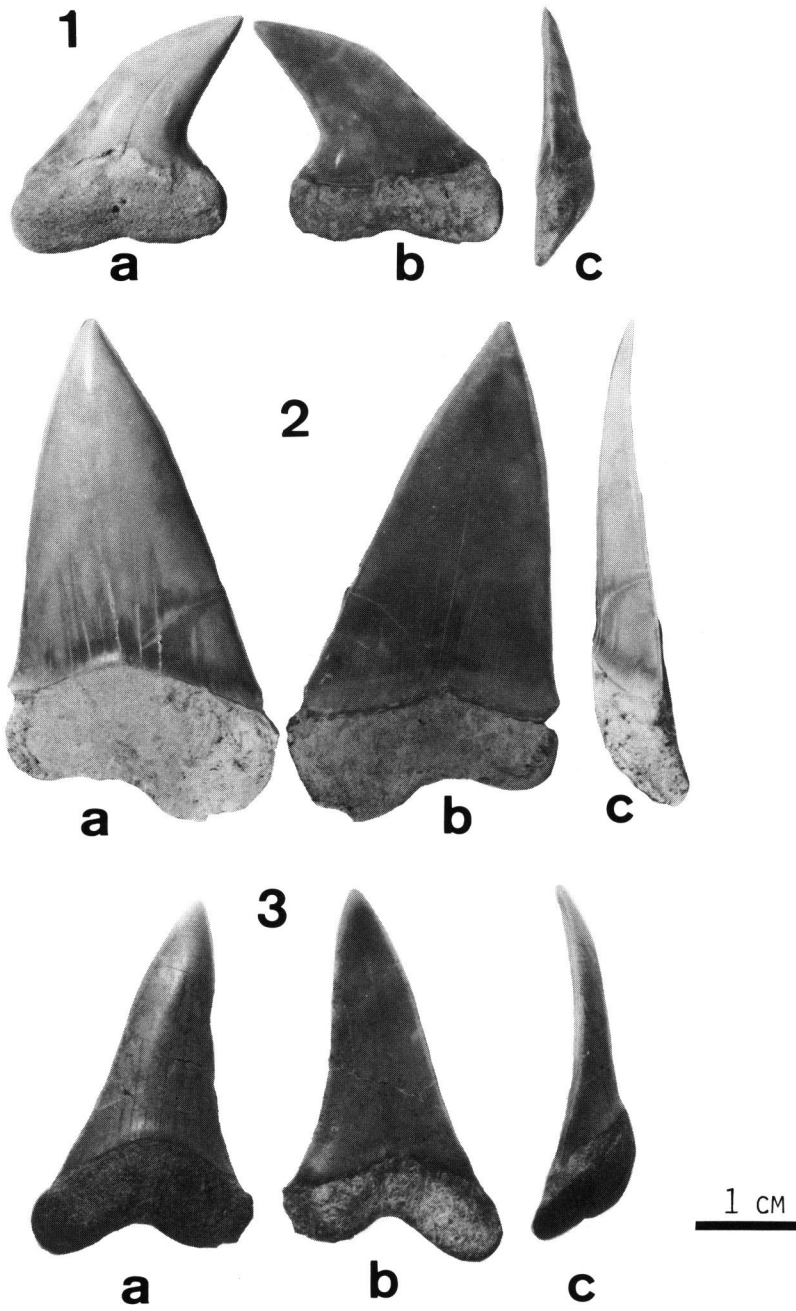


KUGA: Neogene Mackerel Shark Genus *Isurus*

