MAKAIRA SP., CF. M. NIGRICANS LACÉPÈDE, 1802 (TELEOSTEI: PERCIFORMES: ISTIOPHORIDAE) FROM THE EASTOVER FORMATION, LATE MIOCENE, VIRGINIA, AND A REEXAMINATION OF †ISTIOPHORUS CALVERTENSIS BERRY, 1917

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ABSTRACT—An incomplete, disarticulated skull (USNM 375733) is described and referred to *Makaira* sp., cf. *M. nigricans,* and a rostrum, †*Istiophorus calvertensis* Berry, 1917 (USNM 9344, holotype), is re-identified as *Istiophorus* sp., cf. *I. platypterus.* Both specimens are from the Eastover Formation (early late Miocene, Virginia) and are the oldest records in deposits bordering the western North Atlantic Ocean. *Istiophorus* sp., cf. *I. platypterus* (= †*Istiophorus calvertensis*) is the oldest record of the species. Based on ecological requirements of Recent species, the presence of *Istiophorus* sp., cf. *I. platypterus* and *Makaira* sp., cf. *M. nigricans* in the Eastover Formation indicates that deep, warm water probably existed at or near the collection sites for at least part of the year.

INTRODUCTION

Marine Miocene and Pliocene deposits of the Middle Atlantic Coastal Plain occasionally yield remains of istiophorid billfish (Berry, 1917; Kimmel and Purdy, 1984; Fierstine, in press). Remains are usually found as isolated bone fragments, making identification to genus or species difficult and subjective. In an attempt to make identifications more accurate, Fierstine (in press) compared fossil fragments from Lee Creek Mine, North Carolina (Yorktown Formation, early Pliocene) to skeletal material from a large series of Recent istiophorid species. Discovery of a partial istiophorid skull (neurocranium with incomplete upper and lower jaws) from the Eastover Formation (late Miocene, Virginia) offers the first opportunity to examine and identify disarticulated remains of a single individual billfish using the methods of Fierstine and Voigt (1996) and Fierstine (in press). The Eastover specimen is compared morphometrically with other fossil istiophorids, especially †*Istiophorus calvertensis* Berry 1917, the only other billfish species known from the Eastover Formation (Kimmel and Purdy, 1984; Fierstine, in press).

Abbreviations—BMNH, The Natural History Museum, London; **IRSNB**, Institut Royal des Sciences Naturelles de Belgiques, Brussels; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **MNHN**, Museum National d'Histoire Naturelle, Paris; **UCMP**, University of California Museum of Paleontology, University of California, Berkeley, California; **USNM**, United States National Museum of Natural History, Washington, D.C. †, denotes extinct taxa; α, parasphenoidal angle; **a pr**, anterior process; **BO**, basioccipital; **bs pr**, basisphoid process; **cf**, carotid foramen; **DE**, dermethnoid; **d pr**, dorsal process; **F**, frontal; **fv**, facet for articulation with vomer; **i pr**, internal process; **LE**, lateral ethmoid; **m pr**, maxillary process; **N**, nasal; **ORB**, orbit; **PA**, parasphenoid; **PN**, prenasal; **Q-A**, socket of quadrate-articular joint; **tr**, triangular region of maxilla.

MATERIALS

Following Fierstine and Voigt (1996), I use the scientific and common names of Robins et al. (1991) for Recent species of fish and a combination of the osteological terminology of Davie (1990), Gregory (1933), Gregory and Conrad (1937), Jollie (1986), Rojo (1991), and Schultz (1987).

Comparative Material

The species and numbers of whole and partial skeletons of Recent specimens examined are: 50 Sailfish, *Istiophorus platypterus* (Shaw and Nodder, 1792); 11 Black Marlin, *Makaira indica* (Cuvier, 1832); 54 Blue Marlin, *Makaira nigricans* Lacépède, 1802; 21 White Marlin, *Tetrapturus albidus* Poey, 1860; 5 Shortbill Spearfish, *Tetrapturus angustirostris* Tanaka, 1915; 16 Striped Marlin, *Tetrapturus audax* Philippi, 1887; one Mediterranean Spearfish, *Tetrapturus belone* Rafinesque, 1810; three Longbill Spearfish, *Tetrapturus pfluegeri* Robins and deSylva, 1963. See Fierstine (in press) for size range and general collecting locality data for each species, and the institutions that house the material. The museum number, osteological material, geological age, and locality are given in the text for each fossil specimen.

