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I. Introduction

Billfishes (sailfish, spearfish, marlin and swordfish) of the superfamily Xiphiidae (order Perciformes), like tunas, are highly migratory, oceanic fishes which

1) A dissertation submitted to the Faculty of Agriculture, Kyoto University in partial fulfillment of the requirements for the degree of Doctor of Agriculture.

live primarily in tropical and temperate seas and are very important throughout the world as sportfishes and as commercial fishes for fresh and processed foods. They have a high economic value, especially in Japan. There are a variety of fishing methods which have been developed for billfishes and these include longlining, trolling, harpooning, set netting etc. Of the commercial fisheries, surface longline fishing is the most important. Over the past twenty years, the longline fishing grounds have gradually developed by Japanese, Taiwanese and Korean longline fishing fleets ranging from the Pacific Ocean to the Indian and Atlantic oceans. Consequently, as longline fishing for tuna and billfish has assumed greater international importance, problems of control of fisheries have developed between fishing countries and coastal countries, as well as amongst fishing countries themselves. In order to discuss management of the resources, it is first necessary to have complete statistical data. However, the names (including the scientific names) which are used in each country for the different species in this group vary considerably and there has been, up to the present time, no complete compilation of data. Systematic research has been carried out all over the world for a relatively long period of time, but because of the large size of the fish and their high price, it has been very difficult to obtain sufficient samples for study. Until now, research has been limited to those specimens that could be taken from the waters adjacent to the scientist’s own country, and there has not been a large-scale, direct comparison of specimens from different parts of the oceans. Therefore, variations between individuals are often taken as species differences. Because of the lack of agreement on the classification of this group of fishes, too many species have been described which now makes the problem even more complicated. In spite of a remarkable change in form during growth of these fishes, there is a serious lack of information regarding this change and their life histories. Those have made the problem more difficult.

Research on tunas was in a similar situation to that of billfishes some 20 years ago, and consequently an FAO-sponsored World Tuna Meeting was held in La Jolla, California in 1962, where it was decided to promote a world-wide review of the taxonomy of tunas (Rosa, 1963). Three centres (US National Museum, Department of Fisheries of Kyoto University and Muséum National d’Histoire Naturelle) were appointed to carry out this review. The results of this research on tunas were published by Iwai, Nakamura and Matsubara (1965) and by Gibbs and Collette (1965). Subsequently the same kind of research was deemed necessary on billfishes and the results of this research were presented by Nakamura, Iwai and Matsubara (1968). The present study is based primarily on this latter work, but is discussed more from the phylogenetic point of view. As a result, the billfishes which belong to the superfamily Xiphiicae based on Matsubara’s classification (1955) can be classified as follows:

**Superfamily Xiphiicae**

**Family Xiphiidae**

**Genus Xiphias** Linnaeus, 1758
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Xiphias gladius Linnaeus, 1758

Family Istiophoridae

Genus Istiophorus Lacepède, 1803
Istiophorus platypterus (Shaw and Nodder, 1792)
Istiophorus albicans (Latreille, 1804)

Genus Tetrapturus Rafinesque, 1810
Tetrapturus angustirostris Tanaka, 1915
Tetrapturus belone Rafinesque, 1810
Tetrapturus pfluegeri Robins and de Sylva, 1963
Tetrapturus georgei Lowe, 1840
Tetrapturus albidus Poey, 1860
Tetrapturus audax (Philippi, 1887)

Genus Makaira Lacepède, 1803
Makaira mazara (Jordan and Snyder, 1901)
Makaira nigricans Lacepède, 1802
Makaira indica (Cuvier, 1832)

As for Tetrapturus georgei, I have not had the opportunity to study any specimens directly except for the skin imbedded with scales. I therefore tentatively include it in the systematic list and the key, and give a brief description of it based on Robins (1974) for the convenience of comparison with the other species.

II. Materials and methods

Abbreviations used for the institutions cited are as follows:
AMNH: American Museum of Natural History, New York, U.S.A.; AMS: Australian Museum, Sydney, Australia; ANSP: Academy of Natural Sciences, Philadelphia, U.S.A.; BMNH: British Museum (Natural History), London, United Kingdom; BPBM: Bernice P. Bishop Museum, Honolulu, U.S.A.; CAS: California Academy of Sciences, San Francisco, U.S.A.; FAKU: Department of Fisheries, Faculty of Agriculture, Kyoto University, Kyoto, Japan; FRSKU: Fisheries Research Station, Kyoto University, Maizuru, Japan; FSFRL: Far Seas Fisheries Research Laboratory, Shimizu, Japan; LACM: Los Angeles County Museum of Natural History, Los Angeles, U.S.A.; MNHN: Museum National d'Histoire Naturelle, Paris, France; MSNG: Museo Civico di Storia Naturale, Genova, Italy; MZUT: Museo Zoologico, Universita, Torino, Italy; NRFRL: Nankai Regional Fisheries Research Laboratory, Kochi, Japan (in 1967 the name was changed to NSRFRL and the Division of "Tunas and Billfishes" moved to FSFRL); NSRFRL: Nansui Regional Fisheries Research Laboratory, Kochi, Japan; QMB: Queensland Museum, Brisbane, Australia; ROM: Royal Ontario Museum, Toronto, Canada; SIO: Scripps Institution of Oceanography, La Jolla, U.S.A.; SMF: Senckenberg Museum, Frankfurt am Main, West Germany; UMML: Marine Biological Laboratory, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, U.S.A.; USNM: United States National Museum, Washington D.C., U.S.A.

For brevity, the following abbreviations are used:
D1: First dorsal fin rays; D2: Second dorsal fin rays; A1: First anal fin rays; A2: Second anal fin rays; P1: Pectoral fin rays; P2: Pelvic fin rays; GR: Gill-rakers; BS: Branchiostegals; V: Vertebrae; BL: Body length (tip of lower jaw to caudal fork); EF: Eye-fork length (posterior of eye-orbit to caudal fork); TL: Total length (tip of bill to posteriormost point of caudal fin); BW: Body weight.
Billfish materials used for this study were obtained chiefly by R.V. Shoyo Maru, R.V. Toko Maru and R.V. Shunyo Maru from the Atlantic, Indian and Pacific oceans during the past 20 years. Some other materials were purchased through the courtesy of the Nishimaizuru Fish Market of the Fisherman’s Cooperative of Kyoto Prefecture. Formalin-preserved specimens and skeletons are now deposited in the FRSKU, FAKU, FSFRL and NSRFRL. The materials measured and counted to describe each species are registered and listed in the description of each species. The materials used for Figures are mentioned in the explanation below them, where necessary. The register number in parentheses shows that the specimen was not now kept in our laboratories. The descriptions are based on adult specimens, unless otherwise specified. Other materials dissected (including partial dissection), or used for osteological study only are as follows:

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Xiphias gladius: 28 specimens (870–2390 mm BL); northwestern Pacific (16), Japan Sea (2), southeastern Pacific (3), central Pacific (4), South Pacific (2), Indian Ocean (1). Istiophorus platypterus: 225 specimens (710–1830); northwestern Pacific (7), Japan Sea (207), southeastern Pacific (4), western Indian Ocean (7). Istiophorus albicans: 31 specimens (1260–1710); central Atlantic (7), South Atlantic (5), Caribbean Sea (19). Tetrapturus angustirostris: 11 specimens (1170–1490); northwestern Pacific (5), southeastern Pacific (4), eastern Indian Ocean (2). Tetrapturus pfitzneri: 41 specimens (1280–1580); central Atlantic (20), southwestern Atlantic (6), Caribbean Sea (15).

Methods of measuring are shown in Fig. 1 and counts were taken in accordance with Rivas (1956a). The bone structure was examined after the flesh had been removed and the fat dissolved with benzine. For more detailed examination of bone structure, specimens were first cleared and stained with alizarin red and then examined.

Standard names of English and Japanese (in quotation marks) are listed in each description of species, because of their importance in fisheries.

III. Systematics

There have been many studies on the billfishes up to this time, so only comprehensive systematic studies are mentioned here. The history of study on these species goes back to the original description by Linnaeus of Xiphias gladius as Xiphias Gladius in the tenth edition of his work, Systema Naturae (1758). Subsequently, species of billfishes have been described as new to science from the eighteenth to the twentieth centuries as follows: Istiophorus platypterus as Xiphias platypterus by Shaw and Nodder in 1792; Makaira nigricans by Lacepède in 1802; Istiophorus albicans as Makaira albicans by Latreille in 1804; Tetrapturus belone by Rafinesque in 1810; Makaira indica as Tetrapturus indicus by Cuvier in 1832; Tetrapturus georgei as Tetrapturus Georgii by Lowe in 1840; Tetrapturus albidus by Pocé in 1860; Tetrapturus audax as Histiophorus audax by Philippi in 1887; Makaira mazara as Tetrapturus mazara by Jordan and Snyder in 1901; Tetrapturus angustirostris by Tanaka in 1915; Tetrapturus pfitzneri by Robins and de Sylva in 1963. These scientific names, however, have not been consistently used; the generic names have varied and the species names also have been changed through the years. Furthermore, regional studies have been carried out in many parts of the world and new genera and species have been described from time to time, and the classification of billfishes has become more complicated year by year.

Goode (1882, 1883) finally classified the billfishes of the world into one family, 2 subfamilies, 4 genera and 17 species. Jordan and Evermann (1926) divided the same group into 2 families, 4 genera and 32 species. LaMonte and Mercy (1941)
reexamined the billfishes and recognized 4 genera, 13 species and 4 subspecies, while Rosa (1950) recognized 4 genera, 15 species and 4 subspecies. Nakamura et al. (1968) and Nakamura (1974) classified the billfishes of the world into 2 families, 4 genera and 11 species and outlined the history of the systematic study and the confusion of classification of billfishes in detail.

The following key has been devised for the billfishes and is based mainly on external characters for convenience as a field guide. The key, however, has also taken account of some important internal characters in order to clarify presumably phylogenetic relationships of the fishes. When using the key, reference should be made to the illustrations and explanations for the key characters shown in Fig. 2.

![Fig. 2. Schematic external appearance of billfishes. Figures to the left of each species shown cross-sectional view of bill. Figures to the right of each species shown cross-sectional view of bodies taken at the base of pectoral fin. Arrows show the important points used in the key. A: Xiphias gladius; B: Istiophorus platypterus; C: Istiophorus albicans; D: Tetrapturus angustirostris; E: Tetrapturus belone; F: Tetrapturus pfluegeri; G: Tetrapturus georgei; H: Tetrapturus albidus; I: Tetrapturus audax; J: Makaira mazara; K: Makaira nigricans; L: Makaira indica.

Key to families, genera and species of adult billfishes

1a. No pelvic fin. A single caudal keel on side. Snout long and swordlike in shape and depressed in cross-sectional view. No scales on body. No teeth on jaws. Base of first dorsal fin short and well separated from base of second
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dorsal fin. Vertebrae 26 (Xiphiidae, Xiphias).................................
1b. Pelvic fin present. A pair of caudal keels on each side. Snout somewhat shorter and nearly rounded in cross-sectional view. Body covered with small elongate bony scales (Fig. 3). Many small teeth on jaws. Base of first dorsal fin long and close to base of second dorsal fin. Vertebrae 24 (Istiophoridae), Fig. 2 B–L ............................................................... 2

2a. First dorsal fin remarkably higher than body depth at level of mid-body. Pelvic fin rays very long with well developed membrane (Istiophorus), Fig. 2 B, C ............................................................... 3

2b. First dorsal fin only slightly higher to slightly lower than body depth at level of mid-body, not sail-like in shape. Pelvic fin rays not as long, with moderately developed membrane, Fig. 2 D–L ............................................................... 4

3a. Pectoral fin and caudal fin short in specimens of about 90 cm body length. Attains greater size (about 100 kg BW) than Atlantic sailfish (about 60 kg BW). Indo-Pacific Ocean ............................................................... Indo-Pacific sailfish, Istiophorus platypterus, Fig. 2B

3b. Pectoral fin and caudal fin long in specimens of about 90 cm body length. Attains smaller size than Indo-Pacific sailfish. Atlantic Ocean ............................................................... Atlantic sailfish, Istiophorus albicans, Fig. 2C

4a. Height of anterior part of first dorsal fin slightly higher than or nearly equal to body depth. Body well compressed. Nape (external margin of head between preorbital and origin of first dorsal fin) slightly elevated or not elevated. Vertebrae 12+12 (Tetrapturus), Fig. 2 D–I ............................................................... 5

4b. Height of anterior part of first dorsal fin lower than body depth. Body not compressed. Nape highly elevated. Vertebrae 11+13 (Makaira), Fig. 2 J–L ........................................................................................................ 10

5a. Anterior fin rays of first dorsal fin slightly higher than the remainder, later nearly equal in height to end of the fin. Anus situated far anterior to first anal fin origin; the distance between them greater than height of first anal fin, Fig. 2 D–F .......................................................................................... 6

5b. Anterior fin rays of first dorsal fin somewhat higher than remainder of the fin; the height decreasing gradually posteriorly. Anus situated near origin of first anal fin; the distance between them smaller than height of first anal fin, Fig. 2 G–I .......................................................................................... 8

6a. Bill short; bill length usually shorter than head length. Pectoral fin narrow and short, less than 18% of BL, Fig. 2 D, E .......................................................................................... 7

6b. Bill long, bill length usually equal to or longer than head length. Pectoral fin wide and long, more than 18% of BL ........................................................................................................ Longbill spearfish, Tetrapturus fluegleri, Fig. 2 F

7a. Bill very short, less than 15% of BL ........................................................................................................ Shortbill spearfish, Tetrapturus angustirostris, Fig. 2 D

7b. Bill moderately short, about 18% of BL ........................................................................................................ Mediterranean spearfish, Tetrapturus belone, Fig. 2 E
8a. Tip of first dorsal fin and first anal fin round, Fig. 2 G, H .................. 9
8b. Tip of first dorsal fin and first anal fin pointed ........................................ Striped marlin, *Tetrapturus audax*, Fig. 2 I
9a. First dorsal fin unspotted. Scales on mid-body soft and round-shape (Fig. 3 G) .................. Roundscale spearfish, *Tetrapturus georgei*, Fig. 2 G
9b. First dorsal fin spotted. Scales pungent, each elongate with one or two points (Fig. 3 H) .............. White marlin, *Tetrapturus albidus*, Fig. 2 H
10a. Pectoral fin can be folded back against side of body, Fig. 2 J, K .................... 11
10b. Pectoral fin rigid; cannot be folded back against side of body .................................. Black marlin, *Makaira indica*, Fig. 2 L
11a. Lateral line system with simple loops .......................................................... Indo-Pacific blue marlin, *Makaira mazara*, Fig. 2 J
11b. Lateral line system reticulated ........................................................................... Atlantic blue marlin, *Makaira nigricans*, Fig. 2 K

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Fig. 3. Schematic illustration of the arrangement of scales in billfishes (patch 30 x 30 mm from right side behind tip of pectoral fin). A: *Xiphias gladius*, 87 cm BL, northwestern Pacific (scales disappear in adult); B: *Istiophorus platypterus*, 195 cm BL, Japan Sea; B*: *Istiophorus platypterus*, 89 cm BL, Japan Sea; C: *Istiophorus albicans*, 182 cm BL, Caribbean Sea; D: *Tetrapturus angustirostris*, 155 cm BL, northeastern Pacific; E: *Tetrapturus belone*, 172 cm BL, Straits of Messina (CRR-Med-11); F: *Tetrapturus pfluegeri*, 131 cm BL, Caribbean Sea; G: *Tetrapturus georgei*, 157 cm BL, Cape of Santa Maria, Portugal (UMML 11076); H: *Tetrapturus albidus*, 162 cm BL, Caribbean Sea; I: *Tetrapturus audax*, 171 cm BL, northwestern Pacific; J: *Makaira mazara*, 173 cm BL, northwestern Pacific; J*: *Makaira mazara*, ca. 110 cm BL, Japan Sea; K: *Makaira nigricans*, 176 cm BL, Caribbean Sea; L: *Makaira indica*, 184 cm BL, Japan Sea.
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Family Xiphiidae

Premaxilla and nasal elongate to form a long, pointed, depressed rostrum (usually called bill). Scales absent in adults. Branchiostegal membranes united to each other basally and free from isthmus. Pelvic fins and girdles absent. Jaws toothless in adults. Caudal peduncle in adult with single median keel on each lateral side and with a deep notch on both dorsal and ventral sides.

Genus Xiphias Linnaeus

Xiphias Linnaeus, 1758, System naturae, ed. X: 248 (Type-species: Xiphias gladius Linnaeus, by monotypy).


Xiphias gladius Linnaeus

(Fig. 4)

Swordfish, Broadbill swordfish, "Mekajiki"

Xiphias gladius Linnaeus, 1758
Xiphias Gladius Linnaeus, 1758, Systema Naturae, ed. X: 248 (Habitat in Oceano Europae).

Fig. 4. Swordfish, Xiphias gladius, FRSKU (JS 7810221), 1556 mm BL, Japan Sea.
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Xiphias imperator Bloch and Schneider, 1801, illustratum. Post obitum auctoris, 93, pl. 21 (Mediterranean Sea, based on young swordfish copied originally from Aldrovandi).


Xiphias Gradius: Kinder, 1838-1840: Danmarks Fiske. 253-262, 1 fig. 596 (Europe, ? misprint of Xiphias gladius).


Phaethonichthys tuberculous Nichols, 1923, Amer. Mus. Natr. Hist., Novitates, 19 (94) :1-2, fig. 1 (Type-locality: Rapa Island, Austral Group, South Seas; a young swordfish 113 mm from front of anal to base of caudal, taken from gullet of a red-tailed tropic bird, Phaethon rubricaudus by R.H. Beck of the South Sea Expedition). Holotype: AMNH 8257.


Tetrapterus imperator: Riihl, 1942, Fauna descriptiva de Venezuela. 396, fig. 208 (Venezuela).

Xiphias thermaicus Serbetis, 1951, Prakt. Acad. Athen, 22:269-273, fig. 1 (Type-locality: Gulf of Thermaikos, Aegean Sea).


Xiphias estara: Whitley, 1964:244-245, pl. 3 (fig. a) (Australia and New Zealand; as a subspecies of Xiphias gladius based on Xiphias estara Phillipps, 1932, proposed by Whitley).


Diagnosis. Bill long and flat. No pelvic fins or girdles. A median caudal keel on lateral side of caudal peduncle; a deep notch on both dorsal and ventral profiles of caudal peduncle.

Description. Immatures (553-895 mm BL) followed by adults (1520-2538) in parentheses: D 1 34-49 (21-30); D 2 4-6 (3-4); A 1 13-14 (12-13); A 2 3-4 (3); P 1 16-18 (16-18); P 2 0 (0); GR 0 (0); BS 7 (7); V 16-10=26 or 15+11=26 (16+10=26 or 15+11=26).

Measurement expressed in percent of BL: eye-fork length 82.6-84.4 (85.1-87.5); first predorsal length 28.9-33.3 (22.5-27.0); second predorsal length 79.6-84.5 (78.2-82.0); prepectoral length 28.8-33.5 (23.9-26.6); first preanal length...
60.4–64.6 (57.3–59.0); second preanal length 78.2–81.4 (77.0–79.4); tip of mandible to anus 59.1–62.0 (56.1–56.9); greatest depth of body 15.4–19.3 (19.7–20.5); depth of body at origin of first dorsal 15.4–17.7 (19.7–20.0); depth of body at origin of first anal 11.0–13.1 (16.2–18.1); least depth of caudal peduncle 3.1–4.3 (3.9–4.4); width of body at origin of pectorals 7.2–10.8 (10.5–13.5); width of body at origin of first anal 5.4–9.7 (12.4–14.6); head length 29.9–33.5 (23.4–27.6); snout length 11.5–18.1 (6.7–9.5); bill length 49.9–56.3 (54.7–55.6); maxillary length 18.9–25.5 (12.7–17.8); orbit diameter 2.6–4.7 (2.6–4.3); interorbital width 7.4–8.3 (7.2–7.9); anterior height of first dorsal 20.0–26.0 (22.2–26.0); length of middle dorsal spine 2.4–9.4 (—); anterior height of second dorsal 4.2–6.3 (3.2–3.8); height of first anal 13.2–17.4 (12.5–16.3); anterior height of second dorsal 4.2–6.3 (3.2–3.8); height of first anal 13.2–17.4 (12.5–16.3); anterior height of second anal 3.0–5.8 (2.9–3.2); length of pectoral 22.9–25.2 (18.4–20.4); length of second dorsal base 2.4–3.8 (1.7–2.1); length of first anal base 16.2–18.4 (12.0–12.4); length of second anal base 2.4–3.3 (1.6–2.1).

Body elongate (BL about 5 times greatest body depth in adults, more than 5 times in immatures) and cylindrical in shape (BL about 8 times greatest body

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Fig. 5. Schematic drawings of changes of scales with growth in *Xiphias gladius* (A) and *Istiophorus platypterus* (B). A. top: 63 mm BL, Hawaii; middle: 234 mm BL, Hawaii; bottom: 876 mm BL, northwestern Pacific. B. top: 145 mm BL, Japan Sea; middle: 211 mm BL, Hawaii; bottom: 320 mm BL, Hawaii. Each scale indicates 1 mm.
width in adults, 10 times or more in immatures). Snout very elongate, forming long and flat bill (bill length about 2 times head length in adults, less than 2 times in immatures). Lower jaw considerably shorter than upper jaw (bill), but still projected a little. Maxilla tightly fused with premaxilla, nasal and frontal, therefore snout non-protractile. No predentary. Posterior margin of upper jaw beyond posterior margin of eye. Scales with small spines in specimens of about 1 m (Figs. 3A, 5A), but disappearing with growth in larger specimens. Lateral line indistinct, but recognizable on body of specimens more or less 1 m BL as a wavy-shaped line (Fig. 6A–C), disappearing with growth in larger specimens (Fig. 6D).

Fig. 6. Schematic drawings of swordfish, *Xiphias gladius* showing development of lateral line and scales. A: 23.4 cm BL, Hawaii; B: 52.8 cm BL, northwestern Pacific; C: 75.9 cm BL, northwestern Pacific; D: 156 cm BL, Japan Sea.

about 1 m BL with small file-shaped teeth that tend to disappear with growth. Head large (BL about more than 4 times of head length in adults, about 3 times in immatures). Nape not elevated. Both right and left branchiostegal membranes united only basally and free from isthmus. Eye large. Two nostrils close to each other in front of eye, anterior one round with a posterior flap and posterior one oval or slitlike shape. No gill rakers. Pseudobranchiae present. Pectoral fin fairly long (head length about 1.3 times pectoral length), located low on body; falcate and rather rigid fin extending in a downward and backward direction in a natural state. Anterior part of dorsal fin slightly higher than body depth, but height quickly
decreases and fin ends considerably in front of second dorsal fin in adults. Both first and second dorsal fins more continuous in immature specimens. Second dorsal fin small and about the same shape and size as second anal fin, the latter situated a little further forward than the former. First anal fin moderately large and wide sickle-like in shape. No grooves (or sheath) for first dorsal and first anal fins. Caudal fin powerful and deeply forked, caudal fin rays cover most of complex of caudal skeleton. Caudal peduncle slightly depressed, with a deep notch on both dorsal and ventral sides. A large single caudal keel on each lateral side of caudal peduncle. Fin membrane of first dorsal fin dark blackish-brown. Other fins brown or blackish-brown. Dorsal and lateral sides of body blackish-brown, gradually fading to light-brown on ventral side.

Fig. 7. Olfactory rosette of billfishes. A: Xiphias gladius; B: Istiophorus platypterus; C: Istiophorus albicans; D: Tetrapturus angustirostris; F: Tetrapturus pfluegeri; H: Tetrapturus albidus; I: Tetrapturus audax; J: Makaira mazara; K: Makaira nigricans; L: Makaira indica (E: Tetrapturus belone; G: Tetrapturus georgei not examined). Scales indicate 10 mm.

Olfactory rosette radially shaped (Fig. 7A), composed of 32 to 40 olfactory laminae; capillaries can be seen with naked eye on surface of olfactory lamina. Abdominal cavity very large, ending in front of first anal fin. Stomach large and long. Intestine much elongated and folded many times, with separate rectum (Fig. 8A). Pyloric caeca composed of many small sac-like tubules, forming a lump. Liver large with protruding middle lobe. Gall bladder long, only tip of elongate sac can be seen ventrally. Spleen behind gall bladder and therefore cannot be seen ventrally. Air bladder long and sac-shaped. Gonads symmetrical. Kidney much elongate, located below vertebrae. Anus very close to origin of first anal
Fig. 8. Schematic illustration of viscera of billfishes in ventral view. A: Xiphius gladius, 215 cm BL, northwestern Pacific; B: Istiophorus platypterus, 170 cm BL, Japan Sea; C: I. albicans, 162 cm BL, Caribbean Sea; D: Tetrapturus angustirostris, 132 cm BL, northwestern Pacific; E: T. pfluegeri, 143 cm BL, Caribbean Sea; F: T. albidus, 162 cm BL, Caribbean Sea; G: T. audax, 170 cm BL, northwestern Pacific; H: Makaira mazara, 240 cm BL, northwestern Pacific; I: Makaira nigricans, 193 cm BL, Caribbean Sea; J: Makaira indica, 221 cm BL, off Kaohsiung. Each scale indicates 5 cm.

fin. Cranium flat, rather soft and oily, with snout region elongate and postorbital region shorten; temporal crest and pterotic crest somewhat developed posteriorly; posterior projections of epiotic and pterotic slightly developed; supraoccipital crest fairly well developed (Fig. 9). Projection on ventral side of parasphenoid thick and low. Basisphenoid without ventral projection. Nasal parallel with premaxilla, extending forward. Ventral side of vomer and anterior part of ventral surface
of parasphenoid flat and very wide. Number of vertebrae in 10 specimens examined, $15 + 11 = 26$ (6) and $16 + 10 = 26$ (4). Haemal arch in one of "15 + 11 = 26" specimens found to be missing on right side of first caudal vertebra. This fact probably shows that the number of precaudal and caudal vertebrae has not been fixed yet in this species. Neural and haemal spines of central vertebrae slightly flat; neural prezygapophysis projects diagonally in an upward and forward direction, overlapping slightly the preceding neural spine; neural postzygapophysis extending upward and a little smaller than the former (Fig. 10A). Lateral apophysis not developed (Fig. 11A). Parhypural, and last hypurals separated from hypural plate (Fig. 12A).
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Remarks. A bill of *X. gladius* (ca. 1 m BL) which had been caught by Mr. Guillermo Adachi by trolling off Manzanillo, Mexico in 1970, was sent to me. A piece of vinyl cosmetic tube was surrounding on the bill (Fig. 13). This type of example was reported by Ueyanagi and Nishikawa (1973). This probably suggests that *X. gladius* uses the bill for feeding. Jonsgard (1959) reported a snout of this species found lodged in a blue whale, *Balaenoptera musculus* caught in the Antarctic Ocean.