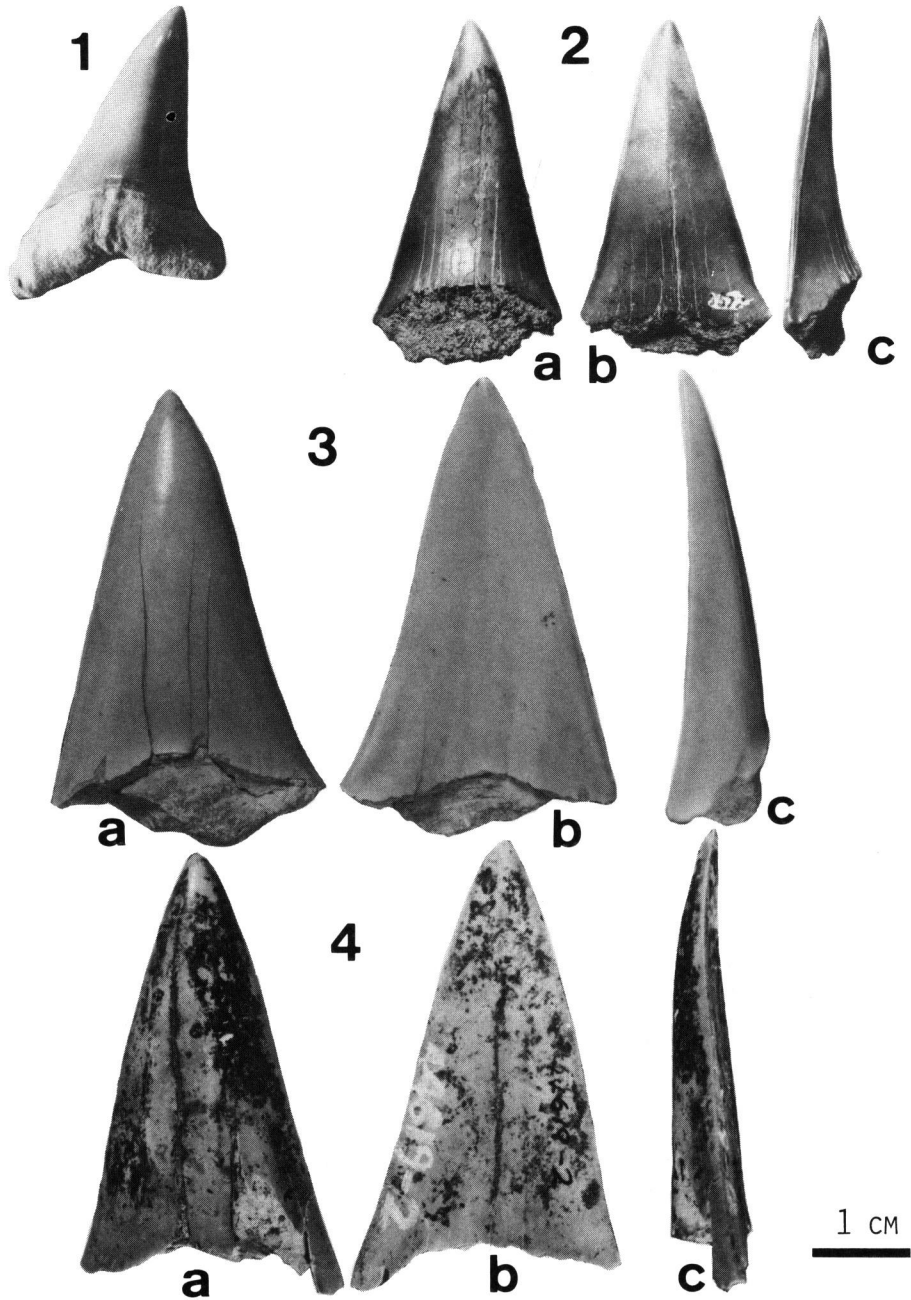




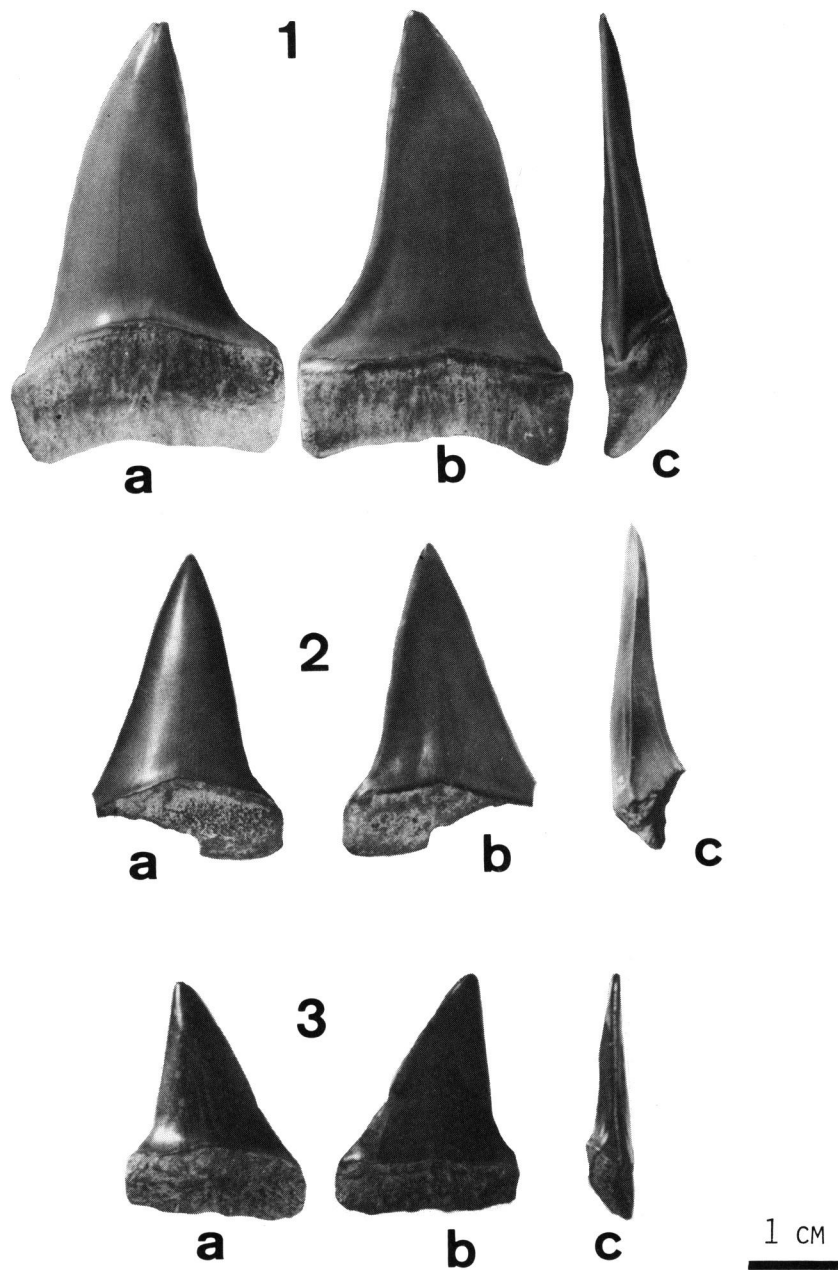