METHODS

Measurements

Although I generally follow the methodology of Fierstine (in press), there are a few differences because some bones and characters in that study are not preserved in the Eastover specimen, whereas in other cases additional bones and characters are preserved. Except for measurements of the rostrum that were taken directly from computer tomography (CT) images, linear measurements were made to the nearest 0.1 mm with dial calipers or metric rule and angular measurements were made to the nearest 0.5° with a protractor. Characters and their definitions for each bone or structure are as follows.

Articular—Five morphometric characters were studied (Fig. 1A, B), all in the region of the socket (main jaw joint) for articulation with the quadrate: length from the anterior margin of the socket to the posterior edge of the articular (ASM); length of the socket from its anterior to posterior margin (AL); length from the apex of the socket to its posterior margin (AAL); width of the socket region from the medial process to the outer margin of the socket (ATW); and width of the socket proper (AW).

Maxilla—Six morphometric characters were studied (Fig. 1C, D), five in the triangular region (tr) that articulates with the nasal, premaxilla, prenasal, and vomer: length of the triangle (ML); height of the triangle (MH); width from the lateral surface of the triangle to the medial margin of the facet (fv) for articulation with the vomer (MW); and height (MVH), and
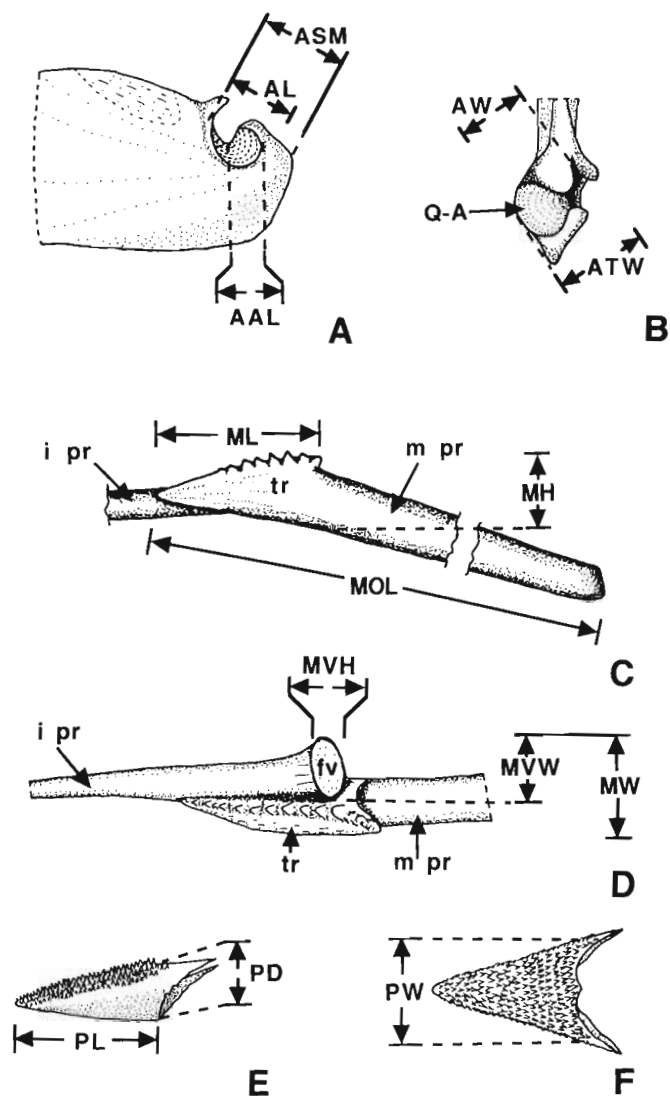
FIGURE 1. Bones of a generalized istiophorid (modified from Fierstine, in press). **A**, left articular, lateral view of posterior region. **B**, left articular, dorsal view of joint with quadrate. **C**, left maxilla, lateral view. **D**, left maxilla, dorsal view of triangular region. **E**, predentary, left lateral view. **F**, predentary, dorsal view. Abbreviations of measurements are defined in Methods section of text.
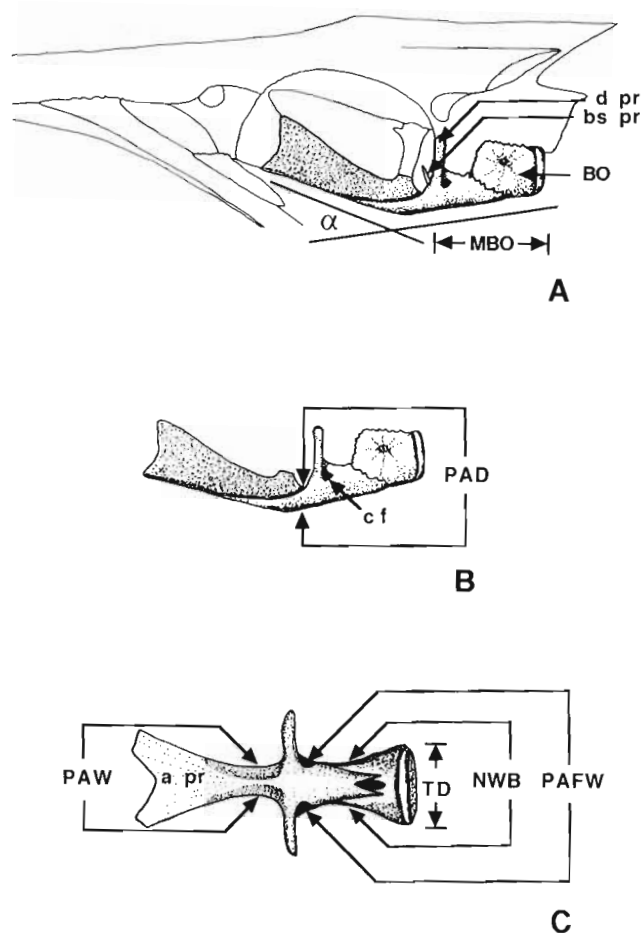