Life history of this species has been extensively studied by Nakamura et al. (1951), Arata (1954) and Yabe et al. (1959). Though there have been many studies on larvae and juveniles of this species, the following are the most representative: Lütken (1880); Sella (1911); Sanzo (1930); Yabe (1951); Tnäing (1955); Padoa

Fig. 12. Caudal complex of billfishes. A: *Xiphias gladius*, Japan Sea; B: *Istiophorus albicans*, Caribbean Sea.

(1956); Jones (1958); Sun (1960); Gorbunova (1969); Tibbo and Lauzier (1969); Kondritskaya (1970); Markle (1974); Nishikawa and Ueyanagi (1974); Yasuda et al. (1978).
Size. There is a record of this species caught at Iquique, Chile on May 7, 1953 which was 445.3 cm TL and 536.2 kg BW (Schwartz, 1961). Since the body is cylindrical in shape, the weight increases rapidly with growth. The range of BL of this species caught by the commercial swordfish longline is 100–270 cm (mostly 120–190 cm) in the northwestern Pacific Ocean.

Distribution. This species is widely distributed in tropical, temperate and cold water zones of the Pacific, Indian and Atlantic oceans (Fig. 14); often coming close to coasts. The swordfish also enters the adjoining seas, such as the Mediterranean, Black, Red and Japan seas. Reports of this species in the Mediterranean Sea are
numerous (e.g., Farber, 1883; Carus, 1893; Sella, 1911; Borcea, 1927; Sanzo, 1931; Luther and Fiedler, 1961; Bini, 1965). There are also many reports of specimens from the Black Sea (Rosa, 1950; Pavlov, 1959), the Marmara Sea (Demir et al., 1956), the Red Sea (Rosa, 1950) and the Japan Sea (Lindberg and Krasykova, 1975). In the north, this species has been reported around Iceland (Saemundson, 1936, 1949) and the North Sea (Andriachev, 1954). Many specimens of larval and juveniles of this species have been collected in the Gulf of Mexico and the Gulf Stream (Arata, 1954), the northwestern Atlantic (Markle, 1974), the tropical and temperate waters of the northwestern Pacific (Nakamura et al., 1951; Yabe et al., 1959), the Indian and Pacific oceans (Nishikawa and Ueyanagi, 1974) and the Indian Ocean (Jones and Kumaran, 1964a). Sanzo (1910, 1922, 1930, 1931) collected extensively the larvae and eggs of this species in the Mediterranean Sea.

Good commercial fishing grounds are located in the northwestern Pacific, off Mexico, off Ecuador, in the Arabian Sea, off Newfoundland and New England, off southern Brazil and the Gulf of Guinea. Based on data from commercial catches, the limits of distribution appear to be about lat. 50°N to 45°S (the western South Pacific) and 35°S (the eastern South Pacific) in the Pacific, lat. 45°S in the Indian Ocean, and lat. 45°N (the western North Atlantic) and more than 60°N in the eastern North Atlantic to 40°–45°S in the South Atlantic. This species is more abundant in coastal waters. The spawning grounds, as presumed by the distribution of larvae and eggs, are surrounded by the 24°C surface isotherm of the summer season (Fig. 14). X. gladius is thought to be essentially a warm water species and generally speaking its migration consists of movement toward temperate or cold waters for feeding and returning to warm waters for spawning.

**Family Istiophoridae**

Premaxilla elongate to form a long, pointed, round rostrum. Elongate scales, each with one to several posterior spines. Branchiostegal membranes united to each other, free from isthmus. One spine and two soft rays of pelvic fin fused, depressible into a groove. Jaws with file-like teeth in adults. Caudal peduncle in adults with two keels on each side; a small shallow notch on dorsal and ventral profiles of caudal peduncle.

**Genus Istiophorus** Lacepède


*Notistium* Hermann, 1804, Observationes zoologicae quibus novae complures...305 (Type-species: *Notistium gladius* Hermann).

*Histiophorus* Cuvier, in Cuvier and Valenciennes, 1832, Histoire naturelle des poissons. 8:291–292 (Type-species: *Histiophorus americanus* Cuvier, based on Maregrave’s Guebucu brasiliensisbus, in Piso, 1648, Historia naturalis Brasiliae; emended spelling to *Istiophorus*).
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**Zanclurus** Swainson, 1839, *On the natural history and classification of fishes*......2:175, 239–240 (Type-species: *Histiophorus indicus* Cuvier).


*Istiophorus platypterus* (Shaw and Nodder)

(Fig. 15)

**Indo-Pacific sailfish, “Bashookajiki”**

*Istiophorus platypterus* (Shaw and Nodder, 1792)


*Scromber gladius* Bloch, 1793, *Naturgeschichte der ausländischen Fisch*. 7:81, pl. 94. Whitehead (1964) indicated the unsatisfactory nature of Bloch’s description of *Scromber gladius*.


*Xiphias velifer* Schneider, in Bloch and Schneider, 1801, *M.E. Blochii Systema Ichthyologiae*:93 (Type-locality: India, after Broussonette, 1786. Replacement name for *Scromber gladius* Bloch, 1793).

*Xiphias platypterus*: Shaw, 1803:101, fig. 15 (Indian Ocean).

![Fig. 15. Indo-Pacific sailfish, *Istiophorus platypterus*, FAKU 41874, 1719 mm BL, Nohara, Wakasa Bay, Japan Sea (above); FAKU 40602, 910 mm BL, Ine, Wakasa Bay, Japan Sea (below).](image-url)
Histiophorus indicus Cuvier, in Cuvier and Valenciennes, 1832, Histoire naturelle des poissons. 8:214–221, pls. 229, 230 (based on a drawing by Sir Joseph Banks from Indian Ocean).

Histiophorus gracilis-rostri Cuvier, in Cuvier and Valenciennes, 1832, Histoire naturelle des poissons. 8:225 (Type-locality: Mauritius ?). Holotype: a spear from a specimen, MNHN A9462.


Xiphias telephus Günther, 1860:512 (Atlantic Ocean)/ Pollen and Van Dam, 1874:100 (Madagascar).

Istiothorax dubius Bleeker, 1873, Ned. Tijdschr. Dierk., 4:151 (China).


Istiothorax triangulatus Hemprich and Ehrenberg, 1849, Symbolae physicae, seu icones adhuc... ... pl. 10. (Type-locality: Red Sea).

Istiothorax japonicus Jordan and Thompson, 1941, Mem. Carnegie Mus., 6 (4):240 (Type-locality: Kobe, Japan).
**Histiophorus magniosi** Jordan and Evermann (date unknown), original description unknown (*side Jordan, 1927*).


I. Nakamura

(I. Nakamura) Grant, 1972:116, 1 fig. (Queensland)/ Grant, 1975:117, 1 fig. (Queensland)/ Kai­
oa, 1975:237 (Port Moreby).

12:48-49, pl. 15 (fig. 2) (Type-locality: Honolulu, Hawaii). Holotype: BPBM 3234, a specimen
6 feet long.

locality: near Cabo San Lucas, Baja California). Holotype: CAS 605, a photograph of a specimen
weighing 135 pounds and 10 feet 1 inch long.


Istiopterus brookei Fowler, 1933, Proc. Acad. Natr. Sci. Philad., 84:403-404, pl. 29 (Type-locality:


Istiopterus brookei: Fowler, 1934:400, fig. 1 (Tahiti, Cooks)/ Curtiss, 1938:78 (Tahiti)/ LaMonte
and Marcy, 1941:14-16 (Tahiti).

Istiopterus immaculatus: LaMonte and Marcy, 1941:14-16 (Red Sea, Indian Ocean)/ Rosa,
1950:152 (Red Sea, Indian Ocean).

Istiopterus amarui Curtiss, 1944, Further notes on the zoology of Tahiti. 6 (Type-locality: Open sea
off Tahiti).

Istiopterus gladius greyi: Nichols and Murphy, 1944:241 (Pacific coast of Panama).

Istiopterus ludibundus: Whitely, 1949:24 (western Australia)/ Ogilby, 1954:91, fig. 112 (Queensland)/
1 fig. (Australia)/ Whitely, 1962:189-190, 1 fig. (Australia)/ Whitely, 1964:245, pl. 3 (figs.
a, c) (Australia).

Istiopterus greyi: de Buen, 1958:21 (Chile) (? misprint of Istiopterus greyi).

Ocean)/ Nakamura, Iwai and Matsubara, 1968:55-57, figs. 9, 12, 14 (indo-Pacific)/ Chirichigno,
1969:76, fig. 149 (Ecuador, Peru, Chile)/ Morrow and Harbo, 1969:34-43 (in part, Indo-Pacific only)/
Bailey et al., 1970:53 (in part, Pacific Ocean only)/ Merrett, 1970:257-360 (Indian Ocean)/
Williams, 1970:831-832 (Kenya)/ Yang, 1970:165-166 (Taiwan)/ Fitch and Lavenberg,
1971:164 (California)/ Hiyama and Yasuda, 1971:112, fig. 161 (Japan)/ Merrett, 1971:
351-360 (equatorial western Indian Ocean)/ Goadby, 1972:255-257, 2 figs. (Pacific Ocean)/
Hiyama and Yasuda, 1972:68, fig. 71 (central and western Pacific Ocean)/ Miller and Lea,
1972:196, 1 fig. (California)/ Randall, 1973a:204 (Tahiti)/ Randall, 1973b:151 (Palau Is-
lands)/ Ueyanagi, 1973:649-658 (indo-Pacific)/ Chirichigno, 1974:93, fig. 23 (Peru)/ Ue-
yanagi, 1974a:73-78, figs. 2, 5, 9 (western Pacific and Indian oceans)/ Ueyanagi,
1974b:189-191 (western Pacific Ocean)/ Walford, 1974:13 (in part, Pacific Ocean)/ Beardsey et al., 1975:
95-98, fig. 1 (in part, Indo-Pacific only)/ Lindberg and Krasykova, 1975:294-296, fig. 232
(Taiwan)/ Nakamura, 1974:50, fig. 1B (indo-Pacific)/ Yoshino et al., 1975:91 (Okinawa,
(Re Santa Island, New Hebrides)/ Gorbunova, 1976:486, fig. 1 (indo-Pacific)/ Klawe, 1977:5
(in part, Indo-Pacific only)/ Klawe, 1978:26 (in part, Indo-Pacific only)/ McClane, 1978:
245-246, 1 fig. (in part, southern California to Ecuador only)/ Nishikawa et al., 1978:70-75
(in part, Indo-Pacific)/ Randall and Sinoto, 1978:304 (Rapa Island, Polynesia)/ Tinker, 1978:
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Diagnosis. Bill long, slender and round in cross section. Sail-like first dorsal fin considerably higher than body depth. Pelvic fin rays very long with well-developed membrane. Relative lengths of pectoral fin and caudal fin to BL smaller than those of I. albicans in immatures. Greatest size attained much larger than in I. albicans.

Description. Young (168–464 mm BL) followed by immatures (616–1078) and adults (1455–1809): D 1 43–49, 44–48, 42–45; D 2 6–7, 6–7, 6–7; A 1 13–17, 12–15, 14–15; A 2 6–7, 6–8, 6–7; P 1 18–19, 18–20, 18–20; P 2 1, 2, 1, 2, 1, 2; GR 0, 0, 0; BS 7, 7, 7; V 12+12=24, 12+12=24, 12+12=24.

Measurement expressed in percent of BL: eye fork length 81.9–83.8, 83.6–86.0, 84.0–88.7; first predorsal length 21.8–27.9, 20.7–23.4, 19.6–21.6; second predorsal length 81.7–84.2, 80.1–83.4, 70.8–83.0; prepectoral length 25.9–28.2 25.1–26.4, 22.1–24.4; prepelvic length 27.0–29.9, 25.5–28.1, 24.0–26.3; first preanal length 62.3–66.8, 61.2–66.8, 59.4–64.1; second preanal length 81.8–91.2, 80.6–84.2, 80.4–82.1; tip of mandible to anus 59.4–62.0, 57.2–62.3, 54.2–59.7; greatest depth of body 10.0–11.2, 12.7–15.8, 14.0–16.1; depth of body at origin of first dorsal 9.3–10.7, 11.6–13.8, 13.1–15.4; depth of body at origin of first anal 7.2–10.7, 9.7–12.4, 10.7–11.9; least depth of caudal peduncle 2.7–3.5, 3.3–4.0, 3.7–4.4; width of body at origin of pectorals 3.9–4.8, 4.7–6.4, 5.1–6.3; width of body at origin of first anal 3.2–5.3, 4.4–6.8, 5.0–5.9; head length 25.8–28.5, 23.8–26.5, 22.2–23.6; snout length 12.1–18.0, 12.0–13.4, 10.9–11.8; bill length 37.1–45.4, 32.2–33.2, 28.9–32.0; maxillary length 15.4–18.4, 14.8–16.5, 13.9–14.6; orbit diameter 3.3–4.1, 2.5–3.0, 1.8–2.5; interorbital width 4.3–5.0, 4.9–5.2, 4.6–5.3; anterior height of first dorsal 14.9–20.2, 16.4–22.5, 19.2–25.4; length of middle dorsal spine 27.8–35.5, 20.9–37.1, 28.5–36.0; anterior height of second dorsal 3.0–4.3, 3.2–4.4, 3.7–4.6; height of first anal 4.5–7.8, 7.1–8.7, 9.8–11.6; anterior height of second anal 2.9–5.3, 3.2–4.1, 3.4–4.0; length of pectoral 7.9–9.2, 7.5–11.9, 16.6–19.6; length of pelvic 28.1–33.2, 31.2–35.4, 28.3–31.6; length of second dorsal base 4.6–5.6, 4.1–6.0, 4.8–5.4; length of first anal base 12.7–15.5, 11.8–14.2, 12.1–18.1; length of second anal base 4.5–6.2, 3.8–5.9, 4.3–5.0; caudal spread 9.2–17.8, 19.3–35.2, 31.3–34.7; length...

Body elongate and compressed. Snout elongate, forming long and round bill (BL about 3.3 times of bill length in adults, relatively smaller with growth). Lower jaw shorter than upper jaw, but still projected a little forward. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Preodontal present. Posterior margin of upper jaw beyond posterior margin of eye. Scales with rather blunt single posterior point (mostly) or two posterior points (sometimes), arranged somewhat randomly (Fig. 3B). Scales on a specimen about 80 cm BL have not yet developed this character very well (Fig. 3B’). Small file-shaped teeth on both jaws and palatine. Lateral line fairly clear, curving above base of pectoral fin and then continuing in a straight line toward caudal fin. Head large (BL about 4.5 times head length in adults, relatively smaller with growth). Eye rather small. Nape fairly elevated. Branchiostegal membranes united completely and free from isthmus. Two nostrils close to each other in front of eye, anterior one slit-like in shape with a posterior flap and posterior one triangular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin fairly long in adults but short in immatures (BL about 5.6 times of length of pectoral, relatively larger with growth) with pointed tip, situated rather low. First dorsal fin sail-shaped; first few rays high, dipping slightly toward middle and then becoming higher, finally gradually tapering off until ending just in front of second dorsal fin. Second dorsal fin small, almost the same size as second anal fin; the latter located a little further forward than the former. First anal fin rather large with an anterior pointed tip. Pelvic fin much longer than pectoral fin, almost extending to anus; its membrane well developed. Grooves for first dorsal and anal fins present. Caudal fin long in adults and rather short in immatures, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeleton as in Scombridae. Caudal peduncle well compressed and slightly depressed, with a pair of caudal keels on its lateral side. Membrane of first dorsal fin dark blue with small black dots scattered on it. Rest of fins blackish brown or sometimes dark blue. Base of first anal and second anal fins tinged with silvery-white. About 20 rows of longitudinal stripes on lateral side of body, each stripe composed of many light blue round dots; individual variation of pattern of stripes observed at Nishimaizuru Fish Market in Kyoto Prefecture. These stripes do not show up clearly in some specimens. Their appearance probably depends on the time passed after capture or the physiological condition of fish before capture. Body dark blue dorsally, light blue spattered with brown laterally and silvery whitish ventrally.

Olfactory rosette radially shaped (Fig. 7B), composed of about 43-50 olfactory laminae; capillaries cannot be seen with naked eye on surface of each olfactory lamina. Abdominal cavity extremely elongate, ending at above middle of base of second anal fin. Stomach long and large when filled with food. Intestine elongate with two bends; rectum not clearly distinguishable (Fig. 8B). Pyloric caeca composed of many small sac-like tubules, forming a large lump. Right lobe
of liver long, left lobe fairly long, but middle lobe not obvious. Gall bladder elongate. Spleen triangular in shape and visible ventrally. Gonads situated beside intestine, and symmetrical. Air bladder composed of many small bubble-shaped sacs which cover most of dorsal side of abdominal cavity, extending to origin of second anal fin. Kidney elongate, located under vertebrae. Anus very close to origin of first anal fin. Cranium hard, stout and fairly wide; anterior dorsal part rather flat; snout portion elongate. Temporal and pterotic crests close to each other anteriorly and run almost parallel to each other medially but abruptly part posteriorly and join at the end (Fig. 16). Ventral parts of vomer and anterior parasphenoid relatively narrow. Width between outer margins of right and left lateral ethmoids moderately wide. Neural and haemal spines of central vertebrae triangular in shape (Fig. 10B); lateral apophysis not well developed (Fig. 11B).

Remarks. There have been many speculations on the role of the remarkably large and sail-like first dorsal fin of the sailfish which were reviewed by Tinsley (1964). The roles or functions of the first dorsal fin have been thought to be as follows: 

Fig. 16. Cranium of *Istiophorus platypterus*, 1672 mm BL, Japan Sea.
a sail of sailing boat to catch the aid of the wind”. “When a sailfish basks in the sun with an extended sail it is absorbing heat or sunlight through the great fin, which thus functions as a respiratory organ”. “It will act like the barb of arrow, and keep the body of the fish on a straight course after it has taken its aim for striking its victim”. “The super fin is thought to help regulate the intricate movements of the sailfish, permit it to make sharp turns, and help reduce or brake the extraordinary speed of fish”. “When a sail fish is chased by any enemy under the sea it suddenly lifts its big fin, thus becoming, in a flash (from the stern view), three times as broad vertically as it was a moment before; the pursuer, assuming this expansion applies overall, is discouraged and abandones the chase”. “One function of the sail that has been observed time and again during the feeding operation is to scare minnows into spherical masses of bait where they will fall easy prey to the sailfish” and so on. The role of the bill of the sailfish and other billfishes have also been speculated by many authors. The bill is generally thought to be used for attacking the prey and many examples of attacking boats are cited.

Fig. 17. Observed behavior of Istiophorus platypterus (see text p. 285).
An aspect of the feeding behavior of the sailfish has often been observed off Manzanillo, Mexico by G. Adachi (Person. Comm.) who informed me as follows (Fig. 17). "When the sailfish found a school of prey fishes (sardine, anchovy or jack mackerel), it began to pursue them at half speed with the fins half folded back in the grooves (A). Then it drove at them at full speed with the fins completely folded back in the grooves (B). After it had caught up with them, it suddenly made a sharp turn with the fins expanded to confront a part of the school (C). Then it hit them with the bill (D). Subsequently it ate the killed and stunned prey fish, usually head first (E).

There have been many studies on the larvae and juveniles of this species. Deraniyagala (1936, 1952) and Jones (1959a, b) studied those from the Indian Ocean, and Yabe (1953a, b) and Sun (1960) studied those from the Pacific Ocean.

**Size.** The largest records of this species caught by sport fishing were a specimen caught at Santa Cruz Island, Galapagos on Feb. 12, 1947 which was 327.7 cm TL and 100.2 kg BW and a specimen caught at La Paz, Mexico on Aug. 23, 1957 which was 340.4 cm TL and 89.8 kg BW. The largest caught by commercial longline is said to have been about 3 m TL. The average size of this species caught by longline and set net around Japan is about 150-230 cm BL.

**Distribution.** This species is distributed in the tropical and temperate waters of the Pacific and Indian oceans (Fig. 18). It shows a strong tendency to come close to shore, but a few are caught in the central parts of oceans. Large numbers of this species migrate in waters off New Guinea, the Solomon Islands, in the Kuroshio Current from the Philippines to Japan and off the Pacific coast of Mexico. This species also has often been reported off the coast of Australia, Tahiti, Hawaiian Islands, India and Sri Lanka, but has been seldom seen off the Pacific coast of southern South America.
Jones and Silas (1964) reported that this species is taken more often than any other species of billfish in Indian coastal waters. Tortone (1961, 1964) believed the invasion of this species to the Mediterranean Sea through the Suez Canal from the Red Sea. In the Japan Sea, some schools of this species migrate northward with the warm Tsushima Current during late summer, southward against the current during early autumn and are caught by the coastal set nets.

Good commercial fishing grounds for longlining this species are located in waters of the eastern Pacific from Baja California to Ecuador, the Coral Sea and around New Guinea, the East China Sea, the adjacent waters of southern India and Sri Lanka, and the Mozambique Channel. Based on the data of commercial catches, the latitudinal limits of *I. platypterus* appear to extend from lat. 40°–45°N in the North Pacific and about lat. 40°S in the South Pacific, and in the Indian Ocean as far south as about lat. 40°S.

Many specimens of larvae and juveniles of this species have been collected in the Kuroshio Current area from the Philippines to southern Japan, and from the Banda, Flores and Coral seas (Ueyanagi, 1964). Many have also been collected from the tropical regions of the northwestern Pacific Ocean (Jones and Kumaran, 1964a; Ueyanagi, 1964), and from the west coast of Sumatra, the west coast of India and near Madagascar (Jones and Kumaran, 1964a). The spawning grounds, presumed by the distribution of larvae and juveniles, are surrounded by the 25°C surface isotherm of the summer season.

*Istiophorus albicans* (Latreille)

*(Fig. 19)*

Atlantic sailfish, "Nishibashookajiki"

*Istiophorus albicans* (Latreille, 1804)

*Makaira albicans* Latreille, in Bosc and Letreille, 1804, Nouveau dictionnaire d'histoire naturelle. 1st ed. 24:104 (Type-locality: Brazil).

*Histiothorus americanus* Cuvier, in Cuvier and Valenciennes, 1832, Histoire naturelle des poissons. 8:222–223 (Type-locality: Off Brazil; Type based on Marcgrave's description and figure in Piso, 1848, Historia naturalis Brasiliæ).


*Skeponopodus guebucu* Nardo, 1833, Isis (Oken), 25 (4):416 (Type-locality: Brazil). Based on Marcgrave’s Guebucu brasiliensibus.

*Histiothorus pulchellus*: Griffith and Smith, 1834:pl. 27 (fig. 4) (Europe)/ Günther, 1860:514 (France)/ Goode, 1882:424 (eastern Atlantic Ocean)/ Goode, 1883:310 (eastern Atlantic Ocean).

*Histiothorus granulifer* Castelnau, 1861; Mem. Poiss. Afrique Austr. 42–43 (Type-locality: Cape of Good Hope).

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Fig. 19. Atlantic sailfish, *Istiophorus albicans*, NRFRL 3216, 2000 mm BL, Caribbean Sea (above); FAKU 39899, 903 mm BL, central Atlantic Ocean (below).


*Xiphias velifer*: Rochebrune, 1882:84 (Dakar).


Istiophorus maguirei: Breder, 1929:130 (Florida Keys, ? misprint for *Istiophorus maguirei*).


Histioplwrus albicans: Whitley, 1936:191 (Britain).


Diagnosis. Bill long, slender and round in cross section. First dorsal sail-like in shape and considerably higher than body depth. Pelvic fin rays very long with
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well developed membrane. Relative lengths of pectoral fin and caudal fin to BL greater than those of I. platypterus in immatures. Greatest size attained much smaller than in I. platypterus.

Description. Young (179.9–202.2 mm BL) followed by immatures (847–1009) and adults (1225–2000): D 1 43–47, 43–45, 42–46; D 2 6–7, 6–7, 6–7; A 1 15–17, 11–12, 11–14; A 2 6–7, 6–7, 6–7; P 1 18–19, 17–20, 18–20; P 2 I, 2, I, 2, I, 2; GR, 0, 0, 0; BS 7, 7, 7; V 12+12=24, 12+12=24, 12+12=24.