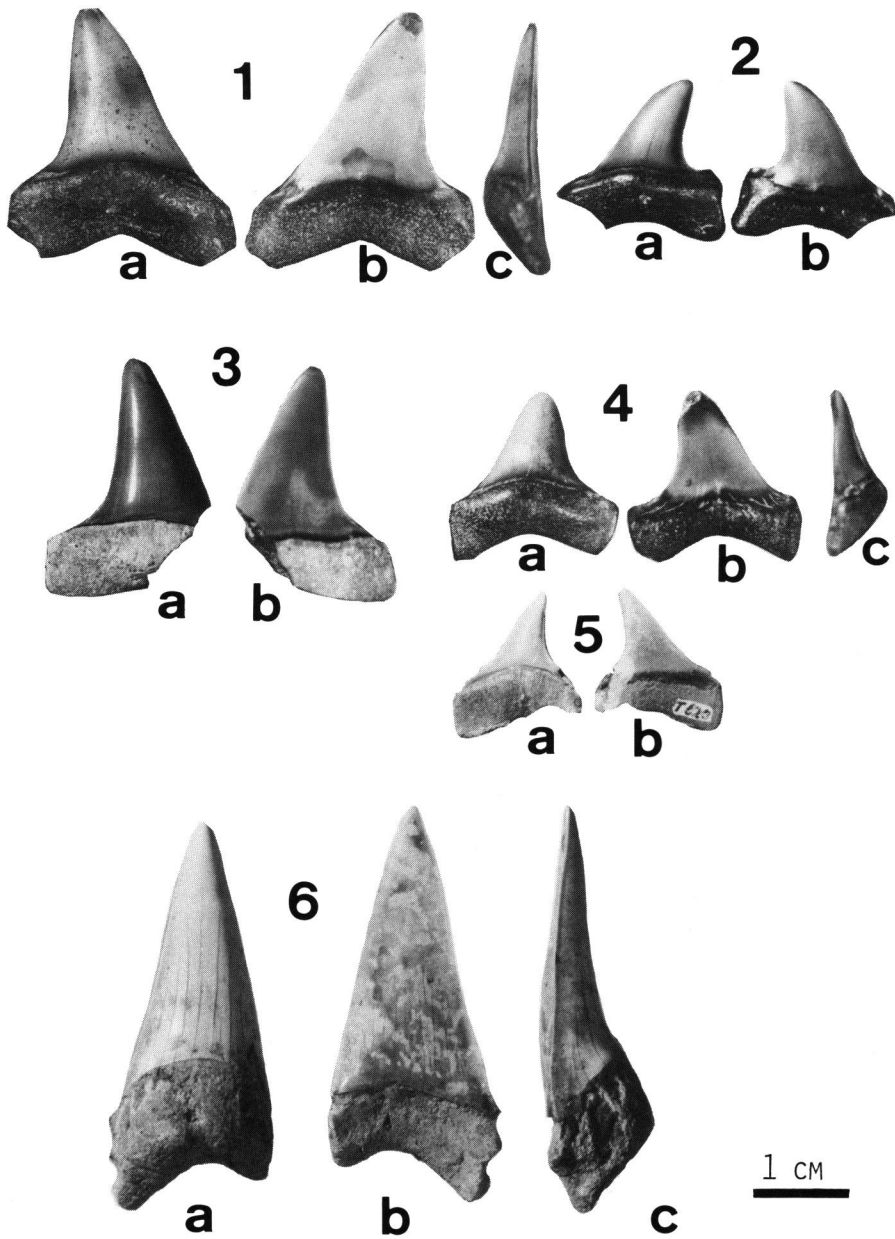


KUGA: Neogeue