FIGURE 2. Parasphenoid of a generalized istiophorid. **A**, left lateral view with outline of adjoining bones. **B**, left lateral view. **C**, ventral view. Abbreviations of measurements are defined in Methods section of text.

width of the facet (MVW). The sixth variable is the length of the posterior limb from the anterior tip of the triangle to the posterior tip of the maxillary process (m pr) at the gape (MOL).

Otico-Occipital Region of Neurocranium—Three morphometric characters were studied (Fig. 2A–C): transverse outside diameter of the basioccipital centrum (TD); anterior edge of the dorsal process (d pr) of the parasphenoid to the posterior margin of the basioccipital centrum (MBO); and narrowest width of the basioccipital bone (NWB). The MBO measurement was made on the right side of the Eastover specimen because it was better preserved than the left side.

Parasphenoid—Four morphometric characters were studied (Fig. 2A–C), three in the central region: width between the carotid foramina (PAFW); depth between the ventral margin of the parasphenoid and the notch posterior to the basisphenoid process (PAD); and narrowest width (PAW) of the anterior process (a pr). The fourth character is the angle (parasphenoidal

angle or α) along the ventral margin of the parasphenoid that the posterior process makes with the anterior process.

Predentary—Three morphometric characters were studied (Fig. 1E, F): length along the ventral mid-line (PL), width across the widest expanse of the denticulated surface (PW), and depth perpendicular to the long axis from the widest expanse of the denticulated surface to the ventral surface of the bone (PD). The posterior extensions of the predentary usually form wing-like processes that are wider than the PW measurement, but since the extensions are often missing in the fossils and broken in the Recent specimens, this measurement of width was omitted.