Measurement expressed in percent of BL: eye-fork length 80.6–85.3, 85.9–88.0, 84.0–86.1; first predorsal length 23.3–25.5, 20.4–22.6, 19.3–23.4; second predorsal length 81.1–82.7, 81.0–81.6, 79.9–83.1; prepectoral length 28.2–30.6, 24.9–25.7, 22.8–25.2; prepectoral length 29.1–32.3, 26.5–27.6, 24.1–26.8; first preanal length 64.0–68.6, 61.1–63.2, 60.7–64.1; second preanal length 79.8–83.6, 80.6–81.6, 80.0–82.5; tip of mandible to anus 60.9–64.9, 57.3–58.5, 55.5–59.7; greatest depth of body 9.1–10.4, 12.7–14.1, 13.8–15.6; depth of body at origin of first dorsal 8.9–10.4, 12.7–13.2, 12.2–14.9; depth of body at origin of first anal 6.8–7.9, 8.7–9.7, 9.9–11.7; least depth of caudal peduncle 2.7–2.9, 3.5–3.8, 3.4–4.1; width of body at origin of pectorals 3.8–4.4, 5.4–5.8, 4.1–5.6; width of body at origin of first anal 2.9–3.3, 4.2–5.2, 4.3–5.4; head length 28.0–30.6, 24.2–25.8, 22.6–24.9; snout length 13.5–15.7, 12.0–13.1, 10.8–12.5; bill length 45.6–49.2, 30.3–30.4, 27.2–31.3; maxillary length 17.7–19.5, 14.8–16.1, 13.9–15.6; orbit diameter 3.8–4.0, 2.3–2.8, 1.8–2.4; interorbital width 3.6–3.9, 4.9–5.3, 4.5–5.5; anterior height of first dorsal 28.6–34.2, 21.5–22.6, 12.7–21.4; length of middle dorsal spine 30.5–35.8, 32.0–35.6, 24.0–37.4; anterior height of second dorsal 2.7–3.5, 3.9–4.8, 3.4–4.9; height of first anal 6.4–7.8, 8.2–9.7, 8.7–10.5; anterior height of second anal 1.6–3.0, 3.4–4.0, 3.2–4.2; length of pectoral 7.6–8.5, 13.5–15.7, 16.2–19.8; length of pelvic 28.3–31.1, 30.9–31.7, 26.4–31.7; length of first dorsal base 56.2–60.0, --------; length of second dorsal base 4.8–5.5, 5.0–5.3, 4.7–6.2; length of first anal base 14.6–16.6, 13.6–14.7, 8.3–14.6; length of second anal base 4.5–8.4, 4.8–5.7, 4.2–5.6; caudal spread 9.3–11.3, 32.3–36.1, 30.0–34.5; length of upper lobe of caudal 14.3–15.4, 26.6–29.9, 22.5–24.1; length of lower lobe of caudal 15.3–16.1, 26.5–28.3, 21.0–22.9.

Body elongate and compressed. Snout elongate forming long and round bill. Lower jaw shorter than upper jaw, but still projected a little. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Scales with rather blunt single posterior point (mostly) or two posterior points (sometimes), arranged somewhat sporadically (Fig. 3C). Small file-shaped teeth on both jaws and palatine. Lateral line fairly clear, curving above base of pectoral fin and then continuing in a straight line toward caudal fin. Head large. Eye rather small. Nape fairly elevated. Both right and left branchiostegal membranes united completely and free from isthmus. Two nostrils close to each other in front of eye, anterior one slitlike in shape with a posterior flap and posterior one triangular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin fairly long with pointed tip, situated rather low. First dorsal fin sail-shaped; first few rays high, dipping slightly
toward middle and then becoming higher, finally gradually tapering off until ending just in front of second dorsal fin. Since shape of first dorsal fin shows fairly individual variation with each specimen, it is difficult to set down any rules as to its shape, but it is almost the same as that of Indo-Pacific sailfish, *I. platypterus*. Second dorsal fin small, almost the same size as second anal fin; the latter located a little more forward than the former. First anal fin rather large with an anterior pointed tip. Pelvic fin much longer than pectoral fin, almost extending to anus; its membrane well developed. Grooves for first dorsal and anal fins present. Caudal fin long, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeleton. Caudal peduncle well compressed and slightly depressed, with a pair of caudal keels on its lateral sides. Membrane of first dorsal fin dark blue or blackish blue with small black dots scattered on it. Rest of fins blackish blue, sometimes tinged with dark brown. Base of first anal and second anal fins often tinged with silvery-white. About 20 rows of longitudinal stripes on lateral side of body, each stripe composed of many light blue round dots. Body dark blue dorsally, light blue splattered with brown laterally and silvery whitish ventrally.

Olfactory rosette radially shaped (Fig. 7C), composed of about 41–48 laminae; capillaries cannot be seen with naked eye on surface of each lamina. Abdominal cavity extremely elongated, ending at about middle of base of second anal fin. Stomach long and large with food. Intestine elongate with two bends; rectum not clearly distinguishable (Fig. 8C). Pyloric caeca composed of many small sac-like tubules, forming a large lump. Right lobe of liver very elongated, left lobe fairly elongated, but middle lobe not obvious. Gall bladder elongated. Spleen triangular in shape and can be seen ventrally. Gonads symmetrical. Air bladder composed of many small bubble-shaped sacs which cover most of dorsal side of abdominal cavity, extending to origin of second anal fin. Kidney elongate, located under vertebrae. Anus very close to origin of first anal fin. Cranium hard, stout and fairly wide; anterior dorsal part rather flat. Snout portion elongate. Temporal and pterotic crests close to each other anteriorly and run almost parallel to each other medially but abruptly part posteriorly and close at the end (Fig. 20). Ventral parts of vomer and anterior parasphenoid relatively narrow. Width between outer margins of right and left lateral ethmoids moderately wide. Neural and haemal spines of central vertebrae triangular in shape (Fig. 10C); lateral apophysis not well developed (Fig. 11C).

Remarks. In adults this species and *I. platypterus* are extremely similar and it is difficult to clearly distinguish between the two species. In immature specimens however, a clear difference can be seen in the relative length of the pectoral and caudal fins (Fig. 21). In the immature stage this species has longer pectoral and pelvic fins than *I. platypterus* (Figs. 15 and 19). In a previous paper (Nakamura et al., 1968), both Indo-Pacific sailfish, *I. platypterus* and Atlantic sailfish, *I. albicans* were recognized only tentatively as valid species, principally because data were claking to establish with certainty whether the two forms were conspecific, subspecies or distinct species. While data are still inadequate, I now feel that both
forms might attain to subspecies differentiation. I consider that some distinctions noted between these two forms, especially in the immature stage, could be referable to subspecific status. These features include differences in maximum body size attained and relative length of pectoral and caudal fins in their immature stage. Morrow and Harbo (1969) reported that analysis of morphometric and meristic characters of sailfish from various localities in the Indian, Pacific and Atlantic oceans indicated that the genus, *Istiophorus* is monotypic, composed of a single species that shows remarkably little variation in the characters examined. Further study of various aspects of the sailfish is necessary to clarify the problems of speciation on the sailfish. Until this is achieved, I retain the use of *Istiophorus platypterus* for the Indo-Pacific sailfish and *Istiophorus albicans* for the Atlantic sailfish. The Japanese name, “Nishibashookajiki” was proposed by Nakamura et al. (1968).

Feeding behavior of this species introduced by Mather (1976) coincides well with Pacific sailfish’s behavior. There have been many studies on larvea, juveniles
Fig. 21. A: Relationships between pectoral fin and body length in sailfish. Open circles show data from the Atlantic sailfish and solid circles show data from the Indo-Pacific sailfish. Data from Vick (1963) and Royce (1957) are included. B: Relationship between spread of caudal fin and body length in sailfish. Open circles show data from the Atlantic sailfish and solid circles show data from the Indo-Pacific sailfish. Data from Vick (1963) and Royce (1957) are included.
and young of this species. The most representative ones are Beebe (1941a), Voss (1953), de Sylva (1963a), Tinsley (1964) and Gehringer (1956, 1970).

**Size.** The largest specimen of this species on record in sportfishing is a specimen caught at Walker Bay, Bahamas, on April 25, 1950 which was 315 cm TL and 55.8 kg BW. The range in BL of this species caught by commercial tuna long-line is about 125–210 cm (mostly 150–195 cm) in both the western and eastern Atlantic Ocean.

**Distribution.** This species is widely distributed in the tropical and temperate waters of the Atlantic Ocean. Compared with the other billfish species, this species is rather coastal. Large numbers migrate in the Gulf of Mexico, the Caribbean Sea, the West Indies and near Florida. There are records of this species caught near New England in the north (Baird, 1873; Kendall, 1908; Nichols and Breder, 1927). This species is also known to migrate to the Mediterranean Sea, but there are only a few reports of this species. Peronaci (1966) reported that the species is common in the eastern Atlantic, but rare in the Mediterranean. The results of tagging experiments (Mather, 1960) indicate that this species probably does not undertake transoceanic migration as do many species of tuna.

Good commercial longlining grounds for this species are found in the Gulf of Mexico, the Gulf of Guinea and the coastal waters off eastern South America from Panama to Brazil (Fig. 22). The distributional limits based on longline catch are about lat. 40°N in the north and lat. 35°–40°S in the south of the Atlantic Ocean.

![Fig. 22. Distribution of *Istiophorus albicans*, based on catch data from Japanese longline fishery. Solid line shows presumed limits of distribution. Dotted area shows presumed spawning ground. Broken line shows summer surface isotherm for 25°C (Sverdrup et al., 1961).](image)

Larvae and juveniles of this species have been collected from the Gulf of Mexico (Jones, 1962), from the Gulf Stream waters, especially near Florida and the tropical waters off West Africa (Beardsley et al., 1975). The spawning grounds presumed by the distribution of larvae and juveniles are surrounded by the 25°C surface isotherm of the summer season.
Genus *Tetrapturus* Rafinesque

*Tetrapturus* Rafinesque, 1810, Caratteri di alcuni nuovi generi e nuove specie di...1810, 54–55, pl. 1 (fig. 1) (Type-species: *Tetrapturus belone* Rafinesque).


*Tetrapturus* Bonaparte, 1841, Iconographia della fauna italica per...3(1):19 (emended spelling of *Tetrapturus*).

*Tetropterus* Agassiz, 1843, Recherches sur les poissons fossiles. 5:7, 89–92, (emended spelling of *Tetrapturus*); Swainson, 1839, On the natural history and classification of fishes...2:175, 239 (? misspelling).


*Tetrapleurus* Radcliffe, 1926, Copeia, (151):112 (? misprint of *Tetropterus*).


*Kajikia* Hirasaka and Nakamura, 1947, Bull. Oceanogr. Inst. Taiwan, (3):13–14, pl. 2 (fig. 1) (Type-species: *Kajikia formosana* Hirasaka and Nakamura [= Immature of *Tetrapleurus audax* Philippi]).


Height of dorsal fin greater than body depth. Pelvic fin fairly long without well developed membrane. Body compressed. Usually no stripes on body except in *T. audax*. Nape almost straight or fairly elevated (in *T. audax* and *T. albidos*). Cranium elongate and narrow. Neural and haemal spines of central vertebrae more or less rectangular in shape. Vertebrae 12+12=24. Lateral apophysis not well developed.

*Tetrapleurus angustirostris* Tanaka

(Fig. 23)

Shortbill spearfish, “Fuuraikajiki”

*Tetrapleurus angustirostris* Tanaka, 1915


Fig. 23. Shortbill spearfish, *Tetrapturus angustirostris*, FRSKU S356, 1570 mm BL, off Angola.


*Tetrapturus illingworthi*: LaMonte and Marcy, 1941:2 (Hawaii)/ Rosa, 1950:161-162 (Hawaii).

*Tetrapturus brevirostris*: Tinker, 1944:165 (Hawaii).

*Tetrapturus belone*: LaMonte, 1945:32, 34 (in part; referring to Hawaii only).

*Pseudohistiophorus angustirostris*: de Buen, 1950:171 (new genus name proposed).

*Pseudohistiophorus illingworthi*: de Buen, 1950:171 (new genus name proposed).

*Tetrapturus indicus*: Deraniyagala, 1964:441 (Sri Lanka; beak short and stout).


Description. \( D_1 45-50; \ D_2 6-8; \ A_1 12-15; \ A_2 6-8; \ P_1 17-20; \ P_2 1, 2; \ GR 0; \ BS 7; \ V 12+12=24. \)

Measurement expressed in percent of BL (977-1784 mm): eye-fork length 85.8-88.9; first predorsal length 18.3-20.7; second predorsal length 79.3-87.8; prepectoral length 21.5-24.3; prepelvic length 22.6-25.6; first preanal length 57.5-66.0; second preanal length 79.2-86.4; tip of mandible to anus 48.3-54.4; greatest depth of body 5.2-12.6; depth of body at origin of first dorsal 6.6-12.2; least depth of caudal peduncle 2.3-3.4; width of body at origin of pectorals 4.5-6.7; width of body at origin of first anal 3.5-6.4; head length 21.1-24.3; snout length 9.8-12.6; bill length 14.3-18.3; maxillary length 12.6-15.4; orbit diameter 2.1-2.9; interorbital width 4.0-5.4; anterior height of first dorsal 12.6-16.0; length of middle dorsal spine 9.1-16.2; anterior height of second dorsal 2.8-3.8; height of first anal 7.2-9.7; anterior height of second anal 2.6-5.2; length of pectoral 8.6-14.3; length of pelvic 20.2-25.9; length of first dorsal base 61.4-74.1; length of second dorsal base 3.6-5.1; length of first anal base 12.1-22.3; length of second anal base 4.1-5.6.

Body elongate; depth of body very low (BL about 9 times greatest depth of body) and compressed. Snout short (head length about 1.6 times snout length); cross-section round. Lower jaw shorter than upper jaw, but still projecting. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with elongate scales; each scale with 3-5 posterior points (Fig. 3D). Small file shaped teeth on both jaws and palatine. Lateral line clear, curving above base of pectoral fin and then continuing in a straight line toward caudal fin. Head rather large (BL about 4.5 times head length). Eye small. Nape straight. Branchiostegal membranes united with each other completely and free from isthmus. Two nostrils close to each other in front of eye, anterior one small slit-like in shape with a posterior flap and posterior one elongate semicircular in shape; parts of olfactory laminae visible through posterior nostril. No gill rakers. Pseudobranchiae present. Pectoral fin short (BL about 8.3 times length of pectoral) with pointed tip, situated rather low. First dorsal fin with pointed anterior lobe, begins above posterior margin of preopercle; higher than body depth anteriorly and then abruptly decreasing height to about 19th ray, increasing height gradually after 19th ray, keeping same height medially and posteriorly, ending gradually in front of second dorsal fin. Second dorsal fin small, almost the same size and shape as second anal fin; the latter situated about half the length of its base further forward than the former. First anal fin rather small, sharply pointed, sickle-shape. Pelvic fin slender, about twice the length of pectoral fin. Grooves for first dorsal, pelvic and anal fins present. Caudal fin rather short among billfish species, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeleton. Caudal pedun-
cle well compressed and slightly depressed with a pair of caudal keels on its lateral sides. First dorsal fin dark blue without dots. Rest of fins brown or dark brown. Base of first and second anal fins often tinged with silvery white. Body dark blue dorsally, blue spattered with brown laterally, and silvery white ventrally. No dots or stripes on body.

Olfactory rosetta radially shaped (Fig. 7D), composed of about 45–52 olfactory laminae; capillaries cannot be seen with naked eye on surface of each lamina. Features of viscera very similar to those of *Istiophorus platypterus* except gonads which form asymmetrical Y-shape (left lobe well developed) (Fig. 8D). Anus situated far forward from origin of first anal fin.

Cranium hard, stout and rather elongate; snout portion elongate (Fig. 24). Temporal and pterotic crests close to each other anteriorly and run almost parallel...
to each other posteriorly. Ventral parts of vomer and anterior parasphenoid narrow. Many small elongated ridges on frontal. Width between outer margins of right and left lateral ethmoids narrow. Neural and haemal spine of central vertebrae low rectangular in shape (Fig. 10D); lateral apophysis not well developed (Fig. 11D).

**Remarks.** Ueyanagi (1960b, 1962) reported on larvae and juveniles of this fish in the Pacific Ocean. Watanabe and Ueyanagi (1963) reported on larvae and juveniles of this fish in the Pacific Ocean. Watanabe and Ueyanagi (1963) reported on the young of this species in the Pacific Ocean.

**Size.** This species is said to reach about 2 m BL. The longest specimen used in this study was 178.4 cm BL. The range of BL of this species caught by commercial tuna longline is about 135-200 cm BL (mostly around 160 cm BL) in the Pacific Ocean.

**Distribution.** The shortbill spearfish, *T. angustirostris* is known originally from the Indo-Pacific Ocean and is thought to be largely oceanic, rarely entering coastal waters. This species is known to be distributed throughout tropical and temperate areas of the Pacific, but its apparent population density (based on catch per unit of effort of longline) is always low except in the northwestern Pacific between lat. 15° and 30°N where it appears high from about November through February (Howard and Ueyanagi, 1965), though there have been very few records of this species from the Indian Ocean. Among the Indo-Pacific istiophorids, this species has most recently received scientific attention. Until recently, its range has often been extended by various authors. To the east its range has been extended as far as the Californian coast with one specimen (Craig, 1958) and off Coquimbo, Chile with a single specimen (Robins and de Sylva, 1961). Yabe et al. (1958) reported a specimen of “Shortnosed spearfish (=shortbill spearfish)” obtained from a position 25°13'S, 99°43'E, which was thought to be the westernmost published record at that time in the Indian Ocean. However, the scientific name and further details were not given. Since then, Penrith (1964) reported a specimen of *T. angustirostris* caught by longline at 29°40'S, 32°32'E, which was to be the westernmost published record in the Indian Ocean. Recently Merrett (1968, 1971) reported the occurrence of several specimens of this species from the equatorial western Indian Ocean off Tanzania, Kenya, and Somalia. To the south around the waters of Australia and New Zealand, McKay (1966) reported an immature male of this species from shallow water inside the reef at North Cottesloe, Western Australia, as the first record for Australian waters. Goadby (1972) reported a specimen of “short-billed spearfish (=shortbill spearfish)” captured by rod and reel off Port Stephens, New South Wales. Moreland (1975) reported a new record of this species with a specimen obtained from off White Island in the Bay of Plenty, North Island, New Zealand. In the Atlantic, Nakamura and Nakano (1978) reported the occurrence of this species in the Gulf of Guinea with three specimens caught by longline. Collections of many larval and juvenile specimens of this species has been reported in the subtropical areas of the northwestern Pacific Ocean (Ueyanagi, 1962; Howard and
Ueyanagi, 1965), but only a few have been found in the Indian Ocean (Jones and Kumaran, 1964b, Ueyanagi, 1963a). Ueyanagi (1962, 1963b, 1964) assumed from the occurrence of larvae and mature fish that spawning of this species is more active in winter months than summer months in the tropical and subtropical waters between lat. 25°N and 25°S. Merrett (1971) provided some data to indicate spawning of *T. angustirostris* in the western Indian Ocean and states that this species is more abundant during the southeast monsoon, when the maturity of female fish is more advanced and the surface temperatures are at the lowest (mean 25.5°C). There has been no report of larvae and juveniles of this species in the Atlantic Ocean. The possibility of the occurrence of *T. angustirostris* in the Atlantic Ocean, reported by Nakamura and Nakano (1978), warrants the following discussion.

Penrith (1964) stated that the finding of *T. angustirostris* so far west in the Indian Ocean suggests that there is no reason why it should not occur at the Cape of Good Hope. Talbot and Penrith (1962b) reported that the black marlin (*Makaira indica*), the striped marlin (*Tetrapturus audax*) and the white marlin (*Tetrapturus albidus*) have been found off the Cape in late summer (December-March). Except for the cold upwelled water of the Benguela Current, surface temperatures of 21°C are found in summer around the Cape of Good Hope (Sverdrup et al., 1961). There therefore appears to be no temperature barrier off the Cape of Good Hope in summer that would prevent *T. angustirostris* from entering the Atlantic Ocean. Therefore, the occurrence of this species in the eastern Atlantic Ocean implies that some strays enter the Atlantic Ocean from the Indian Ocean around the Cape of Good Hope during summer. Although some strays of *T. angustirostris* are found in the Atlantic Ocean, I believe that this species has its spawning grounds and principal populations only in the Indo-Pacific area. The distributional limits based on the longline catch are about lat. 40°N to 35°S in the Pacific Ocean and about lat. 20°N to 35°–45°S in the Indian Ocean (Fig. 25).

![Fig. 25. Distribution of *Tetrapturus angustirostris*, based on catch data from Japanese longline fishery. Solid line shows presumed limits of distribution. Dotted area shows presumed spawning ground. Broken line shows summer surface isotherm for 25°C (Sverdrup, et al., 1961). Dot-dash line shows presumed invasion of this species from the Indian Ocean to the Atlantic Ocean.](image-url)
Tetrapturus belone Rafinesque

(Fig. 26)

Mediterranean spearfish, "Chichuukaifuurai"

Tetrapturus belone Rafinesque, 1810

Tetrapturus belone Rafinesque, 1810, Caratteri di alcuni nuovi generi e nuove specie di .......54-55, pl. 1 (fig. 1) (Type-locality: Sicily, original description). Neotype: a male specimen of body length 1268 mm from Sicily, USNM 196527 designated by Robins and de Sylva (1963).


Skepanopodus typus Nardo, 1833, Isis (Oken), 26 (4):416-420 (Type-locality: Adriatic Sea).

Tetrapterurus belone: Bonaparte, 1841:19 (Italy, emended spelling)/ Bonaparte, 1846:80 (Mediterranean Sea)/ Nardo, 1847:461-463 (Mediterranean Sea).


Fig. 26. Mediterranean spearfish, Tetrapterurus belone, a rough sketch from the photograph of Robins and de Sylva (1963), 1268 mm BL, Strait of Messina (p. 93, fig. 4).
Systematics of Billfishes

_Tetrapturus belone_: Verany, 1847:492–494 (Ligurian Sea; ? misprint for _Tetrapturus belone_).
_Histiophorus belone_: Günther, 1860:513 (Mediterranean Sea)/ Parona, 1898:368 (Ligurian Sea).
_Scheponopodus prototypus_ Canestrini, 1872, Pesci. in Cornalia, Fauna d'Italia. 3:112 (Type-locality: Italy).
_Histiophorus (Tetrapturus) belone_: Lütken, 1876, 5:60–63, pl. 3 (Mediterranean Sea).
_Istiophorus gladius_: Ben-Tuvia, 1953:18–19, fig. 12 (Mediterranean Sea; misidentification [vide Ben-Tuvia, 1966, 1971]).

**Material examined.** USNM 19652 (Neotype of _Tetrapturus belone_ designated by Robins and de Sylva, 1963), 1 specimen (1280 mm BL), 200 m off the coast of Punta S. Ranieri, Sicily, August 2, 1961.

**Diagnosis.** Bill rather short and round in cross section. Anterior fin rays of first dorsal fin higher than body depth; posterior rays about same height. Pectoral fin short and narrow with pointed tip. Anus situated far anterior to origin of first anal fin.

**Description.** _D_ 1 41; _D_ 2 6; _A_ 1 14; _A_ 2 6; _P_ 1 19, _P_ 2 1, 2; _GR_ 0; _BS_ 7; _V_ 12+12=24.

Measurement expressed in percent of BL: first predorsal length 20.5; second predorsal length 81.4; prepectoral length 24.7; prepelvic length 25.9; first preanal length 60.9; second preanal length 78.9; tip of mandible to anus 51.1; greatest depth of body 12.2; depth of body at origin of first dorsal 12.1; depth of body at origin of first dorsal 5.6; width of body at origin of anal 6.6; head length 23.9; snout length 11.8; bill length 18.4; maxillary length 14.7; orbit diameter 2.7; interorbital width 4.6; anterior height of first dorsal 13.5; length of middle dorsal spine 8.4; anterior height of second dorsal 3.1; height of first anal 7.9; anterior height of second anal 3.4; length of pectoral 10.2; length of pelvic 20.4; length of first dorsal base 61.6; length of second dorsal base 4.5; length of first anal base 13.8; caudal spread 4.8; length of upper caudal keel 3.8; length of lower caudal keel 3.4.

Body elongate and fairly compressed. Snout elongate, forming rather short bill with round cross section. Lower jaw shorter than upper jaw, but still projected a little forward. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with elongated scales; each scale with 3–5 posterior points (Fig. 3E). Small file-shaped teeth on both jaws and palatine. Lateral line single, curved anteriorly; arch of it ends between midpoint and tip of pectoral fin. Head rather large. Eye small. Nape almost straight. Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye. No gill rakers. Pseudobranchiae present. Pectoral fin short with pointed tip and situated rather low; upper margin of it curved and lower margin of it nearly straight. First dorsal fin with round anterior lobe, begins above posterior margin of preopercle, higher than body daphth anteriorly and then
abruptly decreasing in height to about 10th ray, then keeping same height medially and posteriorly, ending gradually in front of second dorsal fin. Second dorsal fin small, almost the same size and shape as second anal fin; the latter situated about half length of its base further forward than the former. First anal fin low. Pelvic fin slender, a little shorter than twice pectoral fin length. Grooves for first dorsal and anal fins present. Caudal fin rather short among billfish species, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeleton. Caudal peduncle well compressed and slightly depressed with a pair of caudal keels on its lateral side. Though fresh specimens were not examined, the formalin preserved specimen showed dark blue without dots; other fins dark brown; body without markings or spots, bluish grey dorsally and grey or dull white ventrally. Vertebrae

Fig. 27. Distribution of *Tetrapturus belone* (shaded area) and *Tetrapturus georgei* (surrounded by dotted line, uncertain).
12+12=24 (Robins and de Sylva, 1963).

Remarks. No specimen of T. belone was obtained for anatomical and osteological study. So no description of the internal characters can be given here.

The eggs, larvae and young stages have been studied by Lo Bianco (1903), Sparta (1953, 1961), Padoa (1956), Cavaliere (1962) and Robins and de Sylva (1963).

Size. The largest specimen examined by Robins and de Sylva (1963) was 196.8 cm BL, and by Bini (1965) was 240 cm TL.

Distribution. T. belone is limited in its distribution to the Mediterranean Sea, especially around Italy (Fig. 27). Large numbers of this species congregate in the Straits of Messina in August and September (Cavaliere, 1962). There are other records of this species in the literature from Mallorca to the west, the Ligurian, Adriatic, Ionean and Levant seas and around Malta. The eastern limit of the distribution of T. belone has not been clearly delineated. There has been no record of its occurrence in the Black or Aegean seas. Albuquerque (1956), Maul (1948) and Noronha and Sarmento (1948) reported on the occurrence of this species near Madeira Island. However there is no conclusive evidence that these specimens were certainly T. belone. In August and September, 1961, Robins examined 60 istiophorids obtained from the western Alboran Sea (just east of Gibraltar) and mostly in the Atlantic Ocean from the vicinity of Gibraltar to as far west as southern Portugal, of them, 57 were T. albidas and none was T. belone (Robins and de Sylva, 1963). Eggs and larvae referable to this species have been collected in the Messina Straits (Sparta, 1953, 1961). Thus as far as known, the life cycle of T. belone is completed only inside the Mediterranean Sea.