Mackerel Shark Genus *Isurus*

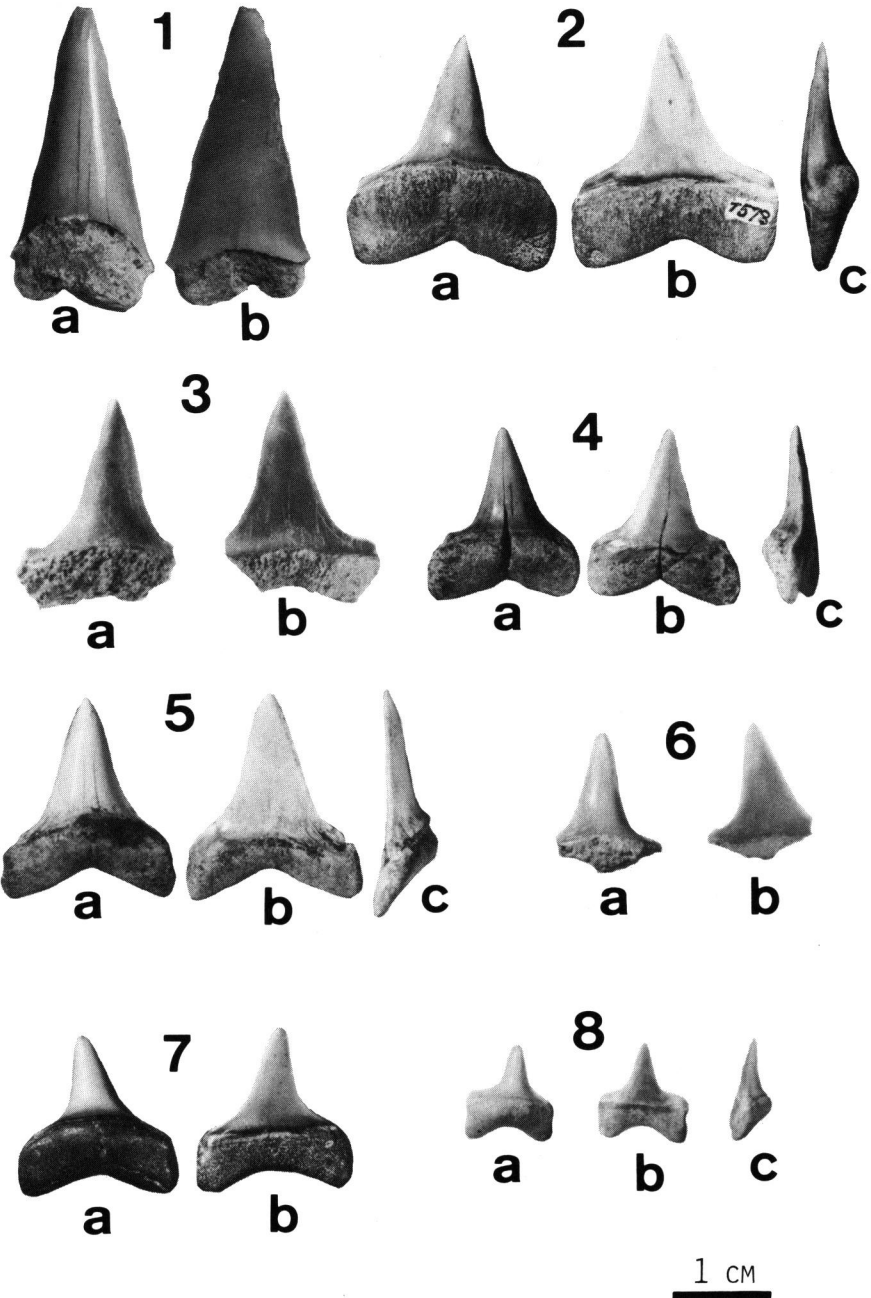