There are no particular fisheries for T. belone. The fisheries of this species, however, are coincidental with the swordfish fisheries (Sparta, 1961; Cavaliere 1962). Small numbers are harpooned or caught with several types of nets in the vicinity of the Straits of Messina.

*Tetrapturus pfluegeri* Robins and de Sylva

(Fig. 28)

Longbill spearfish, “Kuchinagafuurai”

*Tetrapturus pfluegeri* Robins and de Sylva, 1963


Fig. 28. Longbill speargish, *Tetrapturus fluegneri*, 1427 mm BL, Caribbean Sea.

items in synonymy which are based solely on Mediterranean specimens, or accounts and discussion based on photographs of Mediterranean specimens are not referable to *Tetrapturus fluegneri* [vide: Robins and de Sylva, 1963]// Schwartz, 1961:21, 24, 2 figs. (Maryland) // Cavaliere, 1962:171 (in part, reference to western Atlantic material) // Tortone, 1962:8-9 (in part, information referring to Florida only) // Peronaci, 1966:326-364, fig. 79 (in part, referring to Atlantic only).


*Tetrapturus beloni*: Briggs, 1958:287 (Florida; ? misprint of *Tetrapterus belone*).


Diagnosis. Bill long and round in cross section. Anterior fin rays of first dorsal fin higher than body depth; posterior rays about same height. Pectoral fin rather long and wide with rounded tip. Anus situated far anterior to origin of first anal fin.

Description. D1 44-50; D2 6-7; A1 12-17; A2 6-7; P1 18-21; P2 I, 2; GR 0; BS 7; V 12+12=24.

Measurement expressed in percent of BL (1150-1681 mm): eye-fork length
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84.7–86.6; first predorsal length 20.3–23.0; second predorsal length 78.7–86.0; prepectoral length 23.6–25.0; prepelvic length 25.0–26.8; first preanal length 58.0–63.2; second preanal length 77.4–83.5; tip of mandible to anus 48.6–53.2; greatest body depth 10.0–14.8; depth of body at origin of first dorsal 10.4–13.2; depth of body at origin of first anal 7.4–12.9; least depth of caudal peduncle 2.9–3.7; width of body at origin of pectorals 4.2–8.4; width of body at origin of first anal 4.6–8.1; head length 22.6–25.1; snout length 10.8–13.4; bill length 20.0–27.5; maxillary length 13.4–16.4; orbit diameter 2.0–2.9; interorbital width 6.0–6.5; anterior height of first dorsal 8.2–18.7; length of middle dorsal spine 5.5–12.3; anterior height of second dorsal 2.6–4.8; height of first anal 6.8–11.7; anterior height of second anal 3.1–4.7; length of pectoral 17.9–24.9; length of pelvic 21.0–24.8; length of second dorsal base 3.7–5.7; length of first anal base 11.8–19.8; length of second anal base 3.3–5.2.

Body elongate; depth of body very low (BL about 8.5 times greatest depth of body) and very compressed. Snout slender and rather long (head length about 1.1 times snout length); its cross section round. Lower jaw also projected but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with elongate scales; each scale with 2–5 posterior points (Fig. 3F). Small file-shaped teeth on both jaws and palatine. Lateral line clear, curving above base of pectoral fin and then continuing in a straight line toward caudal fin. Head rather large (BL about 4.2 times head length). Eye small. Nape straight. Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye, anterior one small slit-like with a posterior flap and posterior one elongate semi-circular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin long and situated low (length of head about 1.2 times of pectoral fin); its shape varies with individuals and many have round tips. First dorsal fin with rounded anterior lobe in most specimens, begins above posterior margin of preopercle; higher than body depth anteriorly and then abruptly decreasing in height to about 9th ray, decreasing height gradually after 9th ray, keeping almost same height medially and posteriorly, ending gradually in front of second dorsal fin. Second dorsal fin small, almost the same size and shape as second anal fin; the latter situated about 1/3 length of its base further forward than the former. First anal fin rather large with round anterior lobe. Pelvic fin slender and almost equal to or slightly longer than pectoral fin. Grooves for first dorsal, pelvic and anal fins present. Caudal fin large, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeleton. Caudal peduncle compressed and slightly depressed with a pair of caudal keels on its lateral side. First dorsal fin dark blue without dots. Second dorsal fin dark blue. Pectoral fin blackish brown, sometimes tinged with greyish white. First anal fin dark blue, base tinged with silvery white. Second anal fin blackish brown, base tinged with silvery white. Caudal fin blackish brown. Pelvic fin blue black with black membrane. Body blue black dorsally, silvery white spattered with brown laterally.
and silvery white ventrally.

Olfactory rosetta radially shaped (Fig. 4), composed of about 43–52 olfactory laminae; capillaries invisible with naked eye on surface of each lamina. Feature of viscera very similar to those of *Istiophorus platypterus* except gonads which form an asymmetrical Y-shape (left lobe of it well developed) (Fig. 8F). Anus situated far forward to origin of first anal fin.

Cranium hard, rather stout and elongate in general; snout portion elongate and post orbital region rather short (Fig. 29). Temporal and pterotic crests close to each other anteriorly and run almost parallel to each other posteriorly. Ventral parts of vomer and anterior parasphenoid rather narrow. Numerous small elongated ridges on frontal. Width between outer margins of right and left lateral ethmoids narrow. Neural and haemal spines of central vertebrae moderately rectangular in shape (Fig. 10F); lateral apophysis not well developed (Fig. 11F).
Remarks. Ueyanagi (1974a) reported the illustration of a larva of 8.3 mm total length. A specimen of 36.8 cm BL was reported Robins and de Sylva (1963).

Outline drawings of five specimens of this species (Nakamura et al., 1968: fig. 18) which were based on field notes, were thought by de Sylva (1973) not to be of *T. pfluegeri*, but appeared to be of *T. georgei* or even an undescribed species. I believe that those five specimens were *T. pfluegeri*, since very wide individual variations are recognized in the external appearances of *T. pfluegeri* and that none of the specimens sampled had the round scales which are a typical characteristic of *T. georgei*. Further examination of those five specimens, however, is not possible, since none of them was kept. Although this species is not distributed around Japan, it is landed in fish markets of Japan. The Japanese name “Kuchinagafuurai” was therefore proposed (Howard and Ueyanagi, 1963).

Size. The largest specimen measured by Robins and de Sylva (1963) was 180.7 cm BL. The most common size often caught by surface longline average about 165 cm BL throughout the fishing grounds of the Atlantic Ocean.

Distribution. This species was reported only rather recently as a new species by Robins and de Sylva (1963). At that time, *T. pfluegeri* was known with certainty only from the western North Atlantic where it occurs from off southern New Jersey to Venezuela and from Texas to Puerto Rico. Recent surveys of research vessels have clearly showed that this species is widely distributed throughout the Atlantic Ocean (Ueyanagi et al., 1970). This species is chiefly distributed in off-shore waters and much more densely distributed in the western Atlantic than the eastern Atlantic. Larvae of this species have been collected in the tropical and subtropical areas of the Atlantic Ocean. The distributional limits based on catch by surface longline of research vessels are approximately lat. 40°N to lat. 35°S in the Atlantic Ocean (Fig. 30). All the areas where larvae have been collected are surrounded by the 24°C surface isotherm.

Fig. 30. Distribution of *Tetrapturus pfluegeri*, based on catch data from Japanese longline fishery. Solid line shows presumed limits of distribution. Dotted area show presumed spawning ground. Broken line shows summer surface isotherm for 24°C (Sverdrup et al., 1961).
Fig. 31. Roundscale spearfish, *Tetrapturus georgei* based on Robins (1974: p. 56, Fig. 1).

*Tetrapturus georgei* Lowe  
(Fig. 31)

Roundscale spearfish

Based on the Mediterranean and eastern Atlantic specimens described by Robins (1974), the following brief description is given since only a piece of skin with scales (UMML 11076) was available to this study.

**Diagnosis.** Scales on sides of body round anteriorly with usually two or three posterior projections (Fig. 3G), scales only slightly imbricate and soft. Scales dorsally and ventrally elongate imbricate and stiff, more typical of Istiophoridae. Anterior lobe of spinous dorsal and anal fins rounded. Spinous dorsal fin high, unspotted. Nape moderately humped. Anus moderately far from anal fin origin, distance between them equal to about one-half height of first anal fin. Pectoral fin long in adults, subequal to pelvic fins, reaching beyond curve of lateral line. Isthmial groove present. Eye moderate about 2.9 percent of body length. Vertebrae 24 (12 + 12).

**Description.**  

\[
\begin{align*}
D_1 & = 43-48; \\
D_2 & = 6-7; \\
A_1 & = 14-16; \\
A_2 & = 5-7; \\
P_1 & = 19-20; \\
GR & = 0; \\
BS & = 7; \\
V & = 12 + 12 = 24.
\end{align*}
\]

Measurements expressed in percent of BL (1540–1600 mm): first predorsal length 22–23; second predorsal length 81; prepectoral length 24–27; prepelvic length 26–29; first preanal length 59–60; second preanal length 79–80; tip of mandible to anus 52–56; greatest depth of body 15–18; depth of body at origin of first dorsal 14–17; depth of body at origin of first anal 13–14; least depth of caudal peduncle 3.4–4.3; width of body at origin of pectorals 6.1–7.5; width of body at origin of first anal 7.2–8.1; head length 24–27; snout length 12–14; bill length 31; maxillary length 15–17; orbit diameter 2.9; anterior height of first dorsal 18–24; length of middle dorsal spine 5.0–9.2; anterior height of second dorsal 3.8–4.4; height of first anal 12–15; anterior height of second anal 3.0–3.3; length of pectoral 21–26; length of pelvic 21–22; length of first dorsal fin base 58–50; length of upper caudal keel 2.6–3.8; length of lower caudal keel 3.1–3.4.

Dorsal profile concave above posterior part of head, nape being moderately humped. Exclusive of sheath for spinous dorsal fin, dorsal and ventral profiles
nearly parallel. Behind this point body narrows rapidly to caudal peduncle. Body fairly robust, being proportionally wider at pectoral and first anal fins than *T. belone* and nearly equal to *T. albidus* in this regard. Dorsal fin moderately high posteriorly, its height at 25th spine varying widely from 5.0 to 9.2 in percent of body length. Anterior lobe of spinous dorsal fin high (18–24 percent of body length) and broadly rounded; first anal fin high (12–15 percent of body length) and broadly rounded. Dorsal fin completely unspotted. None of frozen specimens exhibited bars on body. Pectoral fin long, nearly as long as pelvic fin. Scales on lateral sides of body slightly imbricate, soft and flexible, each rounds anteriorly with two or three posterior spines; scales on dorsal and ventral sides of body more elongate, stiffer and with only one point or two closely approximated points. Lateral line simple as in all species of *Tetrapturus*. Flesh distinctly redder.

Remarks. There are no published records on eggs, larvae and young stages.

Size. There is very little information on size of this species. Three specimens measured by Robins (1974) were 1540, 1570 and 1600 mm BL and 23.5, 20.0 and 21.5 kg BW, respectively.

Distribution. This species is positively known from the specimens reported by Robins (1974) from Sicily, the Straits of Gibraltar and the adjacent Atlantic Ocean off Portugal (Fig. 27).

*Tetrapturus albidus* Poey

(Fig. 32)

White marlin, "Nishimakajiki"

*Tetrapturus albidus* Poey, 1860

*Tetrapturus albidus* Poey, 1860, Memorias sobre la historia natural de la isla de Cuba. 2:237–244, 258–260, pl. 15 (fig. 1), pl. 16 (figs. 2–13), pl. 17 (figs. 1, 5, 6–9, 19–11, 26) (Type-locality: Cuba, Original description). Holotype: 2150 mm long male specimen.


Fig. 32. White marlin, *Tetrapturus albidus*, NRFRL 3213, 1582 mm BL, Caribbean Sea.


Makaira lessonae: Jordan and Evermann, 1926:56–57 (coast of Italy).

Tetraperus imperator: Radcliffe, 1926:112 (Georges Bank).


Tetrapturus georgii: Tortonese, 1940:3, 5–6 (based on a mounted specimen, MZUT 784).

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Tetrapterus belone: Cabo, 1958:57, fig. 93 (Spain, Morocco, misidentification).


Description. D1 38-46; D2 5-6; A1 12-17; A2 5-6; P1 18-21; P2 1, 2; GR 0; BS 7; V 12+12=24.

Measurements expressed in percent of BL (1190-1622): eye-fork length 83.7-86.2; first predorsal length 21.6-24.3; second predorsal length 79.7-82.7; prepectoral length 25.3-27.1; prepelvic length 26.6-29.0; first preanal length 55.7-60.1; second preanal length 77.2-80.3; tip of mandible to anus 51.3-55.4; greatest body depth 13.8-17.7; depth of body at origin of first dorsal 13.6-17.7; depth of body at origin of first anal 11.5-13.6; least depth of caudal peduncle 3.4-4.1; width of body at origin of pectorals 5.4-8.5; width of body at origin of first anal 5.1-5.8; head length 24.8-27.8; snout length 11.8-16.6; bill length 26.0-31.6; maxillary length 15.6-17.0; orbit diameter 2.3-3.1; interorbital width 6.1-6.8; anterior height of first dorsal 17.2-21.5; length of middle dorsal spine 4.4-12.6; anterior height of second dorsal 3.2-5.2; height of first anal 10.9-15.4; anterior height of second anal 3.3-4.5; length of pectoral 17.3-27.2; length of pelvic 18.8-24.6; length of second dorsal base 3.6-4.9; length of first anal base 13.1-16.8; length of second anal base 4.0-5.6; caudal spread 37.8-41.6.

Body elongate and compressed (BL about 6 or 7 times body length, about 11 to 19 times body width). Snout rather slender and long (head length about 0.8 to 1 times bill length), its cross section round. Lower jaw also projected but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Pre dentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with elongated scales; each scale with 1 or 2 posterior points (Fig. 3H). Small file-shaped teeth on both jaws and palatine. Lateral line clear, curving above base of pectoral fin and then continuing in a straight line toward caudal base. Head large (BL about 4 times head length). Eye relatively small. Nape fairly elevated. Basichistoskeletal membranes united with other and free from isthmus. Two nostrils close to each other in front of eye, ante each rior one small slit-like with a posterior flap and posterior one elongate semi circular or triangular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin long and wide, situated low; its shape varies with individuals and many have round
tips. First dorsal fin with rounded anterior lobe in most specimens, originating above posterior margin of preopercle; higher than body depth anteriorly and then abruptly decreasing height to about 12th ray, decreasing height gradually after it, ending gradually in front of second dorsal fin. Second dorsal fin small, almost the same size and shape as second anal fin; the latter situated slightly further forward than the former. First anal fin fairly large with rounded anterior lobe. Pelvic fin slender and almost equal to or slightly shorter than pectoral fin. Grooves for first dorsal, pelvic and first anal fins present. Caudal fin large, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeletons. Caudal peduncle well compressed and slightly depressed with a pair of caudal keels on its lateral sides and a small notch on both dorsal and ventral sides. First dorsal fin dark blue with many black dots. Second dorsal fin dark blue. Pectoral fin blackish brown,
sometimes tinged with greyish white. First anal fin dark blue, its base tinged with silvery white. Caudal fin blackish brown. Pelvic fin blue black with black membrane. Body blue black dorsally, silvery white spattered with brown laterally and silvery white ventrally. Usually no blotches or marks on body, but sometimes with about 15 rows of obscure white stripes on body.

Olfactory rosette radially shaped (Fig. 7H), composed of about 44–50 olfactory laminae; capillaries cannot be seen with naked eye on surface of each lamina. Features of viscera very similar to those of *Istiophorus platypterus* (Fig. 8H). Anus situated close to origin of first anal fin.

Cranium hard, fairly stout and elongate in general; snout portion elongate and post orbital region rather short (Fig. 33). Temporal and pterotic crests close to each other anteriorly and run almost parallel to each other posteriorly. Ventral parts of vomer and anterior parasphenoid rather wide. Many small elongated ridges on ventral surface of frontals. Distance between outer margins of right and left lateral ethmoids rather wide. Neural and haemal spines of central part of vertebrae high rectangular in shape (Fig. 10H), lateral apophysis not well developed (Fig. 11H).

**Remarks.** The early stages of the life history of this species are not well known. The smallest larva, 3.2 mm long, with heavy, pointed opercular spines and lacking the characteristic bill of the adult was reported by Scotton and de Sylva (1972). Two larvae, 6.5 and 11.2 mm TL, with pointed opercular spine and pointed snout were reported by Ueyanagi (1974a). Ueyanagi (1959), also, suggested that some of the larvae collected in the western North Atlantic and identified by Gehringer (1956) as *Istiophorus americanus* might have been white marlin. Juvenile specimens of 124.9 mm TL from North Carolina (de Sylva, 1963a) and 191 mm TL from northwest coast of Cuba (Anon., 1968) were reported. Although this species is not distributed around Japan, it is landed in Japanese fish markets. The Japanese name "Nishimakajiki" was therefore proposed (Howard and Ueyanagi, 1963).

**Size.** The heaviest record of this species in sportfishing is a specimen caught at Victoria, Brazil on Nov. 1, 1975 which weighed 79 kg. Another large specimen was that caught at Pompano Beach, Florida on April 25, 1953, which was 72.3 kg BW and 274.3 cm TL. The size range caught by commercial longlines is between 130 and 210 cm BL (mostly 165 cm BL). Almost all bigger specimens are female as seen in some other species of istiophorids.

**Distribution.** Based on Japanese commercial longline catches, *T. albidus* is distributed over most of the Atlantic Ocean from lat. 45°N to 45°S (Fig. 34). This species is also known from the eastern North Atlantic near the Straits of Gibraltar (Furnestine et al., 1958; Postel, 1959), from the Mediterranean (Tortonese, 1940, 1961, 1962, 1970; Cabo, 1958; Rodoriguez-Roda and Howard, 1962; de Sylva, 1973), and from Bretagne (Legandre, 1928), though these records would seem to be strays from the main population of this species. Japanese longliners have also taken small numbers of this species in the South Atlantic Ocean between lat. 40°S and 45°S (Ueyanagi et al., 1970) and sporadic catches have been recorded from
near Cape Point, South Africa (Penrith and Cram, 1974). Based on recovery of tagged fish released of this species (Mather, 1960; Mather et al., 1975), there is no indication of an extensive migration such as the transoceanic migrations observed in some tunas (Thunnus thynnus and Thunnus alalunga). Three spawning grounds of this species in the western North Atlantic, off Abaco Island, northeast of the Little Bahama Bank, northwest of Grand Bahama Island, and southwest of Bermuda, were postulated on the basis of the larval collections carried out by RV John Elliot Pillsbury between 24 July and 13., Aug., 1964 (Stephens, 1965). Ueyanagi et al., (1970) postulated that T. albidus migrate to subtropical waters to spawn with peak spawning occurring in early summer. Good longline fishing grounds are located in the Gulf of Mexico, the Caribbean Sea, and the western South Atlantic. All the areas where larvae have been collected by Japanese research vessels are surrounded by the 25°C surface isotherm.

**Tetrapturus audax** (Philippi)

(Fig. 35)

Striped marlin, “Makajiki”

*Tetrapturus audax* (Philippi, 1887)

_Histiophorus audax_ Philippi, 1887, Anal. Univ. Chil. 71:35–38, pl. 8, (figs. 2–3) (Type-locality: Iquique, Chile).

_Histiophorus audax:_ Reed, 1897:24 (Chile)/ Delfin, 1899:82 (Iquique, Chile)/ Porter, 1909:290 (Chile)/ Gotschlich, 1913:119 (Valdivia, Chile)/ Quijada, 1913:49 (Chile)/ Fowler, 1951:289 (Chile).

_Istiophorus audax:_ Abbott, 1899:345 (Peru)/ Delfin, 1901:52 (Chile)/ Delfin, 1902:75 (Chile)/ Gigoux, 1943:11 (Chile)/ Oliver, 1943:101 (Chile)/ Fowler, 1944:499 (Chile)/ Fowler, 1945:63, 1 fig. (Chile)/ Fowler, 1951:289 (Chile).

*Tetrapturus mitsukurii* Jordan and Snyder, 1901, J. Coll. Sci. Imp. Univ. Tokyo, 15:303, pl. 16, fig. 5 (Type-locality: Misaki, Japan).
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Fig. 35. Striped marlin, *Tetrapturus audax*, FRSKU (JS 789081), 2090 mm BL, Ine, Wakasa Bay, Japan Sea.

*Tetrapturus mitsukurii*: Jordan and Starks, 1907:71, fig. 5 (southern California)/ Starks and Morris, 1907:191 (southern California)/ Jordan, Tanaka and Snyder, 1913:125 (Sagami Sea and Otaru, Japan, southern California)/ Jordan and Thompson, 1914:240 (Japan)/ Tanaka, 1921:374, fig. 114 (Japan)/ Jordan and Jordan, 1922:30 (Honolulu, Santa Catalina)/ Fowler, 1923:387 (Hawaii)/ Uii, 1924:89 (Wakayama, Japan)/ Jordan, 1925:339-341, 1 fig. (Santa Catalina)/ Jordan and Evermann, 1925:8 (Hawaii)/ Jordan and Hubbs, 1925:222 (Japan)/ Griffin, 1927:143-146, pl. 14 (New Zealand)/ Fowler, 1931:325 (Honolulu)/ Tanaka, 1936:149-150 (Japan)/ Oshima, 1940:456-457, fig. 540 (given as this species but the figure shows *Makaira indica*, Taiwan)/ Tanaka, 1951:56, fig. 138 (Japan)/ Tanaka and Abe, 1955:90, 1 fig. (Japan)/ Berdegue, 1956:111-112, fig. 116 (Mexico).


Marлина Mitsukuri: Grey, 1928:47–52, 1 fig. (New Zealand).

Marлина kohli: Jordan, Evermann and Clark, 1930:263 (Pacific Ocean).


Tetropeterus brevirostris: Hiyama, 1943:527, fig. 221 (Indo-West Pacific).

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**Kajikia formosana** Hirasaka and Nakamura, 1947, Bull. Oceanogr. Inst. Taiwan, 3:13–14, 1 fig. (Type-locality: Taiwan).

**Kajikia formosana**: Nakamura, 1949:64–65 (Taiwan); Chen, 1951:311 (Taiwan); Chen, 1956:126 (Taiwan); Chen, 1969:305 (Taiwan).

**Tetrapturus tenuirostratus** Deramoyagala, 1951, Ceylon J. Sci., 26(2):139, pl. 1 (fig. b), pl. 2 (fig. b) (Type-locality: Indian Ocean). Holotype: said to be a mounted specimen in BMNH (site: Jones and Silas, 1964).

**Tetrapturus acutirostratus** Deraniyagala, 1952, A coloured Atlas of some vertebrates from Ceylon. I. Fishes. pl. 27 (apparently plate figure is erroneously labelled as *Tetrapturus acutirostratus* instead of *Tetrapturus tenuirostratus* on p. 105).

**Tetrapturus brevirostris** Deraniyagala, 1933:53 (Sri Lanka). Munro, 1955:223, pl. 43 (fig. 655) (Sri Lanka).


**Marlina audax**: Smith, 1956a:30 (South Africa).


**Makaira tenuirostratus**: Devalaj, 1974:312 (Gulf of Mannar).


**Diagnosis.** Bill long, stout and round in cross section. Anterior lobe of first...
dorsal fin higher than body depth mostly, then height decreasing posteriorly. Tips of first dorsal, first anal and pectoral fins pointed. Nape fairly elevated. Anus situated near origin of first anal fin.

**Description.** D₁ 37-42; D₂ 5-6; A₁ 13-18; A₂ 5-6; P₁ 18-22; P₂ 1, 2; GR 0; BS 7; V 12+12=24.

Measurements expressed in percent of BL (993-2550 mm): eye-fork length 83.9-86.1; first predorsal length 23.4-24.5; second predorsal length 23.4-24.4; prepectoral length 26.8-28.2; prepelvic length 27.5-28.8; first preanal length 57.4-62.9; second preanal length 79.0-81.8; tip of mandible to anus 56.2-59.2; greatest depth of body 14.2-16.8; depth of body at origin of first dorsal 13.8-16.6; depth of body at origin of first anal 9.8-13.5; least depth of caudal peduncle 3.8-4.7; width of body at origin of pectorals 6.1-9.3; width of body at origin of first anal 5.4-9.7; head length 25.6-27.7; snout length 12.7-14.4; bill length 27.5-30.2; maxillary length 15.9-17.8; orbit diameter 2.3-3.2; interorbital width 6.1-6.4; anterior height of first dorsal 18.6-24.4; length of middle dorsal spine 6.7-14.4; anterior height of second dorsal 3.9-5.1; height of first anal 11.2-14.0; anterior height of second anal 3.1-4.4; length of pectoral 13.4-23.5; length of pelvic 15.0-26.8; length of first dorsal base 56.2-59.7; length of second dorsal base 3.9-5.0; length of first anal base 12.7-18.2; length of second anal base 4.0-5.4; caudal spread 38.4-42.2; length of upper lobe of caudal 26.6-27.4; length of lower lobe of caudal 24.8-25.5; length of upper keel 3.5-3.6; length of lower keel 3.3-3.4.

Body elongate and compressed (BL about 6 or 7 times body depth, about 11 to 16 times body width). Snout fairly stout and long (head length about 0.9 to 1 times bill length), its cross section round. Lower jaw also projected forward but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with elongated scales, each with 1 or 2 posterior points (Fig. 31). Small file-shaped teeth on both jaws and palatines. Lateral line single and obvious, curving above base of pectoral fin, then running straight to base of caudal fin. Head large (BL about 3.7 times head length). Eye relatively small. Nape fairly elevated. Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye, anterior one small slit-like with a posterior flap and posterior one elongate semi-circular in shape. No gill-rakers. Pseudobranchiae present. Pectoral fin long and narrow, situated low on body, its tip pointed. First dorsal fin with pointed anterior lobe, originating above posterior margin of preopercle; higher than or equal to in few cases body depth anteriorly and then abruptly decreasing height to about 10th ray, decreasing height gradually after it, ending gradually in front of second dorsal fin. First anal fin fairly large and sickle-shaped, with its tip pointed. Second dorsal fin and second anal fin about the same size and shape, the latter located slightly further forward than the former. Pelvic fin slender, slightly shorter than pectoral fin in large specimens and slightly longer than pectoral fin in smaller specimens. Grooves for first dorsal, pelvic and first anal fins present. Caudal fin large, deeply
forked and powerful; caudal fin rays deeply cover complex of caudal skeletons. Caudal peduncle well compressed and slightly depressed with a pair of caudal keels on its lateral sides and a small notch on both dorsal and ventral sides. First dorsal fin dark blue. Other fins usually dark brown, sometimes tinged with dark blue; bases of first and second anal fins tinged with silvery white. Body blue black dorsally and silvery white ventrally. About 15 rows of cobalt-colored stripes on body, each stripe consisting of round dots and/or narrow bands.

Olfactory rosette radially shaped (Fig. 71), composed of about 46–51 olfactory laminae; capillaries cannot be seen with naked eye on surface of each lamina.

Fig. 36. Cranium of *Tetrapturus audax*, 1638 mm BL, northwestern Pacific.
Features of viscera very similar to those of Istiophorus platypterus (Fig. 8I). Anus situated close to origin of first anal fin.

Cranium hard, fairly stout and elongate in general appearance; snout portion elongate and post orbital region rather short (Fig. 36). Temporal and pterotic crests parallel to each other. Ventral surface of frontals rather flat, but having many small elongated slits. Distance between outer margins of right and left lateral ethmoids rather wide. Neural and haemal spines in central part of vertebrae high rectangular in shape (Fig. 101), lateral apophysis not well developed (Fig. 111).

Remarks. Kamimura and Honma (1958) and Honma and Kamimura (1958) proposed the hypothesis that north and south populations are quite separate from each other and may belong to different species. Howard and Ueyanagi (1965) pointed out that striped marlin do occur in their extreme northern range (southern California) during late summer and fall when surface temperatures reach a peak, but it is not clear whether these fish have come from the south or from the west. The postlarval stage of this species is described in detail by Ueyanagi (1959). The study was based on 40 specimens captured by surface larvae net tows. These ranged from 2.9 to 21.2 mm standard length, and were collected from the northwestern Pacific, South Pacific and Indian oceans. Two juveniles of this species (122, 145 mm standard length), collected from the South Pacific and western Indian oceans, were described by Nakamura (1968).

Size. The heaviest record of this species in sportfishing is a specimen caught in the Cavalli Islands, New Zealand on Jan. 14, 1977, weighing 189.4 kg. Another large specimen was caught at Whakatane, New Zealand on Feb. 26, 1972, weighing 165.6 kg and measuring 341.6 cm TL. The size range caught by commercial longlines is mainly between 205 and 225 cm BL in the north of the northwestern Pacific, between 145 and 185 cm BL in the south of the northwestern Pacific, between 235 and 255 cm BL in the centralnorth Pacific and about 280 cm BL in the western-south Pacific.

Distribution. T. audax is chiefly distributed in the tropical and temperate waters of the Pacific and Indian oceans (Fig. 37). Based on Japanese longline catch data, the distributional pattern of this species in the Pacific is horseshoe-shaped with the base located along the central American coast. Talbot and Penrith (1962b) stated that this species is occasionally found on the Atlantic side of the Cape of Good Hope. A specimen of this species was caught off Angola on Oct. 1976 (Nakano, S., Person. Comm.), though it is probable that this specimen may have only strayed from the Indian Ocean as in the case of T. angustirostris and M. indica. Ueyanagi et al. (1970) reported the occurrence of this species west of Cape Town (0–3°E, 30–34°S). The latitudinal limits based on data from the commercial longline fishery are about lat. 45°N to lat. 35–40°S in the Pacific Ocean, as far south as lat. 45°S in the western South Indian Ocean and lat. 35°S in the eastern South Indian Ocean.

Although eggs of this species have not been identified, there are several reports on larvae (Ueyanagi, 1959, 1964; Jones and Kumaran, 1964a, b; Ueyanagi and Wares, 1975). In the Pacific, larvae have been found in the northwestern Pacific.
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Fig. 37. Distribution of *Tetrapturus audax*, based on catch data from Japanese longline fishery. Solid line shows presumed limits of distribution. Dotted area shows presumed spawning ground. Broken line shows summer surface isotherm for 24°C (Sverdrup et al., 1961). Dot-dash line shows presumed invasion of this species from the Indian Ocean to the Atlantic Ocean.

(west of long. 180°E) between lat. 10° and 30°N and in the South Pacific (west of long. 130°W) between lat. 10° and 30°S. The larvae are most abundant in early summer, with peak occurrence in the northwestern Pacific in May and June and in the South Pacific in November and December. In the Indian Ocean, larvae have been reported to occur in the Banda and Timor seas during January and February (Ueyanagi, 1959) and in the western Indian Ocean during December and January between lat. 10°S and 18°S and in the eastern Indian Ocean during October to November between lat. 6°N and 6°S (Jones and Kumaran, 1964a). The spawning grounds presumed by the distribution of larvae and juveniles are surrounded by the 24°C surface isotherm in the summer season (Fig. 37).

**Genus Makaira Lacepède**

*Makaira* Lacepède, 1802, Histoire naturelle des poissons. 1802, 4:688-695, pl. 13 (fig. 3) (Type-species: *Makaira nigricans* Lacepède, based on notes and a sketch of a 365 kg specimen washed up on a beach at Ile du Re, Bay of Biscay and sent to Lacepède by MM Treversay, Fleuriau-Bellevue and Lamathe [vide Morrow, 1959a]).


*Macaira* Nardo, 1833, Isis (Oken), 26(4):418 (emended spelling of *Makaira*).


*Eumakaira* Hirasaka and Nakamura, 1947, Bull Oceanogr. Inst. Taiwan, (3):16, pl. 2 (fig. 2) (Type-species: *Eumakaira nigra* Hirasaka and Nakamura).


Height of dorsal fin less than body depth. Pelvic fin shorter than pectoral

**Makaira mazara** (Jordan and Snyder)

(Fig. 38)

Indo-Pacific blue marlin, “Kurokajiki”

*Makaira mazara* (Jordan and Snyder, 1901)


Fig. 38. Indo-Pacific blue marlin, *Makaira mazara*, NRFRL 3203, 1878 mm BL, western-north Pacific.

**Makaira herscheli**: Barnard, 1927:808 (Table Bay, East London)/ Barnard, 1947 183, pl. 21 (fig. 17) (South Africa)/ Smith, 1949:315, pl. 67 (fig. 875) (South Africa)/ Rosa, 1950:139 (Indian Ocean)/ Smith, 1956a:26, pls. 1-2 (South Africa).


**Eumakaira nigra** Hiraseka and Namakura, 1947, Bull. Oceanog. Inst. Taiwan, 3:16-18, pl. 2 (fig. 2) (Type-locality: Taiwan).


**Makaira mitsukurii**: Herre, 1953:255-256 (in part, Japan, Hawaii only).


**Tetrapturus herschelii**: Ogilby, 1954:91 (Queensland).

**Tetrapturus herschelii**: Ogilby, 1954:91 (Queensland).

**Istiompax howardi**: Whiteley, 1954a, Aust. Zoologist, 12(1):58-60, pl. 3 (fig. 3) (Type-locality: Bermagui, New South Wales).


**Makaira ampla**: Rivas, 1956b:59-72, fig. a (in part, northeastern Pacific Ocean)/ Royce, 1957:532-538, fig. 2 (f), fig. 3 (b) (Pacific Ocean)/ Gosline and Brock, 1960:264, fig. 258d (Hawaii)/ Munro, 1958a:115, fig. 764 (Australia)/ Grant, 1965:178, 1 fig. (Queensland)/ Grant, 1972:115, 1 fig. (Queensland)/ Jaleel and Uddin, 1972:12 (Pakistan)/ Grant, 1975:176, 1 fig. (Queensland).
**Isiompax mazara:** Whitley, 1968b:74 (New Zealand).

**Makaira herschelii:** Smith, 1956b:758 (East Africa).

**Makaira nigra:** Abe, 1957:320-321, 1 fig. (Japan).

**Makaira (Makaira)nigricans:** Robins and de Sylva, 1961:406 (Indo-Pacific, subgenus name proposed).


**Diagnosis.** Bill long, extremely stout and round in cross section. Anterior lobe of first dorsal fin lower than body depth. Pectoral fin can lie flat. Nape extremely elevated. Lateral line system forms loop pattern. Anus situated near origin of first anal fin.

**Description.** Immatures (810-1209 mm BL) followed by adults (1322-1878) in parentheses: D 1 40-45 (40-43); D 2 6-7 (6-7); A 1 12-17 (14-15); A 2 6-7 (6-7); P 1 21-23 (20-22); P 2 I, 2 (I, 2); GR 0 (0); BS 7 (7); V 11+13=24 (11 + 13=24).

Measurements expressed in percent of BL: eye-fork length 88.6-89.6 (86.8-87.8); first predorsal length 18.2-22.3 (16.7-22.5); second predorsal length 75.3-78.5 (77.3-77.8); prepectoral length 22.3-24.3 (22.8-23.8); prepelvic length 22.9-25.3 (23.1-24.3); first preanal length 55.2-55.9 (55.7-58.4); second preanal length 74.6-76.5 (75.2-76.3); tip of mandible to anus 50.9-55.3 (51.8-55.3); greatest depth of body 13.3-16.0 (13.9-18.5); depth of body at origin of first dorsal 13.0-16.0 (13.5-17.9); depth of body at origin of first anal 10.3-12.9 (7.9-14.6); least depth of caudal peduncle 2.7-4.3 (2.8-3.9); width of body at origin of pectorals 6.6-8.5 (6.2-8.4); width of body at origin of first anal 5.1-8.5 (4.5-9.2); head length 22.8-24.3 (23.1-24.9); snout length 7.9-10.8 (8.6-10.6); bill length 8.9-17.0 (24.0-28.2); maxillary length 13.1-14.0 (12.3-14.4); orbit diameter 2.8-5.3 (2.9-4.8); interorbital width 6.3-6.5 (6.3-7.0); anterior height of first dorsal 11.0-22.4 (16.1-18.0); length of middle dorsal spine 3.1-11.6 (3.5-4.2); anterior height of second dorsal 3.2-5.1 (3.2-4.3); height of first anal 9.4-11.0 (12.4-14.2); anterior height of second anal 3.2-4.0 (3.0-3.6); length of pectoral 11.3-13.1 (10.4-23.5); length of pelvic 22.6-26.4 (19.9-29.1); length of second dorsal base 4.3-6.8 (5.1-7.0); length of first anal base 14.3-17.7 (16.0-16.1); length of second anal base 5.5-7.2 (5.4-9.1); caudal spread 17.7-20.0 (36.8-42.9).

Body elongate but robust and less compressed (BL about 5.0 to 5.4 times body depth, about 10.5 to 11 times body width in adults; about 6.3 to 7.4, about 12-16 respectively in immatures). Snout extremely stout and long (head length about 0.9 to 1 times bill length in adults, about 1.4 to 1.8 in immatures); snout cross section round. Lower jaw also stout and projected forward but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with thick elongated scales, each with 1 or...
2 sometimes 3 posterior points (Fig. 3J). Small file-shaped teeth on both jaws and palatine. Lateral line forms complicated loop pattern, obvious in immatures but obscure in adults, becoming imbedded in skin with size; however, line becomes visible if epidermis removed (Fig. 39). Head large (BL about 4.2 times head length in adults, about 4.4 in immatures). Eye relatively small. Nape extremely elevated. Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye, anterior one small slit-like with a posterior flap and posterior one small elongate semi-circular in shape. No gillrakers. Pseudobranchiae present. Pectoral fin long and narrow in adults, rather short and narrow in immatures. First dorsal fin with pointed anterior lobe, originating above posterior margin of preopercle; lower than body depth throughout its entire length. First anal fin fairly large and sickle-shape with its tip pointed. Second dorsal fin and second anal fin about the same size and shape, the latter located slightly further forward than the former. Pelvic fin slender, shorter than pectoral fin in the largest

![Diagram of lateral line systems](image)

Fig. 39. Schematic drawings of lateral line systems of the Indo-Pacific blue marlin (A–L) and the Atlantic blue marlin (M–T). Body length: A. 18 cm, B. 19 cm, C. 81 cm, D. 84 cm, E. 113 cm, F. 120 cm, G. 121 cm, H. 121 cm, I. 132 cm, J. 185 cm, K. 260 cm, L. ca. 400 cm, M. 20 cm, N. ca. 60 cm, O. ca. 135 cm, P. 140 cm, Q. ca. 155 cm, R. ca. 160 cm, S. 188 cm, T. 205 cm. Lateral line systems of the Atlantic blue marlin are partly visible. Scales are not the same.
specimen examined and longer than pectoral fin in other (smaller) specimens. Deep grooves for first dorsal, pelvic and first anal fins present. Caudal fin large, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeletons. Caudal peduncle fairly compressed and slightly depressed with a pair of caudal keels in its lateral side and a small notch on both dorsal and ventral sides. First dorsal fin blackish dark blue. Other fins usually brown black, sometimes tinged with dark blue; bases of first and second anal fins tinged with silvery white. Body blue black dorsally and silvery white ventrally. About 15 rows of pale cobalt-colored stripes on body, each stripe consisting of round dots and/or narrow bands. Stripes not visible in long preserved specimens.

Olfactory rosette radially shaped (Fig. 7J), composed of about 48–51 olfactory
laminae; no capillaries visible with naked eye on surface of each lamina. Features of viscera very similar to those of Istiophorus platypterus (Fig. 8J). Anus situated close to origin of first anal fin.

Cranium hard, extremely stout; snout portion elongate and post orbital region rather short (Fig. 40). Temporal and pterotic crests parallel to each other. Ventral surface of frontal rather flat, but having many small elongated slits there. Distance between outer margins of right and left lateral ethmoids wide. Neural and haemal spines of central part of vertebrae high trapezoid in shape (Fig. 10J). Lateral apophysis remarkably developed (Fig. 11J).

Remarks. “Black marlin” as the English common name for Makaira mazara was often used among Japanese scientists until the mid-1960's. The name, “Black marlin” is a direct translation of the Japanese common name, “Kurokajiki” for this species. Although the general appearance of both the Indo-Pacific blue marlin and the Atlantic blue marlin is so similar, the lateral line system of each species is quite different as shown in Fig. 39. Therefore, I recognize the Indo-Pacific blue marlin as Makaira mazara and the Atlantic blue marlin as Makaira nigricans. Many authors have held that Makaira nigricans constitutes a single species occurring in the Atlantic, Indian and Pacific oceans (e.g., Rivas, 1975; Royce, 1957; Briggs, 1960; Robins and de Sylva, 1961; Jones and Silas, 1964; Morrow, 1964).

Eight larval specimens of this species, ranging in length from 2.9 to 23.2 mm TL were collected in the western Pacific (Ueyanagi and Yabe, 1959). Ueyanagi (1964) reported on 1015 larvae from the Pacific and 35 larvae from the Indian Ocean including the Banda and Timor seas, ranging in length from 3 to 33 mm TL. Juveniles and young of this species, ranging from 111 to 755 mm EF, were reported from the western Pacific, South Pacific and Indian oceans (Ueyanagi, 1957a).

Feeding behavior of this species has been observed off Baja California by T. Sato (Person. Comm.) who informed me as follows (Fig. 41). “After a blue marlin, about 3 m BL found the squids (Dosidicus gigas, about 40 cm mantle length) gathering under the night light of a squid fishing boat, it came near the squids with almost full speed with fins completely held back in the grooves (A). Then it suddenly hit them with the bill (B). It subsequently nudged the stunned squid (C) and ate it head first (D)”.

This species has often been observed to swallow skipjack, Katsuwonus pelamis and bigeye tuna, Thunnus obesus, head first and those fishes usually had deep scars on their body (Togo, S., Person. Comm.). These observations confirm Wisner's (1958) extensive discussions which show that it is most likely that the billfishes often use the bill for feeding.

Size. The heaviest record of this species in sportfishing is 818 kg “Choys monster” from Hawaii (Mather, 1976), and second is a specimen caught at Ritidian Point, Guam on Aug. 21, 1969, which weighed 523 kg and measured 447 cm TL. Another large specimen was caught at Le Morne, Mauritius on Feb. 20, 1966, weighing 499 kg and measuring 420.4 cm TL. I observed a specimen which has been caught by a commercial longliner in the Java Sea and landed at Yaizu Fish Market on May 31, 1967, which was 3.51 m BL and 490 kg BW without viscera, bill and
tips of each fin removed. Size ranges caught by commercial longlines average between 200 and 285 cm BL in the equatorial waters of the North Pacific Ocean and between 215 and 300 cm BL in the Indian Ocean.

**Distribution.** This species is distributed chiefly in the tropical and temperate waters of the Indian and Pacific oceans (Fig. 42). The Indo-Pacific blue marlin is the most tropical of the billfish species and it is primarily distributed in equatorial waters. The latitudinal limits based on data from the commercial longline fishery are about lat. 45°N in the western North Pacific Ocean, lat. 35°N in the eastern North Pacific Ocean, lat. 35°S in the South Pacific Ocean, lat. 40–45°S in the western South Indian Ocean and lat. 35°S in the eastern South Indian Ocean. Good fishing grounds for commercial longlining are found in the equatorial central and tropical North Pacific, the South Pacific and the equatorial Indian Ocean.

Laevae of this species have been extensively collected in the Pacific Ocean, around northern New Guinea, the Carolines, the Gilberts, the Marshalls, the Bonin Islands, Wake Island, the Marcus Islands, the Coral Sea, the Kuroshio current and in the central equatorial Pacific (Jones and Kumaran, 1964b; Ueyanagi, 1964; Howard and Ueyanagi, 1965) and in the Indian Ocean, off northwestern Australia, the west coast of Sumatra, the east coast of Madagascar and the south coast of Sri
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Fig. 42. Distribution of *Makaira mazara*, based on catch data from Japanese longline fishery. Solid line shows presumed limits of distribution. Dotted area shows presumed spawning ground. Broken line shows summer surface isotherm for 24°C (Sverdrup et al., 1961).

Lanka (Jones and Kumaran, 1964b; Ueyanagi, 1964). All these areas of larval collections are surrounded by the 24°C surface isotherm in the summer season (Fig. 42).

*Makaira nigricans* Lacepède

(Fig. 43)

Atlantic blue marlin, "Nishikurokajiki"

*Mathyrnigricans* Lacepède, 1802


Fig. 43. Atlantic blue marlin, *Makaira nigricans*, NRFRL 3201, 2036 mm BL, Caribbean Sea.
Xiphias makaira Shaw, 1803, General zoology or systematic natural history ...... 4:104 (after Lacepède).


Histiophorus herschelii: Günther, 1860:513 (Table Bay).

Tetrapturus amplus Poey, 1860, Memorias sobe la historia natural de la isla de Cuba. 2:237, 243–244, pl. 15 (fig. 2), pls. 16–17 (figs. 12–25) (Type-locality: Cuba). Holotype: a specimen 2453 mm long, Poey Collection Reg. No. 190.


Makaira herschelii: Jordan and Evermann, 1926:69 (Cape of Good Hope)


Makaira eisii: Jordan and Evermann, 1926:57–58, fig. 1 (West coast of France).


Makaira bermudae: Beebe and Tee-Van, 1933:98–99, 1 fig. (Bermuda).
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Makaira nigricans nigricans: Nichols and LaMonte, 1935b:328 (France).
Makaira nigricans ampla: Nichols and LaMonte, 1935b:328 (Cuba)/ Conrad and LaMonte, 1937: 207–220 (Bahama)/ Shapiro, 1938:1–17, fig. 2 (Bahama)/ Shapiro, 1943:87–103 (South Atlantic coast of US and Gulf of Mexico)/ LaMonte, 1944:258 (Cuba)/ LaMonte, 1945:31 pl. 12 (northwestern Atlantic)/ Rosa, 1950:145 (Caribbean Sea, northwestern Atlantic Ocean)/ Allyn, 1951:72 (Gulf Stream)/ LaMonte, 1952:24, pl. 24 (North Atlantic Ocean)/ Mather and Day, 1954:186, pl. 2 (tropical Atlantic Ocean)/ Pew, 1954:32, fig. 31 (Texas).
Orthocraeros bermudae: Smith, 1956a:31–32, pl. 1 (fig. I) (Bermuda, new genus name proposed).
Tetrapterus belone: Cabo, 1958:57, fig. 94 (Spain and Morocco, misidentification).
Makaira (Makaira) nigricans: Robins and de Sylva, 1961:406 (subgenus name proposed).

Material examined. FSRFL B113, 1 specimen (1992 mm), 20°29'N, 70°31'W, June 6, 1957; FRSKU (A6701081), 1 (1879), 4°54'N, 34°51'W, Jan. 8, 1967; NRFRL 3201, 1 (2036), June 1, 1957, 17°25'N, 68°45'W, June 1, 1957; FRSKU (A6701311), 1 (2059), 12°34'N, 63°14'W, Jan. 1, 1967; FRSKU (C6912001–6912005), 5 (1866–2220), Caribbean Sea, Dec. 1969.


Description. D 1 39–43; D 2 6–7; A 1 13–16; A 2 6–7; P 1 19–22; P 2 I, 2; GR 0; BS 7; V 11 + 13 = 24.

Measurements expressed in percent of BL (1866–2220 mm): eye-fork length 86.1–89.6; first predorsal length 20.1–25.0; second predorsal length 76.2–78.9; prepectoral length 22.3–25.3; prepelvic length 22.6–25.3; first preanal length 55.1–58.4; second preanal length 73.6–76.6; tip of mandible to anus 50.3–54.1; greatest depth of body 17.8–20.4; depth of body at origin of first dorsal 17.8–19.2; depth of body at origin of first anal 16.3–18.0; least depth of caudal peduncle 4.0–4.6; width of body at origin of pectorals 8.0–10.7; width of body at origin of first anal 9.1–10.8; head length 22.3–25.0; snout length 10.0–12.9; bill length 24.2–26.5; maxillary length 14.0–15.9; orbit diameter 2.2–3.1; interorbital width 6.2–6.8; anterior height of first dorsal 15.3–19.6; length of middle dorsal spine 2.9–5.4; anterior height of second dorsal 2.6–4.8; height of first anal 11.7–15.1; anterior height of second anal 3.0–4.1; length of pectoral 19.4–24.0; length of pelvic 15.3–22.3; length of second dorsal base 4.5–5.4; length of first anal base 15.7–17.8; length of second anal base 5.2–5.5.

Body elongate but robust and less compressed (BL about 5.2 to 5.6 times body depth, about 9.3 to 11.0 times body width). Snout extremely stout and long (head length about 0.9 to 1 times bill length); its cross section round. Lower jaw also stout and projected forward but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout non-protractile. Predentary present.
Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with thick elongated scales, each with mostly 1, sometimes 2 or 3 posterior points (Fig. 3K). Small file-shaped teeth on both jaws and palatine. Lateral line forms complicated network pattern, obvious in immatures but obscure in adults, being imbedded in skin with size. However, the line becomes visible, if epidermis removed (Fig. 39). Head large (BL about 4 to 4.5 times head length). Eye relatively small. Nape extremely elevated. Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye, anterior one small and slit-like with a posterior flap, and posterior one small and elongate semi-circular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin long and narrow. First dorsal fin with pointed anterior lobe, originating above posterior margin of preopercle; lower than body depth throughout its entire length. First anal fin fairly large and sickle-like in shape with pointed lobe. Second dorsal fin and second anal fin almost the same size and shape, the latter located slightly further forward than the former. Pelvic fin slender, shorter than pectoral fin in the specimens examined (rather larger adult specimens). Deep grooves for first dorsal, pelvic and first anal fins present. Caudal fin large, falcated and deeply forked; caudal fin rays deeply cover complex of caudal skeletons. Caudal peduncle fairly compressed and slightly depressed with a pair of caudal keels on its lateral side and a small notch on both dorsal and ventral sides. First dorsal fin blackish dark blue. Other fins usually brown black, sometimes tinged with dark blue; bases of first and second anal fins often tinged with silvery white. Body blue black dorsally and silvery white ventrally. About 15 rows of pale cobalt-colored stripes on body, each stripe consisting of round dots and/or narrow bands.

Olfactory rosette radially shaped (Fig. 7K), composed of about 47–54 olfactory laminae; no capillaries visible with naked eye on surface of each lamina. Features of viscera very similar to those of *Istiophorus platypterus* (Fig. 8K). Anus situated close to origin of first anal fin.

Cranium hard, extremely stout; snout portion elongate and post orbital region rather short (Fig. 44). Temporal and pterotic crests parallel to each other. Ventral surface of frontals rather flat, but covered with many small elongated slits. Distance between outer margins of right and left lateral ethmoids wide. Neural and haemal spines of central part of vertebrae high trapezoid in shape (Fig. 10K). Lateral apophysis remarkably developed (Fig. 11K).

Remarks. This species is very similar to the Indo-Pacific blue marlin, *Makaira mazara*, but the lateral line system of this species is different from that of *Makaira mazara* as previously stated. The Japanese standard name for this species was proposed as “Nishikurokajiki” by Nakamura et al. (1968), because of the importance of this species to the Japanese commercial longline fisheries.

Three unidentified larvae reported by Gehringer (1956) from the western Atlantic off Georgia were later identified as this species by Ueyanagi and Yabe (1959). Eschmeyer and Bullis (1968) reported 4 larvae from the western Atlantic. Bartlett and Haedrich (1968) reported 85 larvae from off Brazil between Cabo de Sao Roque.
Juveniles were reported from Jamaica by de Sylva (1963b) and Caldwell (1962b). Ueyanagi et al. (1970) discussed the seasonal distribution of larvae of this species in the Atlantic Ocean.

**Size.** The heaviest record of this species in sportfishing is a specimen caught at St. Thomas, Virgin Islands on Aug. 6, 1977, which weighed 581.5 kg. Many anglers claim to have seen this species over 682 kg or 1,500 lbs. (Mather, 1976). Schwartz (1961) stated that the record length for this species was specimen measuring about 3.9 m TL. However, gamefishing records indicate a specimen measuring 398.8 cm TL and weighing only 319.8 kg. The most common length range caught by Japanese commercial longlines is 200–275 cm BL. Throughout the Atlantic, the size range caught by commercial longlines is 115 cm to 345 cm TL. However, in the equatorial Atlantic, the proportion of small fish in the overall catch
increases between November and April, thereby decreasing the overall size range. It is well recognized that females attain much larger sizes than males.