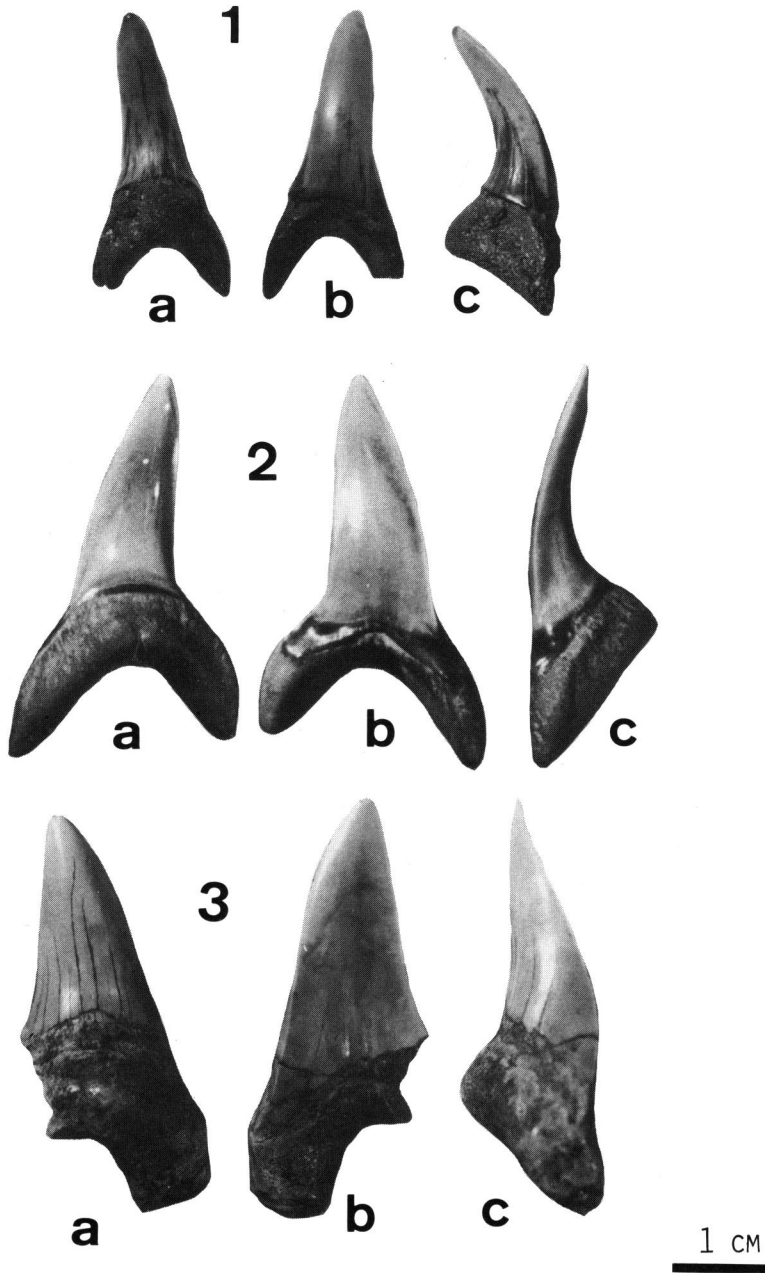
KUGA: Neogene Mackerel Shark Genus *Isurus*