**Distribution.** This species is distributed mainly in the tropical and temperate waters of the Atlantic Ocean and is the most tropical species of the Atlantic billfishes (Fig. 45). The rate of hooks set in the commercial longline fishery is high in the western Atlantic and low in the eastern Atlantic. Good fishing grounds are found in the Gulf of Mexico and the Caribbean Sea between May and October (especially from July to September) and in the Brazil Current between November and April (especially from January to March). The latitudinal limits based on data from the commercial longline fishery are about lat. 40°N to 40°S in the Atlantic Ocean.

Based on larval collections and occurrence of mature adults, the spawning grounds of this species are found off Brazil between lat. 10° and 30°S from November through April. All the areas where larvae have been collected are surrounded by the 25°C surface isotherm.

**Makaira indica** (Cuvier)

(Fig. 46)

Black marlin, “Shirokajiki”

*Makaira indica* (Cuvier, 1832)


*Tetrapturus Australis* Macleay, 1854, Illus. Sydney News, 1 (23):179, 1 fig. (Locality: Broken Bay, Australia; *nomen nudum*).
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**Fig. 46.** Black marlin, *Makaira indica*, FAKU 29323, 1848 mm BL, Tai, Wakasa Bay, Japan Sea.


*Histiophorus brevirostris*: Pollen, 1874:75 (Madagascar)/ Day, 1878:199, fig. 3, pl. 17 (Madras, India)/ Day, 1889:132–133, fig. 52 (India)/ Qureshi, 1955:43 (Pakistan).


Makaira indicus: Deraniyagala, 1933b:55-56, pl. 3 (Sri Lanka).


Makaira nigricans tahitiensis Nichols and LaMonte, 1935a, Amer. Mus. Novit., (807):1-2, fig. 1 (Type locality: Tahiti).


Makaira brevirostris: LaMonte and Marcy, 1941:2 (Zanzibar).

Makaira ampla marlina: LaMonte and Marcy, 1941:2 (Pacific Ocean)/ Nichols and LaMonte, 1952:65 (Pacific Ocean)/ Rosa, 1950:144 (Pacific Ocean).


Makaira brevirostris: LaMonte and Marcy, 1941:2 (Zanzibar).

Makaira ampla marlina: LaMonte and Marcy, 1941:2 (Pacific Ocean)/ Nichols and LaMonte, 1941:8, fig. 1 (Pacific Ocean)/ Bini and Tortonese, 1955:33-34 (Peru, Chile).

Makaira ampla tahitiensis: LaMonte and Marcy, 1941:2 (Tahiti, Hawaii)/ Nichols and LaMonte, 1941:8, fig. 3 (Tahiti, Hawaii).


Malina malina: Chen, 1951:311 (Taiwan; misprint for Martina marlina).

Makaira marlina: Mori, 1952:138 (southern Korea; misprint for Makaira marlina)/ Chyung, 1961:515-516, fig. 162 (southern Korea; misprint for Makaira marlina).
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*Makaira nigricans*: LaMonte, 1952:62, 65, pl. 23 (Pacific Ocean).


*makaira marlina*: Chuyng, 1954:368 (Korea; misprint for *Makaira marlina*).


*Makaira mazara tahitiensis*: LaMonte, 1955:342-343, pl. 10 (Pacific Ocean)/ LaMonte, 1958b:396 (Mexico).


*Istiompax marlina*: Royce, 1957:524-528, figs. 2d, 3a (Pacific Ocean)/ Munro, 1958a:115, fig. 765 (Australia)/ Gosline and Brock, 1960:264, fig. 258c (Hawaii)/ Caldwell, 1962a:467-468 (Pacific coast of Mexico)/ Talbot and Penrith, 1962a:468 (South Africa)/ Munro, 1967:205, pl. 22 (New Guinea)/ Grant, 1975:174, 1 fig., colour pl. 42 (Queensland).


*Istiompax indicus*: Abe, 1963:92, fig. 274 (Japan; misprint of *Istiompax indicus*)/ Temiyama, Abe and Tokioka, 1969:213, fig. 632 (Japan; misprint of *Istiompax indicus*).


*Makaira mitsukurii*: Ueno, 1971:79 (Hokkaido; adopted erroneously to *Makaira indica*).


**Description.** Immature (1080 mm BL) followed by adults (1620-3620) in parentheses. $D_1$ 35 (34-42); $D_2$ 7 (5-7); $A_1$ 11 (10-14); $A_2$ 6 (6-7); $P_1$ 20 (18-20); $P_2$ I, 2 (I, 2); GR O (0); BS 7 (7); $V = (11+13=24)$. 
Measurements expressed as percent of BL: eye-fork length 85.6 (86.5–87.9); first predorsal length 19.8 (20.8–25.5); second predorsal length 78.8 (76.4–86.6); prepectoral length 23.6 (20.6–27.1); prepelvic length 25.6 (22.9–30.4); first preanal length 58.5 (54.5–67.6); second preanal length 78.2 (77.2–80.5); tip of mandible to anus 53.2 (51.7–59.5); greatest depth of body 16.6 (17.3–22.7); depth of body at origin of first dorsal 16.5 (18.2–19.6); depth of body at origin of first anal 14.0 (15.5–16.6); least depth of caudal peduncle 4.0 (4.0–4.6); width of body at origin of pectorals 7.6 (7.4–10.1); width of body at origin of first anal 8.5 (8.0–9.9); head length 23.5 (22.7–26.8); snout length 11.3 (11.3–11.7); bill length 24.3 (23.2–28.2); maxillary length 14.6 (11.9–15.3); orbit diameter 2.6 (1.2–2.4); interorbital width 6.8 (5.9–7.8); anterior height of first dorsal 15.3 (12.0–16.6); length of middle dorsal spine 5.1 (3.5–4.8); anterior height of second dorsal 4.4 (3.2–4.9); height of first anal 10.4 (9.6–14.3); anterior height of second anal 3.0 (2.8–4.3); length of pectoral 17.3 (12.3–21.6); length of pelvic 16.1 (8.2–16.3); length of second dorsal base 5.2 (4.5–6.4); length of first anal base 19.6 (11.5–19.4); length of second anal 4.6 (4.8–5.6); caudal spread 36.6 (34.8–43.2); length of upper lobe of caudal 26.9 (21.8–27.8); length of lower lobe of caudal 24.5 (21.5–26.4).

Body elongate but robust and less compressed (BL about 4.4 to 5.8 times body depth, about 10 to 12 times body width). Snout extremely stout and long (head length slightly less than bill length), its cross section round. Lower jaw also stout and projected forward but shorter than upper jaw. Maxilla tightly fused with premaxilla and nasal, therefore snout nonprotractile. Predentary tightly fused with dentary. Posterior margin of upper jaw beyond posterior margin of eye. Body densely covered with thick elongated scales, each with 1 or 2 (mostly 1) posterior points (Fig. 3L). Small file-shaped teeth on both jaws and palatine. Lateral line single, but obscure especially in larger specimens. Head large (BL about 3.7 to 4.4 times head length). Eye relatively small. Nape steeply elevated.

Branchiostegal membranes united with each other and free from isthmus. Two nostrils close to each other in front of eye, anterior one small slit-like with a posterior flap and posterior one elongate and semi-circular in shape. No gill rakers. Pseudobranchiae present. Pectoral fin long and narrow with pointed tip, situated low on body and cannot be folded back against side of body. First dorsal fin with pointed anterior lobe, originating above posterior margin of preopercle, lower than body depth throughout its entire length. Second dorsal fin and second anal fin about the same size and shape, the former located slightly further forward than the latter. First anal fin rather small and sickle-shaped with its tip pointed. Pelvic fin slender, shorter than pectoral fin. Deep grooves for first dorsal, pelvic and first anal fins present. Caudal fin large, deeply forked and powerful; caudal fin rays deeply cover complex of caudal skeletons. Caudal peduncle fairly compressed and slightly depressed with a pair of caudal keels on its lateral side and a small notch on both dorsal and ventral sides. First dorsal fin blackish dark blue. Other fins usually dark brown, sometimes tinged with dark blue. No blotches or stripes on body in adults, and young fish have vertical bars (Pepperell, J., Person. Comm.). Body
dark blue black dorsally and silvery white ventrally. After death, color of body changes into a dull greyish white, thereby explaining its Japanese so called “Shirokajiki (=White marlin)”.

Olfactory rosetta radially shaped (Fig. 7L), composed of about 44–50 olfactory laminae; no capillaries visible with naked eye on surface of each lamina. Features of viscera very similar to those of *Istiophorus platypterus* (Fig. 8L). Anus situated close to origin of first anal fin.

Cranium hard and extremely stout; snout portion elongate and post orbital region rather short (Fig. 47). Temporal and pterotic crests parallel to each other. Width between outer margins of right and left lateral ethmoids wide. Neural and haemal spines of central part of vertebrae high trapezoid in shape (Fig. 10L). Lateral apophysis extremely well developed, but slightly smaller than those of *Makaira*

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**Fig. 47.** Cranium of *Makaira indica*, 2109 mm BL, Ine, Wakasa Bay, Japan Sea.
Remarks. The English common name, "Black marlin" for *Makaira indica* was not universally accepted until the mid-1960's. Prior to this agreement, some authors, principally Japanese, called this species "White marlin" which is a direct translation of the Japanese common name, "Shirokajiki" for *M. indica*.

Only a very few larvae have been obtained from the tropical western North Pacific, the tropical Indian Ocean, tropical waters off northwestern Australia and the Coral Sea (Ueyanagi, 1960a, 1964; Ueyanagi and Yabe, 1960; Jones and Kumaran, 1964b; Howard and Ueyanagi, 1965; Howard and Starck, 1975).

Size. The heaviest record of this species in sportfishing is a specimen caught at Cabo Blanco, Peru on Aug. 4, 1953, which weighed 708 kg and measured 442 cm TL. Black marlin weighing in excess of 500 kg are often caught off Cairns, Queensland. Measurements taken on female black marlin in excess of 1,000 lb caught during the First Black Marlin Tournament held at Cairns, Queensland on October, 1973 were 448.0 cm TL and 481.4 kg and 437.2 cm TL and 484.3 kg (Nakamura, I., unpublished data). LaMonte (1955) reported that this species attains about 4.1 m in length around Tahiti. Other examples in game fishing records are a specimen measuring 426.7 cm TL and weighing 509.8 kg, one measuring 436.9 cm TL and weighing 691.7 kg and one of 447.0 cm TL and 552.5 kg. The size range caught by the commercial longline fishery is 150–310 cm BL (mostly 170–210 cm BL) in the western Indian Ocean and 170–310 cm BL (mostly 185–240 cm BL) in the Coral Sea.

Distribution. This species is distributed in the Indian and Pacific oceans, principally in the tropical and temperate waters. The occasional stray black marlin may invade the Atlantic Ocean by way of the Cape of Good Hope (Fig. 48). This
species has only been rarely recorded by Japanese commercial longliners operating in the Atlantic Ocean (Shiohama et al., 1965; Ueyanagi et al., 1970). Nakamura et al. (1968) indicated that the occurrence of this species in the Atlantic was not certain since the records could possibly refer to the Atlantic blue marlin, *Makaira nigricans*. Some authors had postulated that the occasional stray black marlin may enter the Atlantic from the Indian Ocean and attempted to find more accurate evidence on the occurrence of this species in the Atlantic (Ueyanagi et al., 1970; Nakamura, 1974, 1975). Recent evidence has confirmed this occurrence as follows: A photograph of a black marlin taken in 1929 by commercial fishermen in Baia Farta, Lobito, Angola was identified by Rivas (1974 MS). A male black marlin measuring 174 cm EF and weighing 56 kg was caught by Longliner No. 12 Kaki Maru on September 5, 1972 at 33°46'N, 74°31'W, surface temperature 28°C (Sato, T., Person. Comm.). A black marlin weighing 91 kg was caught by Longliner of No. 28 Ryooei Maru on December 31, 1975 at 32°03'N, 21°42'W, surface temperature 18–19°C (Warashina, 1977).

There is very little information relating to spawning grounds and spawning seasons of this species. Nakamura (1941, 1942) surmised that spawning occurs in the vicinity of the Hainan Island and in the South China Sea in May or June. Ueyanagi (1960a) further presumed spawning to occur in the northwestern part of the Coral Sea between October and December. Mature females of this species with large gonads were examined at Cairns in October 1973, and it was also observed that females attained a larger size than males, with limited samples (Nakamura, I., unpublished data). All of these spawning areas, postulated on the basis of occurrence of larvae and mature females, are situated in tropical waters (Fig. 48).

**IV. Evolutionary relationships**

Phenetic similarity among the billfishes is based on the examination of 66 (37 external and 29 internal) characters. These characters were selected by comparative morphological examination on the basis of their intrageneric stability and intergeneric variability. They are summarized in Tables 1 (for external) and 2 (for internal) and rearranged later in Tables 4, 5 and 6 together with a discussion on possible evolutionary directions of the billfishes.

Table 3 shows a similarity matrix, based on the percentage of external, internal and total numbers of characters shared in the same state between each pair of species of the billfishes, regardless of whether the states are primitive or derived. Greater phenetic similarity is seen in the internal characters than in the external characters among each pair of species of Istiophoridae but *vice versa* between *Xiphias gladius* and each species of Istiophoridae.

*Xiphias gladius* shows greater similarity to species of *Makaira* than to species of either *Istiophorus* or *Tetrapturus* in both external and internal character states (consequently the total character states also). However, any one of these three character states which *X. gladius* shares with each species of Istiophoridae, is less than
Table 1. Comparison of counts and external characters in the adult billfishes examined.

<table>
<thead>
<tr>
<th>Character</th>
<th>Xiphiidae</th>
<th>Istiophorus platypterus</th>
<th>Istiophorus albicans</th>
<th>Istiophorus angustirostris</th>
<th>Istiophorus belone</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (D_1)</td>
<td>21–30</td>
<td>42–45</td>
<td>42–46</td>
<td>45–50</td>
<td>41</td>
</tr>
<tr>
<td>2 (D_2)</td>
<td>3–4</td>
<td>6–7</td>
<td>6–7</td>
<td>6–8</td>
<td>6</td>
</tr>
<tr>
<td>3 (A_1)</td>
<td>12–13</td>
<td>14–15</td>
<td>11–14</td>
<td>12–15</td>
<td>14</td>
</tr>
<tr>
<td>4 (A_2)</td>
<td>3</td>
<td>6–7</td>
<td>6–7</td>
<td>6–8</td>
<td>6</td>
</tr>
<tr>
<td>5 (P_1)</td>
<td>16–18</td>
<td>18–20</td>
<td>18–20</td>
<td>17–20</td>
<td>19</td>
</tr>
<tr>
<td>6 (P_2)</td>
<td>absent</td>
<td>I, 2</td>
<td>I, 2</td>
<td>I, 2</td>
<td>I, 2</td>
</tr>
<tr>
<td>7 GR</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8 BS</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>9 Caudal keels</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>10 V</td>
<td>16+10 or 15+11</td>
<td>12+12</td>
<td>12+12</td>
<td>12+12</td>
<td>12+12</td>
</tr>
<tr>
<td>11 Olfactory laminae</td>
<td>32–40</td>
<td>43–50</td>
<td>41–48</td>
<td>50–52</td>
<td>?</td>
</tr>
<tr>
<td>12 Bill</td>
<td>extremely stout</td>
<td>slender</td>
<td>slender</td>
<td>stout</td>
<td>stout</td>
</tr>
<tr>
<td>13 Length of bill</td>
<td>very long</td>
<td>long</td>
<td>long</td>
<td>very short</td>
<td>short</td>
</tr>
<tr>
<td>14 Cross section of bill</td>
<td>flat</td>
<td>round</td>
<td>round</td>
<td>round</td>
<td>round</td>
</tr>
<tr>
<td>15 Profile of nape</td>
<td>steep</td>
<td>convex</td>
<td>convex</td>
<td>straight</td>
<td>straight</td>
</tr>
<tr>
<td>16 Left and right branchiostegal membranes</td>
<td>separate</td>
<td>united</td>
<td>united</td>
<td>united</td>
<td>united</td>
</tr>
<tr>
<td>17 Length of pectoral fin</td>
<td>long</td>
<td>long</td>
<td>long</td>
<td>short</td>
<td>short</td>
</tr>
<tr>
<td>18 Rigidity of pectoral fin</td>
<td>a little</td>
<td>none</td>
<td>none</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>19 Continuity of dorsal fins</td>
<td>separate</td>
<td>continuous</td>
<td>continuous</td>
<td>continuous</td>
<td>continuous</td>
</tr>
<tr>
<td>20 First dorsal fin</td>
<td>anteriorly falcate, pointed</td>
<td>sail-like pointed</td>
<td>sail-like pointed</td>
<td>high posteriorly, anterior lobe pointed</td>
<td>high posteriorly, anterior lobe pointed</td>
</tr>
<tr>
<td>21 Second dorsal fin</td>
<td>very small</td>
<td>small</td>
<td>small</td>
<td>small</td>
<td>small</td>
</tr>
<tr>
<td>22 Pectoral fin</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
</tr>
<tr>
<td>23 Pelvic fin</td>
<td>absent</td>
<td>long</td>
<td>long</td>
<td>moderate</td>
<td>moderate</td>
</tr>
<tr>
<td>24 First anal fin</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
<td>pointed</td>
</tr>
<tr>
<td>25 Second dorsal fin</td>
<td>very small</td>
<td>small</td>
<td>small</td>
<td>small</td>
<td>small</td>
</tr>
<tr>
<td>26 Caudal fin</td>
<td>very strong, lunate</td>
<td>strong, falcate</td>
<td>strong, falcate</td>
<td>strong, falcate</td>
<td>strong, falcate</td>
</tr>
<tr>
<td>27 Caudal keel</td>
<td>very large</td>
<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
</tr>
<tr>
<td>28 Notches on caudal peduncle</td>
<td>deep</td>
<td>shallow</td>
<td>shallow</td>
<td>shallow</td>
<td>shallow</td>
</tr>
<tr>
<td>29 Grooves for fins</td>
<td>not developed</td>
<td>developed</td>
<td>developed</td>
<td>developed</td>
<td>developed</td>
</tr>
<tr>
<td>30 Anus to first anal fin</td>
<td>very near</td>
<td>near</td>
<td>near</td>
<td>far forward</td>
<td>far forward</td>
</tr>
<tr>
<td>31 Lateral line</td>
<td>absent</td>
<td>single</td>
<td>single</td>
<td>single</td>
<td>single</td>
</tr>
<tr>
<td>32 Scale</td>
<td>absent</td>
<td>pungent with few points</td>
<td>pungent with few points</td>
<td>pungent with few points</td>
<td>pungent with few points</td>
</tr>
<tr>
<td>33 Cross section of body</td>
<td>round</td>
<td>compressed</td>
<td>compressed</td>
<td>compressed</td>
<td>compressed</td>
</tr>
<tr>
<td>34 Spots on first dorsal fin</td>
<td>unspeckted</td>
<td>spotted</td>
<td>spotted</td>
<td>unspeckted</td>
<td>unspeckted</td>
</tr>
<tr>
<td>35 Stripes on body</td>
<td>none</td>
<td>striped</td>
<td>striped</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>36 Second dorsal to second anal fin</td>
<td>second anal forward</td>
<td>second anal forward</td>
<td>second anal forward</td>
<td>second anal forward</td>
<td>second anal forward</td>
</tr>
<tr>
<td>37* Approximate maximum BL (cm)</td>
<td>380</td>
<td>300</td>
<td>275</td>
<td>200</td>
<td>210</td>
</tr>
<tr>
<td>38* Approximate maximum BW (kg)</td>
<td>540</td>
<td>100</td>
<td>55</td>
<td>20</td>
<td>20</td>
</tr>
</tbody>
</table>

* To compile Tables 3 and 4, size of body was estimated as 3 categories (large, very large and
**Systematics of Billfishes**

Data are based on Robins (1974) and my estimation in case of *Tetrapturus georgei*.

<table>
<thead>
<tr>
<th></th>
<th><em>Tetrapturus</em></th>
<th><em>Makaira</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>pfluegeri</em></td>
<td><em>georgei</em></td>
<td><em>albidus</em></td>
</tr>
<tr>
<td>6-7</td>
<td>6-7</td>
<td>5-6</td>
</tr>
<tr>
<td>12-17</td>
<td>14-16</td>
<td>12-17</td>
</tr>
<tr>
<td>6-7</td>
<td>5-7</td>
<td>5-6</td>
</tr>
<tr>
<td>18-21</td>
<td>19-20</td>
<td>18-21</td>
</tr>
<tr>
<td>I, 2</td>
<td>I, 2</td>
<td>I, 2</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>12 +12</td>
<td>12+12</td>
<td>12+12</td>
</tr>
<tr>
<td>43-52</td>
<td>?</td>
<td>44-50</td>
</tr>
<tr>
<td>stout</td>
<td>stout</td>
<td>very stout</td>
</tr>
<tr>
<td>long</td>
<td>long</td>
<td>long</td>
</tr>
<tr>
<td>round</td>
<td>round</td>
<td>round</td>
</tr>
<tr>
<td>straight</td>
<td>straight</td>
<td>convex</td>
</tr>
<tr>
<td>united</td>
<td>united</td>
<td>united</td>
</tr>
<tr>
<td>long</td>
<td>long</td>
<td>long</td>
</tr>
<tr>
<td>none</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>continuous</td>
<td>continuous</td>
<td>continuous</td>
</tr>
<tr>
<td>high posterior-</td>
<td>low posterior-</td>
<td>low posterior-</td>
</tr>
<tr>
<td>small</td>
<td>small</td>
<td>small</td>
</tr>
<tr>
<td>round</td>
<td>round</td>
<td>round</td>
</tr>
<tr>
<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
</tr>
<tr>
<td>small</td>
<td>small</td>
<td>small</td>
</tr>
<tr>
<td>strong, falcate</td>
<td>very strong, falcate</td>
<td>very strong, falcate</td>
</tr>
<tr>
<td>moderate</td>
<td>moderate</td>
<td>fairly large</td>
</tr>
<tr>
<td>shallow</td>
<td>shallow</td>
<td>shallow</td>
</tr>
<tr>
<td>developed</td>
<td>developed</td>
<td>developed</td>
</tr>
<tr>
<td>far forward</td>
<td>near</td>
<td>near</td>
</tr>
<tr>
<td>single</td>
<td>single</td>
<td>single</td>
</tr>
<tr>
<td>pungent with</td>
<td>pungent with</td>
<td>pungent with</td>
</tr>
<tr>
<td>a few points</td>
<td>few points</td>
<td>few points</td>
</tr>
<tr>
<td>compressed</td>
<td>compressed</td>
<td>fairly round</td>
</tr>
<tr>
<td>unspotted</td>
<td>unspotted</td>
<td>sometimes striped</td>
</tr>
<tr>
<td>none</td>
<td>none</td>
<td>second anal forward</td>
</tr>
<tr>
<td>second anal</td>
<td>160</td>
<td>280</td>
</tr>
<tr>
<td>forward</td>
<td>250</td>
<td>25</td>
</tr>
</tbody>
</table>

*extremely large* based on 37 and 38.
Table 2. Comparison of internal (osteological and soft anatomical) characters

<table>
<thead>
<tr>
<th>Xiphiidae</th>
<th>Xiphius</th>
<th>Istiophorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xiphius</td>
<td>gladius</td>
<td>platypterus</td>
</tr>
<tr>
<td>Infraorbitals</td>
<td>minute</td>
<td>developed</td>
</tr>
<tr>
<td>Lachrymal</td>
<td>minute or absent</td>
<td>present</td>
</tr>
<tr>
<td>Predentary</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Nasal</td>
<td>narrow, forming a part of bill</td>
<td>broad, not forming a part of bill</td>
</tr>
<tr>
<td>Cranium</td>
<td>oily, rather soft</td>
<td>hard, fairly stout</td>
</tr>
<tr>
<td>Basisphere</td>
<td>not articulated with parasphenoid</td>
<td>articulated with parasphenoid</td>
</tr>
<tr>
<td>Vomer</td>
<td>wide</td>
<td>moderate</td>
</tr>
<tr>
<td>Temporal crest</td>
<td>developed only posteriorly</td>
<td>convex proximally</td>
</tr>
<tr>
<td>Centra</td>
<td>Cubic</td>
<td>hour-glass shape</td>
</tr>
<tr>
<td>Lateral apophys</td>
<td>not developed</td>
<td>not developed</td>
</tr>
<tr>
<td>Neural spines</td>
<td>a little flat</td>
<td>flat, triangular</td>
</tr>
<tr>
<td>Haemal spines</td>
<td>a little flat</td>
<td>flat, triangular</td>
</tr>
<tr>
<td>Anterior neural zygaphyses</td>
<td>long, oblique</td>
<td>very long</td>
</tr>
<tr>
<td>Posterior neural zygaphyses</td>
<td>remarkably produced</td>
<td>slightly produced</td>
</tr>
<tr>
<td>Anterior haemal zygaphyses</td>
<td>very slightly produced</td>
<td>quite long, horizontal</td>
</tr>
<tr>
<td>Posterior haemal zygaphyses</td>
<td>very slightly produced</td>
<td>not produced</td>
</tr>
<tr>
<td>Pelvic girdle</td>
<td>none</td>
<td>well developed</td>
</tr>
<tr>
<td>Hypurals</td>
<td>parahypural and last one separated</td>
<td>fused to a plate</td>
</tr>
<tr>
<td>Posttemporal</td>
<td>2 forks</td>
<td>3 forks</td>
</tr>
<tr>
<td>Postcleithrum</td>
<td>slender</td>
<td>wide anteriorly</td>
</tr>
<tr>
<td>Abdominal cavity</td>
<td>ended in front of first anal</td>
<td>ended at middle of second anal</td>
</tr>
<tr>
<td>Liver</td>
<td>middle lobe slightly produced</td>
<td>left and right lobes elongate</td>
</tr>
<tr>
<td>Gall bladder</td>
<td>not elongate</td>
<td>elongate</td>
</tr>
<tr>
<td>Spleen</td>
<td>not visible ventrally</td>
<td>visible ventrally</td>
</tr>
<tr>
<td>Air bladder</td>
<td>single compartment</td>
<td>bubble-shaped</td>
</tr>
<tr>
<td>Intestine</td>
<td>folded many times</td>
<td>folded twice</td>
</tr>
<tr>
<td>Rectum</td>
<td>thick</td>
<td>slender</td>
</tr>
<tr>
<td>Gonad</td>
<td>not Y-shaped</td>
<td>not Y-shaped</td>
</tr>
</tbody>
</table>
Systematics of Billfishes

in the adult billfishes examined. Descriptions in parentheses are estimated.

<table>
<thead>
<tr>
<th>Stiophoridae</th>
<th>Tetrapturus</th>
</tr>
</thead>
<tbody>
<tr>
<td>helone</td>
<td>pfluegeri</td>
</tr>
<tr>
<td>(developed)</td>
<td>developed</td>
</tr>
<tr>
<td>(present)</td>
<td>present</td>
</tr>
<tr>
<td>(present)</td>
<td>present</td>
</tr>
<tr>
<td>(broad, not forming a part of bill)</td>
<td>broad, not forming a part of bill</td>
</tr>
<tr>
<td>(hard, fairly stout)</td>
<td>hard, fairly stout</td>
</tr>
<tr>
<td>(articulated with parasphenoid)</td>
<td>articulated with parasphenoid</td>
</tr>
<tr>
<td>(narrow)</td>
<td>narrow</td>
</tr>
<tr>
<td>(narrow)</td>
<td>narrow</td>
</tr>
<tr>
<td>?</td>
<td>slightly convex proximally</td>
</tr>
<tr>
<td>(hour-glass shape)</td>
<td>hour-glass shape</td>
</tr>
<tr>
<td>(not developed)</td>
<td>not developed</td>
</tr>
<tr>
<td>(flat, rectangular)</td>
<td>flat, rectangular</td>
</tr>
<tr>
<td>(very long horizontal)</td>
<td>very long horizontal</td>
</tr>
<tr>
<td>(slightly produced)</td>
<td>slightly produced</td>
</tr>
<tr>
<td>(quite long, horizontal)</td>
<td>quite long, horizontal</td>
</tr>
<tr>
<td>(not produced)</td>
<td>not produced</td>
</tr>
<tr>
<td>(well developed)</td>
<td>well developed</td>
</tr>
<tr>
<td>(fused to a plate)</td>
<td>fused to a plate</td>
</tr>
<tr>
<td>(3 forks)</td>
<td>3 forks</td>
</tr>
<tr>
<td>(wide anteriorly)</td>
<td>wide anteriorly</td>
</tr>
<tr>
<td>(ended at middle of second anal)</td>
<td>ended at middle of second anal</td>
</tr>
<tr>
<td>(left and right lobes elongate)</td>
<td>left and right lobes elongate</td>
</tr>
<tr>
<td>(elongate)</td>
<td>elongate</td>
</tr>
<tr>
<td>(visible ventrally)</td>
<td>visible ventrally</td>
</tr>
<tr>
<td>(bubble-shaped)</td>
<td>bubble-shaped</td>
</tr>
<tr>
<td>(folded twice)</td>
<td>folded twice</td>
</tr>
<tr>
<td>(slender)</td>
<td>slender</td>
</tr>
<tr>
<td>(Y-shaped)</td>
<td>Y-shaped</td>
</tr>
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</table>
Table 2. (Continued)

Istiophoridae

<table>
<thead>
<tr>
<th></th>
<th>Makaira mazara</th>
<th>Makaira nigricans</th>
<th>Makaira indica</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Infraorbitals</td>
<td>developed</td>
<td>developed</td>
<td>developed</td>
</tr>
<tr>
<td>2 Lachrymal</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>3 Predentary</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>4 Nasal</td>
<td>broad, not forming a part of bill</td>
<td>broad, not forming a part of bill</td>
<td>broad, not forming a part of bill</td>
</tr>
<tr>
<td>5 Cranium</td>
<td>hard, massive</td>
<td>hard, massive</td>
<td>hard, massive</td>
</tr>
<tr>
<td>6 Basisphenoid</td>
<td>articulated with parasphenoid</td>
<td>articulated with parasphenoid</td>
<td>articulated with parasphenoid</td>
</tr>
<tr>
<td>7 Parapharynx</td>
<td>wide</td>
<td>wide</td>
<td>wide</td>
</tr>
<tr>
<td>8 Vomer</td>
<td>wide</td>
<td>wide</td>
<td>wide</td>
</tr>
<tr>
<td>9 Temporal crest</td>
<td>nearly straight</td>
<td>nearly straight</td>
<td>nearly straight</td>
</tr>
<tr>
<td>10 Centra</td>
<td>hour-glass shape</td>
<td>hour-glass shape</td>
<td>hour-glass shape</td>
</tr>
<tr>
<td>11 Lateral apophyses</td>
<td>well developed</td>
<td>well developed</td>
<td>well developed</td>
</tr>
<tr>
<td>12 Neural spines</td>
<td>flat, square</td>
<td>flat, square</td>
<td>flat, square</td>
</tr>
<tr>
<td>13 Haemal spines</td>
<td>flat, square</td>
<td>flat, square</td>
<td>flat, square</td>
</tr>
<tr>
<td>14 Anterior neural zygaphyses</td>
<td>very long horizontal</td>
<td>very long horizontal</td>
<td>very long horizontal</td>
</tr>
<tr>
<td>15 Posterior neural zygaphyses</td>
<td>slightly produced</td>
<td>slightly produced</td>
<td>slightly produced</td>
</tr>
<tr>
<td>16 Anterior haemal zygaphyses</td>
<td>quite long, horizontal</td>
<td>quite long, horizontal</td>
<td>quite long, horizontal</td>
</tr>
<tr>
<td>17 Posterior haemal zygaphyses</td>
<td>not produced</td>
<td>not produced</td>
<td>not produced</td>
</tr>
<tr>
<td>18 Pelvic girdle</td>
<td>well developed</td>
<td>well developed</td>
<td>well developed</td>
</tr>
<tr>
<td>19 Hypurals</td>
<td>fused to a plate</td>
<td>fused to a plate</td>
<td>fused to a plate</td>
</tr>
<tr>
<td>20 Posttemporal</td>
<td>3 forks</td>
<td>3 forks</td>
<td>3 forks</td>
</tr>
<tr>
<td>21 Postcleithrum</td>
<td>wide anteriorly</td>
<td>wide anteriorly</td>
<td>wide anteriorly</td>
</tr>
<tr>
<td>22 Abdominal cavity</td>
<td>ended at middle of second anal</td>
<td>ended at middle of second anal</td>
<td>ended at middle of second anal</td>
</tr>
<tr>
<td>23 Liver</td>
<td>left and right lobes elongate</td>
<td>left and right lobes elongate</td>
<td>left and right lobes elongate</td>
</tr>
<tr>
<td>24 Gall bladder</td>
<td>elongate</td>
<td>elongate</td>
<td>elongate</td>
</tr>
<tr>
<td>25 Spleen</td>
<td>visible ventrally</td>
<td>visible ventrally</td>
<td>visible ventrally</td>
</tr>
<tr>
<td>26 Air bladder</td>
<td>bubble-shaped</td>
<td>bubble-shaped</td>
<td>bubble-shaped</td>
</tr>
<tr>
<td>27 Intestine</td>
<td>folded twice</td>
<td>folded twice</td>
<td>folded twice</td>
</tr>
<tr>
<td>28 Rectum</td>
<td>slender</td>
<td>slender</td>
<td>slender</td>
</tr>
<tr>
<td>29 Gonad</td>
<td>not Y-shaped</td>
<td>not Y-shaped</td>
<td>not Y-shaped</td>
</tr>
</tbody>
</table>
Table 3. Similarity matrix of the billfishes based on the characters shared in the same state based on Tables 1 and 2 regardless of whether the states are primitive or derived. Absolute value on the upper, percentage on the lower. The figures show external, internal (in parentheses) and total (italic) characters shared between species.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>X. gladius</td>
<td>8( 2) 10</td>
<td>8( 2) 10</td>
<td>10( 1) 11</td>
<td>9( 1) 10</td>
<td>8( 1) 9</td>
<td>8( 1) 9</td>
<td>7( 2) 9</td>
<td>9( 2) 11</td>
<td>15( 4) 19</td>
<td>15( 4) 19</td>
<td>15( 4) 19</td>
<td></td>
</tr>
<tr>
<td>I. platypterus</td>
<td>22( 7) 15</td>
<td>36( 29) 65</td>
<td>26( 26) 52</td>
<td>25( 25) 50</td>
<td>26( 26) 52</td>
<td>26( 26) 49</td>
<td>28( 28) 56</td>
<td>30( 26) 56</td>
<td>45 45</td>
<td>45 43</td>
<td>45 43</td>
<td></td>
</tr>
<tr>
<td>I. albicans</td>
<td>22( 7) 15</td>
<td>97(100) 98</td>
<td>26( 26) 52</td>
<td>25( 25) 50</td>
<td>26( 26) 52</td>
<td>26( 26) 49</td>
<td>28( 28) 56</td>
<td>30( 26) 56</td>
<td>45 45</td>
<td>45 43</td>
<td>45 43</td>
<td></td>
</tr>
<tr>
<td>T. angustirostris</td>
<td>27( 3) 17</td>
<td>70( 90) 79</td>
<td>70( 90) 79</td>
<td>34( 27) 61</td>
<td>33( 29) 62</td>
<td>31( 25) 56</td>
<td>23( 23) 46</td>
<td>23( 23) 46</td>
<td>41 41</td>
<td>41 41</td>
<td>41 41</td>
<td></td>
</tr>
<tr>
<td>T. belone</td>
<td>24( 3) 15</td>
<td>68( 86) 76</td>
<td>68( 86) 76</td>
<td>92( 93) 92</td>
<td>31( 27) 58</td>
<td>29( 25) 49</td>
<td>23( 23) 47</td>
<td>24( 23) 42</td>
<td>43 43</td>
<td>43 43</td>
<td>43 43</td>
<td></td>
</tr>
<tr>
<td>T. pfluegeri</td>
<td>22( 3) 14</td>
<td>70( 90) 79</td>
<td>70( 90) 79</td>
<td>89(100) 88</td>
<td>32( 25) 57</td>
<td>26( 23) 46</td>
<td>23( 23) 43</td>
<td>24( 23) 41</td>
<td>41 41</td>
<td>41 41</td>
<td>41 41</td>
<td></td>
</tr>
<tr>
<td>T. georgi</td>
<td>22( 3) 14</td>
<td>70( 79) 74</td>
<td>70( 79) 74</td>
<td>84( 86) 85</td>
<td>78( 86) 86</td>
<td>86( 86) 86</td>
<td>25( 23) 48</td>
<td>23( 23) 44</td>
<td>43 43</td>
<td>43 43</td>
<td>43 43</td>
<td></td>
</tr>
<tr>
<td>T. albidus</td>
<td>19( 7) 14</td>
<td>76( 97) 85</td>
<td>76( 97) 85</td>
<td>62( 79) 70</td>
<td>62( 79) 70</td>
<td>68( 79) 73</td>
<td>31( 29) 49</td>
<td>20( 24) 44</td>
<td>44 44</td>
<td>44 43</td>
<td>44 43</td>
<td></td>
</tr>
<tr>
<td>T. audax</td>
<td>24( 7) 17</td>
<td>81( 90) 85</td>
<td>81( 90) 85</td>
<td>62( 79) 70</td>
<td>65( 79) 70</td>
<td>62( 79) 70</td>
<td>62( 79) 70</td>
<td>62( 79) 70</td>
<td>25( 24) 49</td>
<td>25( 24) 49</td>
<td>22( 24) 46</td>
<td></td>
</tr>
<tr>
<td>M. mazara</td>
<td>41( 14) 29</td>
<td>62( 76) 68</td>
<td>62( 76) 68</td>
<td>51( 72) 61</td>
<td>51( 72) 64</td>
<td>51( 72) 65</td>
<td>51( 72) 65</td>
<td>54( 83) 67</td>
<td>68( 83) 74</td>
<td>36( 29) 65</td>
<td>31( 29) 60</td>
<td></td>
</tr>
<tr>
<td>M. migratorius</td>
<td>41( 14) 29</td>
<td>62( 76) 68</td>
<td>62( 76) 68</td>
<td>54( 72) 62</td>
<td>54( 72) 65</td>
<td>54( 72) 62</td>
<td>54( 72) 62</td>
<td>54( 72) 62</td>
<td>68( 83) 74</td>
<td>81(100) 98</td>
<td>32( 29) 61</td>
<td></td>
</tr>
<tr>
<td>M. indica</td>
<td>41( 14) 29</td>
<td>57( 76) 65</td>
<td>57( 76) 65</td>
<td>54( 72) 65</td>
<td>54( 72) 65</td>
<td>54( 72) 65</td>
<td>54( 72) 65</td>
<td>54( 72) 65</td>
<td>84(100) 84</td>
<td>84(100) 84</td>
<td>84(100) 84</td>
<td></td>
</tr>
</tbody>
</table>
any one of those shared among each pair of species of Istiophoridae. These facts suggest that the similarities between X. gladius and the fishes of the Istiophoridae are due to convergent development in large, fast-swimming forms, and that the fishes of the Istiophoridae undoubtedly compose a natural group without very close phylogenetic relationships to X. gladius (Xiphiidae).

The greatest phenetic similarity in internal characters is found between Istio­phorus platypterus and Istiophorus albicans, between Tetrapturus angustirostris and Tetrapturus pfluegeri, between Tetrapturus audax and Tetrapturus albidus, between Makaira mazara and Makaira nigricans, and between Makaira nigricans and Makaira indica, each pair sharing 100 percent of their internal characters in the same state. The greatest phenetic similarity in external characters is found between I. platypterus and I. albicans and between M. mazara and M. nigricans, each pair sharing 97 percent of their characters in the same state.

Table 4. Presumed phylogenetically important characters selected from Tables 1 and 2 as coded states for comparison of istiophorid species. The characters are index numbered in the left column. The states with the lower code values are presumably the more primitive and those with a higher code values are presumably the more derived.

<table>
<thead>
<tr>
<th>Character index</th>
<th>Character</th>
<th>Coded State</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Bill</td>
<td>slender, stout long</td>
</tr>
<tr>
<td>2</td>
<td>Length of bill</td>
<td>very short, short</td>
</tr>
<tr>
<td>3</td>
<td>Profile of nape</td>
<td>straight, convex</td>
</tr>
<tr>
<td>4</td>
<td>Length of pectoral fin</td>
<td>short, long</td>
</tr>
<tr>
<td>5</td>
<td>Rigidity of pectoral fin</td>
<td>none, a little</td>
</tr>
<tr>
<td>6</td>
<td>First dorsal fin</td>
<td>very low posteriorly, high posteriorly, sail-like</td>
</tr>
<tr>
<td>7</td>
<td>Anterior lobe of first dorsal fin</td>
<td>pointed, round</td>
</tr>
<tr>
<td>8</td>
<td>Pectoral fin</td>
<td>pointed, round</td>
</tr>
<tr>
<td>9</td>
<td>Pelvic fin</td>
<td>short, moderate</td>
</tr>
<tr>
<td>10</td>
<td>First anal fin</td>
<td>pointed, round</td>
</tr>
<tr>
<td>11</td>
<td>Caudal fin</td>
<td>strong, very strong</td>
</tr>
<tr>
<td>12</td>
<td>Caudal keel</td>
<td>moderate, fairly large, large</td>
</tr>
<tr>
<td>13</td>
<td>Anus to first anal fin</td>
<td>very near, near</td>
</tr>
<tr>
<td>14</td>
<td>Lateral line</td>
<td>single, looped</td>
</tr>
<tr>
<td>15</td>
<td>Scale</td>
<td>with few point, with a few point</td>
</tr>
<tr>
<td>16</td>
<td>Cross section of body</td>
<td>compressed, fairly round, round</td>
</tr>
<tr>
<td>17</td>
<td>Cranium</td>
<td>fairly stout, stout</td>
</tr>
<tr>
<td>18</td>
<td>Paraphenoid</td>
<td>narrow, moderately wide, wide</td>
</tr>
<tr>
<td>19</td>
<td>Vomer</td>
<td>narrow, moderately wide, wide</td>
</tr>
<tr>
<td>20</td>
<td>Neural spines</td>
<td>triangular, rectangular, trapezoid square</td>
</tr>
<tr>
<td>21</td>
<td>Haemal spines</td>
<td>triangular, rectangular, trapezoid square</td>
</tr>
<tr>
<td>22</td>
<td>Gonad</td>
<td>not Y-shaped, Y-shaped</td>
</tr>
<tr>
<td>23</td>
<td>Size of body</td>
<td>large, very large, extremely large</td>
</tr>
</tbody>
</table>
Table 5. Comparison of istiophorid species by coded states based on Table 4. Total score shows "index of primitiveness".

<table>
<thead>
<tr>
<th>Species</th>
<th>Coded states of characters by character index</th>
<th>Total score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1   2  3  4  5  6  7  8  9  10  11  12  13  14  15  16  17  18  19  20  21  22  23</td>
<td></td>
</tr>
<tr>
<td><em>I. platypterus</em></td>
<td>1 3 2 2 1 3 1 1 3 1 1 1 2 1 1 1 1 2 2 1 1 1 2</td>
<td>35</td>
</tr>
<tr>
<td><em>I. albicans</em></td>
<td>1 3 2 2 1 3 1 1 3 1 1 1 2 1 1 1 1 2 2 1 1 1 2</td>
<td>35</td>
</tr>
<tr>
<td><em>T. angustirostris</em></td>
<td>2 1 1 1 1 2 1 1 2 1 1 1 3 1 2 1 1 1 2 2 2 2 1</td>
<td>32</td>
</tr>
<tr>
<td><em>T. belone</em></td>
<td>2 2 1 1 1 2 1 1 3 1 1 1 3 1 2 1 1 1 1 2 2 2 2</td>
<td>33 or 34</td>
</tr>
<tr>
<td><em>T. pfluegeri</em></td>
<td>2 3 1 2 1 2 2 2 2 1 1 3 1 2 1 1 1 1 2 2 2 2</td>
<td>38</td>
</tr>
<tr>
<td><em>T. georgei</em></td>
<td>2 3 1 2 1 2 2 2 2 1 2 2 2 2 2 2 1 2 2 2 2 2</td>
<td>35 or 36</td>
</tr>
<tr>
<td><em>T. albidus</em></td>
<td>3 3 2 2 1 2 2 2 2 2 2 2 2 1 2 2 2 2 2 2 2 2</td>
<td>43</td>
</tr>
<tr>
<td><em>T. audax</em></td>
<td>3 3 2 2 1 1 1 1 2 1 2 2 2 1 1 3 2 2 2 2 2 2</td>
<td>41</td>
</tr>
<tr>
<td><em>M. mazara</em></td>
<td>3 3 3 2 2 1 1 1 1 3 3 1 2 1 3 3 3 3 3 3 1 3</td>
<td>50</td>
</tr>
<tr>
<td><em>M. nigricans</em></td>
<td>3 3 3 2 2 1 1 1 1 3 3 1 3 1 3 3 3 3 3 3 3 1 3</td>
<td>51</td>
</tr>
<tr>
<td><em>M. indica</em></td>
<td>3 3 3 2 3 1 1 1 1 3 3 1 1 1 3 3 3 3 3 3 3 1 3</td>
<td>50</td>
</tr>
</tbody>
</table>

Fig. 49. Dendrogram schematically showing phenetic similarities of the billfishes based on the 66 characters (Table 3). The length of each horizontal line indicated the percentage of character states not shared between related species. Dashed line indicate the relationships between non-adjacent species which have high percentage of shared characters in the same state.
The greatest similarity in total characters is found between *I. platypterus* and *I. albicans*, and between *M. mazara* and *M. nigricans*, each pair sharing 98 percent of their characters in the same state. Thus the phenetic similarities among the billfishes, based on the total character states, are schematically illustrated in the form of a dendrogram (Fig. 49).

In order to make interrelationships among the species of Istiophoridae clearer, a set of tables (Tables 4, 5 and 6) was devised to compile the dendrogram shown in Fig. 50. This figure is largely based on numerical taxonomic methods of Ebeling and Weed (1973) and Pietsch (1974). A hypothetical model of the ancestral istiophorid is imagined in Fig. 51. This imaginary fish possesses every code state 1 of all the characters shown in Table 4. Consequently, Tables 5 and 6 were compiled on the species of Istiophoridae to produce the dendrogram depicted in Fig. 50.

Among living istiophorids, *T. angustirostris* seems to be the most similar to the ancestor model. Comparing Fig. 49 with Fig. 50, the conventional taxonomy (see above) can be regarded as a good approximation to the supposed natural evolutionary sequence. Among the species of *Tetrapturus*, *T. audax* is closer to *T. albidus*.
Table 6. Similarity matrix of the billfishes based on presumed phylogenetically important characters. Number of characters shared in the same states between each pair of the istiophorid species with figures showing absolute value on the upper and percentage of the 23 characters on the lower. The character and comparative states are based on Tables 4 and 5.

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Fig. 51. A hypothetical ancestor of istiophorid fish which has every code state 1 of all the characters in Table 4.

on one hand, and T. pfluegeri, T. georgei, T. belone and T. angustirostris are closer to each other as a group on the other hand. Species of Istiophorus (I. platypterus and I. albicans) are more closely related to the T. audax–T. albidus group than the T. pfluegeri–T. georgei–T. belone–T. angustirostris group of the genus Tetrapturus and do not show close relationships with the species of Makaira (M. mazara, M. nigricans and M. indica). The M. mazara–M. nigricans–M. indica group is rather independent from the other species. Thus comparison of the results of numerical taxonomy with conventional taxonomy indicates that the conventional adoption of the genera
for the istiophorid group can be considered to be appropriate to a considerable extent.

Ueyanagi (1963b) speculated the relationships of the Indo-Pacific istiophorid species based on the ontogenetic development in their snouts and dorsal fins. He considered that *I. platypterus*, *T. angustirostris* and *T. audax* are grouped into A, and *M. mazara* and *M. indica* are grouped into B and that among the three species of Group A, *T. audax* seems to have the closest relation to Group B. Matsubara (1963) agreed with Ueyanagi's speculation and recognized that the istiophorid fishes form a natural group based on the intermediate condition of *T. audax* which connects Ueyanagi's Group A with Group B. The results here discussed are summarized in Figs. 50 and 52, which support their speculations in some extent.

Assuming that the evolution of the billfishes has selected for a large body and

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**Fig. 52.** Proposed phylogenetic relationships of the billfishes. Solid line show istiophorid-stem and dashed line shows xiphiid-stem; similarities between both stems are considered due to convergence.
become more adapted for fast-swimming, the presumed living billfishes’ phylogenetic relationships are depicted in Fig. 52.

V. Origins of the billfishes

Relationships among the fishes of the very large and very diverse order Perciformes are rather poorly understood (Gosline, 1968). Within this vast and poorly charted assemblage, a suborder Scombroidei has long been recognized by Regan (1909), Starks (1911) and Greenwood et al. (1966) to include the families Scombridae (mackerels, skipjack, bonitos, tunas etc.), Gempylidae (snake mackerels, escolars etc.), Trichiuridae (cutlass fishes, hair tails, frost fish, ribbon fishes etc.), Xiphiidae (swordfish), Istiophoridae (sailfishes, spearfishes and marlins) and Luvaridae (louvar).

Gosline (1968, 1971) and Fierstine (1974), however, differ somewhat from the above authors in placing the suborder Xiphioidei which comprises the families, Istiophoridae, Xiphiidae and, provisionally, the Luvaridae, alongside the suborder, Scombroidei. Recently, the family Scombrolabracidae has also been included in the suborder, Trichiuroidei (Parin and Bekker, 1972, 1973), though some authors (Lindberg, 1971; Nelson, 1976) included the monotypic Scombrolabrax heterolepis in the family Gempylidae. To a large extent, these families have been grouped together because they share external morphological features related to rapid locomotion in an epipelagic environment.

Collette (1978) indicated that the Scombridae have been successful in adapting to the epipelagic fast-swimming lifestyle in both near shore and off shore environments. I would propose that the Istiophoridae and the Xiphiidae have been equally successful in this type of adaptation. Another trend of morphological specialization, shown by the series Scombrolabracidae-Gempylidae-Trichiuridae in adaptation to the mesopelagic and benthopelagic life, is toward elongation of the body. However, the latter trend is beyond the scope of this study.

To date it is felt that there has been no satisfactory attempt to determine the relationships among the families or genera of the Scombroidei, and there are no satisfactory published discussions for considering the suborder, as currently composed, to be a monophyletic group. The billfishes, in particular, are the subject of great controversy. It has long been believed that the swordfish (Xiphias gladius) is a highly specialized end-stage of the scombriform series. Cuvier, in Cuvier and Valenciennes (1832), Regan (1909), and Berg (1940) all closely agreed in placing X. gladius (Xiphiidae) in the division Xiphiiformes, along with the living marlins and sailfishes (Istiophoridae) and extinct families (Palaeorhynchidae, Blochiidae and Xiphiorhynchidae).

Gregory and Conrad (1937), moreover supposed the following hypothetical evolutionary route: All these families data back to Eocene times, while Aestras (Xiphiidae) and Xiphiorhynchus are found in Lower Eocene deposits; The Scombridae also begin in the Lower Eocene, whereas the other scombroids do not appear
until the Oligocene period; The fact that the structurally primitive family (Scombridae) and its highly specialized offshoots (Xiphiiformes) were living side by side in early Eocene times seems to indicate that the latter branched off from the scombrids in the Cretaceous. Fraser-Brunner (1950) supposed that the Xiphiiformes has been derived from the *Scomberomorus–Acanthocybium* route in the family Scombridae.