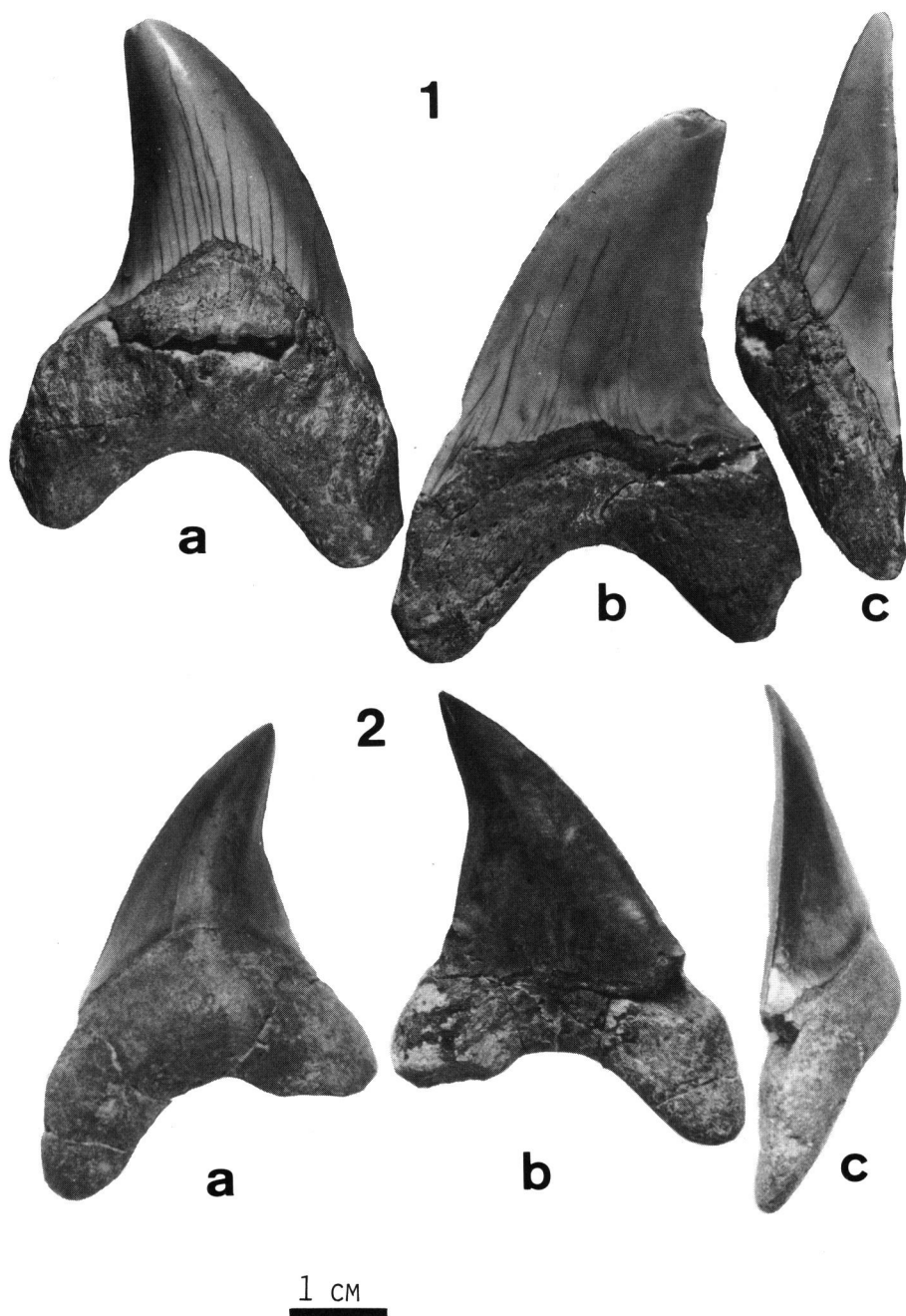


KUGA: Neogene Mackerel Shark Genus *Isurus*





KUGA: Neogene Mackerel Shark Genus *Isurus*



KUGA: Neogene Mackerel Shark Genus *Isurus*