Nevertheless, I consider that both the external and internal structures of the billfishes (Xiphiidae and Istiophoridae) are extremely different from those of the other families of Scombroidei. As discussed in the previous chapter, the great similarity among the fishes of Scombridae, Istiophoridae and Xiphiidae is probably due to convergence in large and fast-swimming forms. The number of vertebrae (Fig. 53) of Luvaridae (22 or 23), Istiophoridae (24) and Xiphiidae (26) is more generalized (typical of the percoid condition) than the number of vertebrae of the Scombridae (more than 30). This does not support the speculations proposed by the above mentioned authors that the billfishes have been derived from certain members of Scombridae.

Another difficult problem is to suggest a true ancestor of the billfishes (both for the Xiphiidae and Istiophoridae). Based on the number of vertebrae (24–26), it would seem that the billfishes are related to some lower percoid fishes. Further study is needed to determine what living fish or group of living fishes is most closely related to the billfishes.
Systematics of Billfishes

related to the present billfishes. There seems to be no easy method to resolve this problem, unless certain fossil records which connect the billfishes with other living fishes (most likely lower percoid fishes) are found.

VI. Some considerations on morphological adaptation of the billfishes

In the previous chapter, I speculated that the evolutionary directions taken by the Istiophoridae and the Xiphiidae have occurred independently and have both tended towards the body becoming enlarged and adapted for fast-swimming. On this basis some aspects of morphological adaptation of the billfishes are now discussed.

The basic differences between *X. gladius* and the istiophorids are summarized in Tables 1, 2 and 3. These differences may trace the different evolutionary routes. Therefore, for simplicity sake, I shall describe here some aspects of morphological adaptation of the billfishes chiefly in accordance with the istiophorid route. As the occasion may demand, *X. gladius* will be referred to.

*Enlargement of body.* It is quite likely that enlargement of the body has been an evolutionary trend in both the Istiophoridae and Xiphiidae. Maximum body sizes of the living billfishes is schematically shown in Fig. 54. Enlargement of the body is most extreme in *Makaira* and *Xiphias* and is quite extreme in a species of *Istiophorus* (*I. platypterus*) and a species of *Tetrapturus* (*T. audax*). As fish become larger, the body seems to become more robust.

*Cranium.* The cranium is oilier, lighter and less ossified in Xiphiidae than in
I. Nakamura

Fig. 55. Relation between length and width of cranium in billfishes. CL: cranium length; ACW: anterior cranium width; PTW: cranium width at pterotics. Indo-Pacific species were based on adult specimens from the northwestern Pacific and the Japan Sea and Atlantic species were based on adult specimens from the Caribbean Sea.

Istiophoridae. The cranium of Istiophoridae is stouter and greatly ossified. The shape of the cranium in the Istiophoridae is analyzed graphically in Fig. 55. This shows that it is wide and extremely stout (even massive) in Makaira, moderately wide and stout in Istiophorus, and of various shapes in Tetrapturus. Among the species of Tetrapturus, T. audax and T. albidus have a stouter and wider cranium while those of T. pfluegeri and T. angustirostris are moderately stout and rather elongate. It is most likely that the cranium has become stouter and wider with the enlargement of the body.

Vertebrae. The vertebrae are more flattened and much more specialized in Istiophoridae than in Xiphiidae. The vertebrae of Xiphiidae are not very different from typical percoid vertebrae (Fig. 10A). The vertebrae of the Istiophoridae
however are completely different from typical percoid vertebrae. The shape of the vertebrae in Istiophoridae is analyzed graphically in Fig. 56. This shows that *Makaira* has high and wide, square neural spines, *Tetraprurus* has moderately high and wide, rectangular or trapezoid spines, whilst *Istiophorus* has rather low and narrower, triangular spines. The vertebral structure of the Istiophoridae is possibly adapted for jumping, since istiophorid fishes often leap above the sea surface. The vertebrae of Istiophoridae are firmly joined and overlap each other by means of extremely elongate anterior neural zygapophyses and elongate haemal zygapophyses (Fig. 10). This structure would seem to act as a spring for the jumping behaviour of istiophorid fishes.

**Caudal fin.** The caudal fin rays completely cover the hypural plate in both the Xiphiidae and Istiophoridae (Fig. 57). The members of the Scombridae possess the same kind of condition of the caudal fin as members of the Xiphiidae and Istiophoridae. This is also considered to be due to convergence towards large, fast-swimming forms. In general, the caudal fin is large and strong in all species of billfishes. It is somewhat lunate in *Xiphius gladius* and falcate in Istiophoridae. The relative powerfulness of the caudal fin can be evaluated in order of development: *T. angustirostris, T. belone, T. pfluegeri, I. albicans, I. platypterus* < *T. albidus, T. audax* < *X. gladius* < *M. mazara, M. nigricans, M. indica.* The caudal keel is single
in *X. gladius* and double in Istiophoridae. The degree of development of the caudal keels in Istiophoridae can be relatively evaluated in the following order: *T. angustirostris*, *T. belone*, *T. pfluegeri* (< *I. albicans*, *I. platypterus* < *T. albidus*, *T. audax* < *M. nigricans*, *M. mazara*, *M. indica*. The well developed single caudal keel of *X. gladius* is very similar to that of tunas, *Thunnus* or Mako shark, *Isurus*, because of convergence. Both the powerfulness of the caudal fin and the development of caudal keels in billfishes correlates very well with the tendency towards enlargement of the body in evolution.

**Pectoral fin.** The pectoral fin is generally well developed in all species of billfishes, though it is rather short but still strong in *T. angustirostris* and *T. belone*. The pectoral fin is low on the body in all species of istiophorids, particularly in *M. indica* whose pectoral fin is fixed (secondarily resembling the condition of a shark’s fin). The condition of the pectoral fin of *M. indica* (remarkably rigid and extended in adults) is approached by *X. gladius* (to a considerable extent), and *M. mazara* and *M. nigricans* (to a lesser extent). The low position and rigidity of the pectoral fin would thus seem to be an adaptation for buoyancy of a heavy body while swimming fast.

**Air bladder.** The air bladder is large and well developed in all species of billfishes, though it is a single compartment in *X. gladius* and many bubble shaped small chambers in Istiophoridae (Fig. 58). Development of the air bladder would also seem to be an adaptation for keeping a heavy body buoyant.

**Dorsal fin.** The first dorsal fin of the sailfish (*Istiophorus*) is sail-like in shape. As stated in Chapter III, the sailfish uses its first dorsal fin when attacking and scar­ring prey fishes, or when turning suddenly. Among the istiophorid fishes, the sailfish is considered to have trace of a somewhat different evolutionary route from the istiophorid’s main route, in its using the sail-like first dorsal fin effectively in its way of life. The pelvic fin is longest in *Istiophorus* among istiophorids, while *X. gladius* has no pelvic fin. The pelvic fin of *Istiophorus* seems to function in relation with the first dorsal fin.
Fig. 58. Diagrammatic drawings of air bladder in *Xiphias gladius* (A) from the Japan Sea (ca. 200 cm BL) and *Makaira indica* (B) from the Japan Sea (ca. 185 cm BL).

Fig. 59. Diagrammatic drawings of shapes and conditions of first dorsal and first anal fins in *Xiphias gladius* (A) from the Japan Sea (ca. 200 cm BL) and *Istiophorus platypterus* (B and B') from the Japan Sea (ca. 175 cm BL). A: during linear movement, B: during slow movement and turn or stop; B': during linear movement with high speed. Black fins show first dorsal and anal fins. Obliquely lined parts in *I. platypterus* show the grooves for the fins.
**Grooves for fins.** *Xiphias gladius* has no groove for receiving the folded fins. On the other hand, all the members of Istiophoridae have well developed grooves for the folded pelvic, first dorsal and first anal fins (Fig. 59). Instead of the groove, *X. gladius* has smaller fins for adaptation to fast swimming. This feature may show a typical example of convergence that they trace independently different routes for fast-swimming.

**Caudal notch.** *Xiphias gladius* has a deep notch on both the dorsal and ventral sides of the caudal peduncle. The members of the Istiophoridae however have a shallow notch on each side (Fig. 60). Though the basic structures of both types of notches are different, these seem to act effectively in allowing the caudal fin to control the caudal span. This may assist the fishes’ maneuverability during fast-swimming. Same kind of condition, possessing notches (or pits) on caudal peduncle region, is seen in large pelagic fast-swimming sharks, such as *Alopias, Lamna, Isulus, Sphyrna* and *Carcharinus.*

![Diagram of caudal part of Xiphias gladius and Istiophorus platypterus](image)

*Fig. 60.* Diagrammatic drawings of the caudal part of *Xiphias gladius* (A) from the Japan Sea (ca. 200 cm BL) and *Istiophorus platypterus* (B) from the Japan Sea (ca. 175 cm BL).
**Bill.** The bill is extremely long and flat in cross section in *Xiphias gladius*, and has various lengths and is round in cross section in the Istiophoridae. It is the shortest in *Tetrapturus angustirostris* among istiophorids, fairly short in *Tetrapturus belone* and long in other species of Istiophoridae. As discussed by Wisner (1958), billfishes use their bills for feeding. Relative strength of bill can be evaluated in istiophorids in order of stoutness: *Tetrapturus angustirostris* < *Tetrapturus belone* < *Tetrapturus pfluegeri* < *Istiophorus platypterus*, *Istiophorus albicans* < *Tetrapturus albidus*, *Tetrapturus audax* < *Makaira mazara*, *Makaira nigricans*, *Makaira indica*. Bill stoutness in istiophorids coincides well with the enlargement of body of this group of fish. The extremely large and flat bill of *X. gladius* is considered to have no relation with the bill of Istiophoridae from the phylogenetic viewpoint.

**Gill.** The billfishes have no gill-raker in both Xiphiidae and Istiophoridae. The way of life is very similar both in billfishes and tunas, but the latter has well developed gill-rakers. Billfishes are believed to be carnivorous and more predaceous than tunas. So that the lack of gill-raker in billfishes may suggest that they are ranked in the highest trophic level among the teleostean fishes.

Ovchinnikov (1970) recognized that the gross morphological features of the billfishes (Xiphiidae and Istiophoridae) show evidence of two principal adaptations: toward high speed and toward control of movement.

**VII. Distribution**

As the distribution of each species was stated in Chapter III, the general distribution pattern of billfishes (Fig. 61) is discussed here in comparison with that of tunas which have similar way of life as billfishes. *Xiphias gladius* has world-wide distribution. While none of istiophorid species has worldwide distribution, there are some authors who recognize a single cosmopolitan species of sailfish, *Istiophorus platypterus*. I prefer to retain the traditional usage of *I. platypterus* for the Indo-Pacific sailfish and *I. albicans* for the Atlantic sailfish, because some differences are recognized between two forms as mentioned above. Thus five species of Istiophoridae are basically distributed in the Indo-Pacific area. In comparison with this, six species are recognized in the eastern Atlantic area, (if we can recognize *Tetrapturus georgei* as a valid species), and four species are recognized in the western Atlantic area. Moreover, three species, *Makaira indica*, *Tetrapturus angustirostris* and *Tetrapturus audax* are incidentally recognized as occurring in the eastern Atlantic (Fig. 61). If these three species are added, there are nine species of Istiophoridae which are at least occasionally present in the eastern Atlantic.

Though the Cape of Good Hope seems to be a hidden barrier to istiophorids (Penrith and Cram, 1974), it does not completely prevent the movement of istiophorids from the Indian Ocean to the Atlantic Ocean or *vice versa*. Cape Horn, however, does completely prevent interoceanic migration of istiophorids. As far as I know, interoceanic migration of istiophorids from the Indian Ocean to the Atlantic Ocean has been recorded occasionally, but no instances of istiophorids
movements from the Atlantic Ocean to the Indian Ocean are known. Thus, Atlantic istiophorids are believed to be confined to that ocean, whereas Indo-Pacific species are not always so.

Compared with the some species of tuna, such as *Thunnus albacares*, *Thunnus obesus* and *Thunnus alalunga*, which have very wide geographical distributions, istiophorids tend to be rather limited in their geographical distribution. Suzuki et al. (1977) studied average swimming layers of tunas and billfishes by comparing catches of regular (shallow) longline gear set in 50-120 m depth with catches of deep longline gear set in 50-250 m depth in the western and central equatorial Pacific Ocean. The following ratios were determined: *Istiophorus platypterus* and *Tetrapturus angustirostris* (Ratio of mean hook rates of deep longline / regular longline — 0.06); *Tetrapturus audax* (0.28); *Makaira indica* (0.34); *Makaira mazara* (0.55); *Thunnus albacares* (0.73); *Xiphias gladius* (0.79); *Thunnus alalunga* (0.82); *Thunnus obesus* (1.79). The smaller the ratio, the more "surface dwelling" a species is, at least for fish taken by longline in the above mentioned areas. This analysis shows that billfishes are generally surface dwellers, (except *X. gladius*, which has the widest distribution amongst the billfishes), and that tunas are deeper dwellers, particularly *Thunnus obesus*. *Thunnus albacares* is the exception to this rule. These results suggest that dwelling in deeper waters may confer an advantage for surpassing natural barriers to movement, thus resulting in a wider distribution. In my opinion, this could explain the fact that the tunas generally have a wider distribution than billfishes,

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</table>

Fig. 61. Schematic explanation of the distribution of the billfishes. W: Western; E: Eastern; N: Northern Hemisphere; S: Southern Hemisphere. Dotted part shows the area where each species is distributed primarily with reproduction and/or principal population. Cross-hatching part shows the area where each species is distributed incidentally (or invades into) without reproduction and principal population.
and that *Xiphias gladius* has the widest distribution amongst the billfishes. Differences in distribution can also be considered from a morphological viewpoint. Tunas have a pineal window and frontoparietal fenestra on the dorsal surface of the cranium whereas billfishes possess neither. Rivas (1953) hypothesized that the pineal window (his pineal apparatus) in tunas functions as a light receptor and assists in migration. Murphy (1971) demonstrated the following facts: In tunas, light can be transmitted through the pineal window but not through the adjacent thick layers of muscle and bone; Electron microscopy showed that the pineal sensory cells of bluefin tunas possess the structural characteristics of vertebrate retinal photoreceptor cells; A nerve runs from the pineal end-organ to the junction of the pallium and habenular commissure of the brain. These findings support the Rivas' hypothesis. Collette (1978) considered that the pineal may deliver periodic photo stimuli to the central nervous system.

The frontoparietal fenestra of tunas are not true foramina since the openings are covered with parchment-like connective tissue where no nerves and blood vessels penetrate through. Collette (1978) speculated that the frontoparietal fenestra may serve as a pressure valve in that the tissue-covered holes may permit expansion of the blood vessels supplying the brain without increasing pressure within a restricted space which could damage sensitive brain tissues. The brains of tunas are very tightly enclosed in a nearly complete bony box and they are warmer than the surrounding water. I consider that another function of the frontoparietal fenestra is possible. Since external pressure can easily be transmitted through the parchment-like connective tissue to the semicircular canals, depth changes could be quickly sensed by tunas during rapid vertical diving or surfacing.

I also consider that the pineal window of tunas functions as a light receptor in migration over a long time span (*i.e.*, monthly or seasonally) and that the frontoparietal fenestra functions as an aid for sensing depth over a short time span (*i.e.*, immediately). Thus these structures could be greatly advantageous for extending distribution.

Since billfishes have no pineal window or frontoparietal fenestra on the cranium, I would suggest that this could be one of the reasons why billfishes except *Xiphias gladius* have rather restricted distributions when compared with the wider distribution of most tunas. Though *X. gladius* does not have these structures, they have a wide distribution. They might have another ability to get wide distribution.

**VIII. Fisheries**

The total world production of billfishes, according to FAO statistics, presently stands at approximately 100 thousand metric tons per year, of which more than 90 percent is caught by the surface longline fisheries. Billfishes are caught primarily as a by-catch of tuna longlines. Japan currently produces between 60 and 70 percent of the world's catch of billfishes and is the principal consumer nation of billfishes. Taiwan and South Korea follow Japan. Japan's average annual total
catch of billfishes is about 60 thousand metric tons in recent years. Comparing the longline catches of tunas and billfishes, the billfish catch comprises approximately 18 percent of the total landings. The proportion of the total catch contributed by all species of billfishes is about the same as that of albacore, *Thunnus alalunga* and both fall below the proportions contributed by the yellowfin tuna, *Thunnus albacares* and the bigeye tuna, *Thunnus obesus*. Among the billfishes, the striped marlin, *Tetrapturus audax* and the swordfish, *Xiphias gladius* predominate, each accounting for approximately 30% of the total catch. The blue marlin (*Makaira mazara* and *Makaira nigricans* combined) and the black marlin, *Makaira indica* together account for about 25% and the sailfish (*Istiophorus platypterus* and *Istiophorus albicans* combined) about 14% of the total landings. Besides longlining, billfishes are also caught by harpooning, trolling, set netting and occasionally by drift netting.

Billfishes are of considerable importance among the fishery products utilized by Japan, because of their high demand from the consumer, which generates high prices. The world commercial fisheries for billfishes was reviewed in detail by Ueyanagi (1974c).

The principal utilization of billfishes in Japan is as follows:

**Striped marlin:** sashimi (fresh or frozen; sliced raw fish with soy-sauce and horse-radish), ingredient of sushi (fresh or frozen; sliced raw fish on vinegared boiled rice with horse-radish).

**Blue marlin** (both Indo-Pacific and Atlantic): sashimi, ingredient of sushi (fresh or frozen); sausages and hams (frozen)

**Black marlin:** sashimi, ingredient of sushi (fresh or frozen); sausages and hams (frozen)

**Swordfish:** steak, sashimi (fresh or frozen)

**Sailfish** (both Indo-Pacific and Atlantic): sashimi (fresh), sausages and hams (frozen)

**Shortbill spearfish:** sausages and hams (frozen)

**White marlin:** sashimi, sausages and hams (frozen)

**Longbill spearfish:** sausages and hams (frozen)

Mediterranean and round scale spearfishes have not been exploited as commercial fishes.

Sportfishing, utilizing trolled lures or baits is directed towards billfishes in most of the world's tropical and subtropical waters. de Sylva (1974) reviewed sportfishing for billfishes as follows: In the likely order of decreasing catch rate, the principal species caught by anglers are sailfish, blue marlin, striped marlin, black marlin, swordfish, and longbill spearfish. The shortbill and Mediterranean spearfishes are rarely taken by anglers; Important sportfisheries are presently centred from Massachusetts to North Carolina, and off Bermuda, southeastern Florida, the northern and northeastern Gulf of Mexico, the Bahamas, the larger islands of the Caribbean, Venezuela, the eastern tropical Pacific between southern California and Chile, Hawaii, New Zealand and eastern Australia, Kenya to Cape Town, South Africa, the Ivory coast to Senegal, West Africa, and off Portugal, Spain and
Both the commercial and sportfisheries of the billfishes are briefly summarized in Fig. 62. The areas where the commercial fisheries confront the sportfisheries, have recently developed conflicts and political problems in relation to the declaration of the 200 miles fishing zone by various nations.

IX. Conclusive discussion

In conclusion, I would like to briefly compare the usual conventional taxonomic studies with the results of this study.

It has been confirmed that Xiphias gladius of Xiphiidae differs completely from all species of Istiophoridae in both external and internal characters (Tables 1, 2 and 3). Some superficial phenetic similarities however are recognized in both X. gladius and the species of Makaira but these are certainly due to convergent evolution. Conventional taxonomic concepts agree well with these findings.

Considering the three genera of Istiophoridae, various opinions have often been put forward. The sailfishes have been included in Istiophorus, the small spearfishes have been included in Tetrapturus, and the large (blue and black) marlins have been included in Makaira in most cases. This system agrees well with my results. The smaller (striped and white) marlins, however, have been included in both Tetrapturus and Makaira by various authors. On the basis of this study, it seems clear that the smaller marlins, T. albidus and T. audax should be included in the genus, Tetrapturus together with the small spearfishes, T. angustirostris, T. belone and T. pfluegeri. On the basis of the following osteological features Makaira can be clearly distinguished from the other two genera, Istiophorus and Tetrapturus: (1) well ossified and massive cranium; (2) wide and flat ventral sides of vomer and parasphenoid; (3) high square shaped neural and haemal spines of central vertebrae; (4) well developed lateral apophyses of central vertebrae; (5) number of
vertebrae $11 + 13 = 24$. *Istiophorus* and *Tetrapturus* can be clearly distinguished from each other by external characters, but are very similar in their internal characters, as shown in Tables 1, 2 and 3.

*Istiophorus* has been recently considered to be monotypic (Morrow and Harbo, 1969). However, I prefer to recognize the Indo-Pacific sailfish as *Istiophorus platypertus* and the Atlantic sailfish as *Istiophorus albicans* on the bases of maximum size attained and on certain differences in the young from each ocean. Further study is needed before this issue is solved beyond doubt.

*Tetrapturus* contains five species; *T. angustirostris*, *T. belone*, *T. pfluegeri*, *T. albidus* and *T. audax*, or six species, if *T. georgei* is added. Since I did not have the opportunity to examine any specimens of *T. georgei* other than some skin imbedded with scales (UMML 11076), I shall exclude *T. georgei* in this discussion. I have, however, included Robins' (1974) brief description for convenience. Further study is much needed on the *Tetrapturus* group. *T. georgei*, *T. angustirostris*, *T. belone* and *T. pfluegeri* have many common features, and *T. albidus* and *T. audax* have also many common features, both external and internal. Some differences can be seen between the former four species and the latter two species, but these differences are considered insufficient to divide them at a generic, or subgeneric level, since important characters such as the features of the cranium and the vertebrae are so similar.

The genus *Makaira* contains three species, *M. mazara*, *M. nigricans* and *M. indica*. The Indo-Pacific blue marlin, *M. mazara* and the Atlantic blue marlin, *M. nigricans* are extremely similar to each other, the only real difference being in the shape of the lateral line system. Many authors still consider that both blue marlins are conspecific, adopting *Makaira nigricans* as the name for the cosmopolitan blue marlin (Parin, 1968; de Sylva, 1973; Rivas, 1975; Klawe, 1977). It should be pointed out, however, that the lateral line systems of individuals larger than 200 cm BL of both the Indo-Pacific and Atlantic blue-marlins are often difficult to observe since the lateral line system is covered by thick skin. In specimens of both forms measuring less than 100 cm BL, the characteristic pattern of the lateral line system is easily recognized. At Yaizu Fish Market, Shizuoka Prefecture, which is recognized as the world's biggest landing market for tuna longliners, I often compared both species directly and was able to separate many specimens of both forms with ease when the lateral line systems were visible. I could not distinguish between large specimens in which the lateral line system was covered by thick skin, however, even then the lateral line system is concealed, it still exists under the skin, I therefore consider that the difference in the lateral line system is important enough to warrant recognition of both species of blue marlin *Makaira mazara* and *Makaira nigricans*. A number of authors have placed *Makaira indica* in a separate genus, (either *Istiompax* or *Martina*), on the basis of the rigidity of the pectoral fin. However, since all the three species of *Makaira* are very similar each other except for the rigidity of the pectoral fin and lateral line systems, (Tables 3, 5 and 6), I consider that it is reasonable to place these three species in the same genus, *Makaira*. 
Hirasaka and Nakamura (1974) and Nakamura (1949) include *Martina* and *Eumakaira* in the subfamily Marlinae, and *Tetrapturus, Istiophorus* and *Kajikia* in the subfamily Tetrapturinae, on the basis of the number of vertebrae, the width of the body, the height of the first dorsal fin, depth of the body, length of the pelvic fin and the lateral line system. Robins and de Sylva (1961) support this classification, adding changes of bill with growth and body size to these criteria, but they do not agree with placing these two groups into subfamilies. Matsubara (1955) is also against the establishment of subfamilies, considering that the dividing features are not enough of a basis for establishing subfamilies. Instead, he includes three genera, *Histiophorus, Tetrapturus* and *Makaira*, in the family Histiophoridae. Taking into consideration the growth pattern of bill with size, the changes in shape of the first dorsal fin during growth and certain ecological aspects, Ueyanagi (1963b) divides the species of Istiophoridae into two groups (A and B): *T. angustirostris, I. platypterus* and *T. audax* are placed in group A, and *M. mazara* and *M. indica* in group B. He considers that *T. audax* of group A is more closely related to group B than the others in group A, but he does not agree with the establishment of subfamilies. Ueyanagi and Watanabe (1965) support this opinion on the basis of comparison of vertebrae.

I recognize that *Makaira* can be clearly separated from the other two genera, *Istiophorus* and *Tetrapturus*, but do not consider that it is necessary to establish subfamilies in the family Histiophoridae.

Recently, the so-called “hatchet marlin (marlin hacha)” has been proposed as a probable new species from the western Atlantic Ocean (Pristas, 1980). The most distinctive characters of this “new” species are reported to be a truncate lobe on the first dorsal fin, dark spots along the base of the dorsal fin and a pointed tip on the pectoral fin. I have no proof of the validity of this species, since I have not had a chance to examine it. However, I would question the validity of this species, since there are seven species of Istiophoridae in the western Atlantic and Mediterranean which is such a restricted area compared with the vast Indo-Pacific area where only five species occur. Further study is obviously needed on this possibility.

**X. Summary**

All the currently recognized billfishes (superfamily Xiphiidaceae) were diagnosed and described and were classified into two families, Xiphiidae and Istiophoridae, the former containing the monotypic *Xiphias gladius* and the latter containing three genera and 11 species.

Numerical analyses of the 23 presumed phylogenetically important characters, both external and internal, selected from 66 (37 external and 29 internal) of the characters examined, were made to establish the phylogenetic relationships of the billfishes. The results of these analyses demonstrated the following: The similarities between *Xiphias gladius* and the species of Istiophoridae are due to convergent evolution in large, fast-swimming forms; The species of Istiophoridae
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undoubtedly compose a natural group without phylogenetic relationships to Xiphiidae; Adaption of genera of the istiophorids, as determined by conventional taxonomy, can be considered to be relevant to the phylogenetic situation to a large extent.

It is most likely that the evolutionary trends in both Istiophoridae and Xiphiidae have independently tended towards the body becoming enlarged and adapted for fast-swimming. Based on this view, some aspects of morphological adaptation in the billfishes were discussed.

The general distribution pattern of billfishes, compared with that of tunas was briefly discussed.

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