Rostrum—Because the Eastover rostrum is a distal segment, only features of the distal part of the rostrum were studied (Fig. 3A–C). Using the size of the prenasal as a guide (Fierstine, in press), 0.25L (one-fourth the distance between the distal tip and the orbital margin of the lateral ethmoid) was estimated to be 144 mm from the distal tip. Morphometric characters studied at 0.25L (Figs. 3A–C, 8A) were depth (D2) and width (W2) of the rostrum, height (H2) of the nutrient canal (as seen in cross-section), and distance (DD2) of the nutrient canal from the dorsal surface (as seen in cross section). In order to prevent damage caused by sectioning, the rostrum was measured at 0.25L from a CT image (Fig. 8A). Characters studied without reference to region were the distribution of denticles on the dorsal
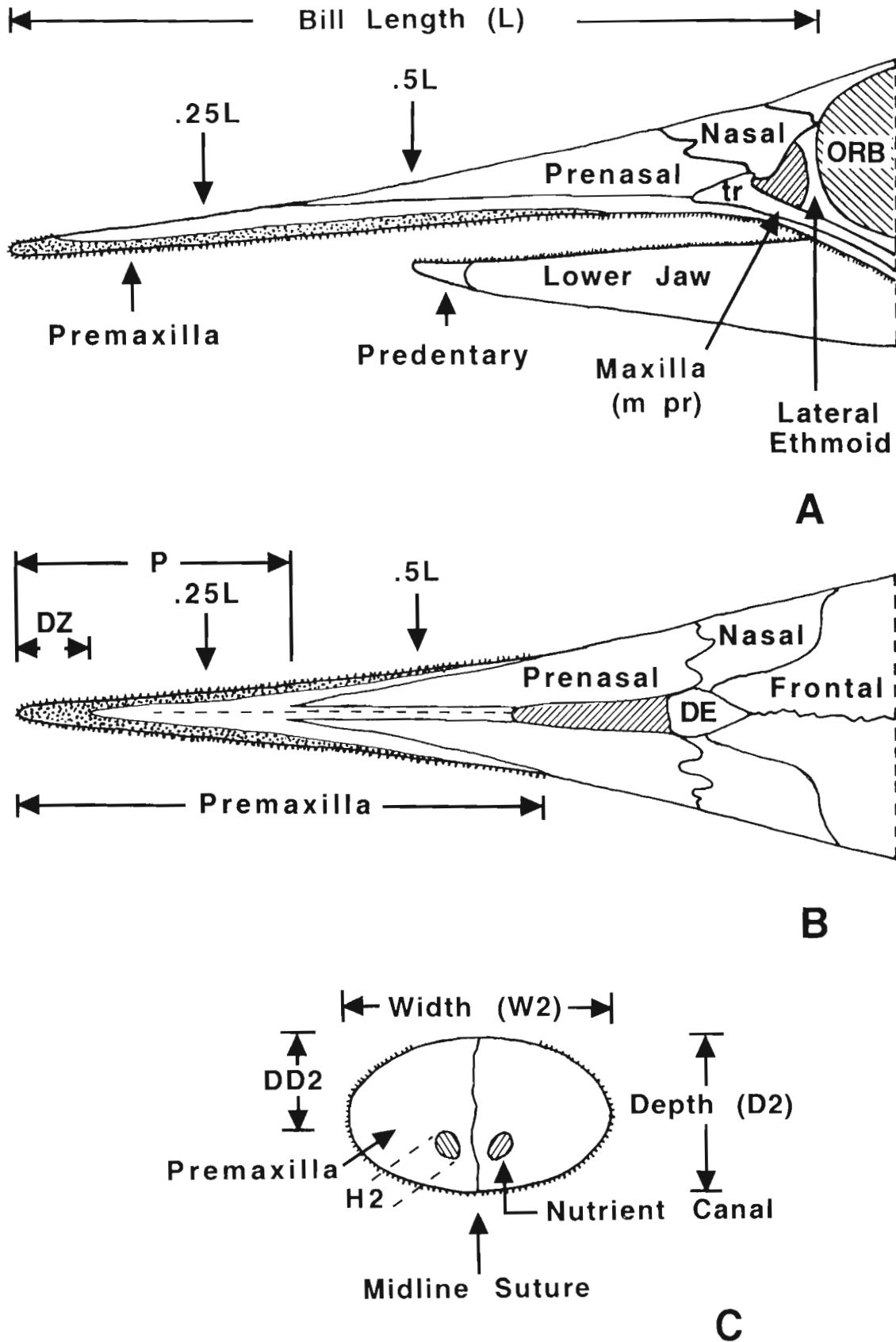
FIGURE 3.   Rostrum of a generalized istiophorid (modified from Fierstine and Voigt, 1996). **A**, left lateral view. **B**, dorsal view. **C**, cross section at one-fourth bill length (0.25L). Abbreviations of measurements are defined in Methods section of text.
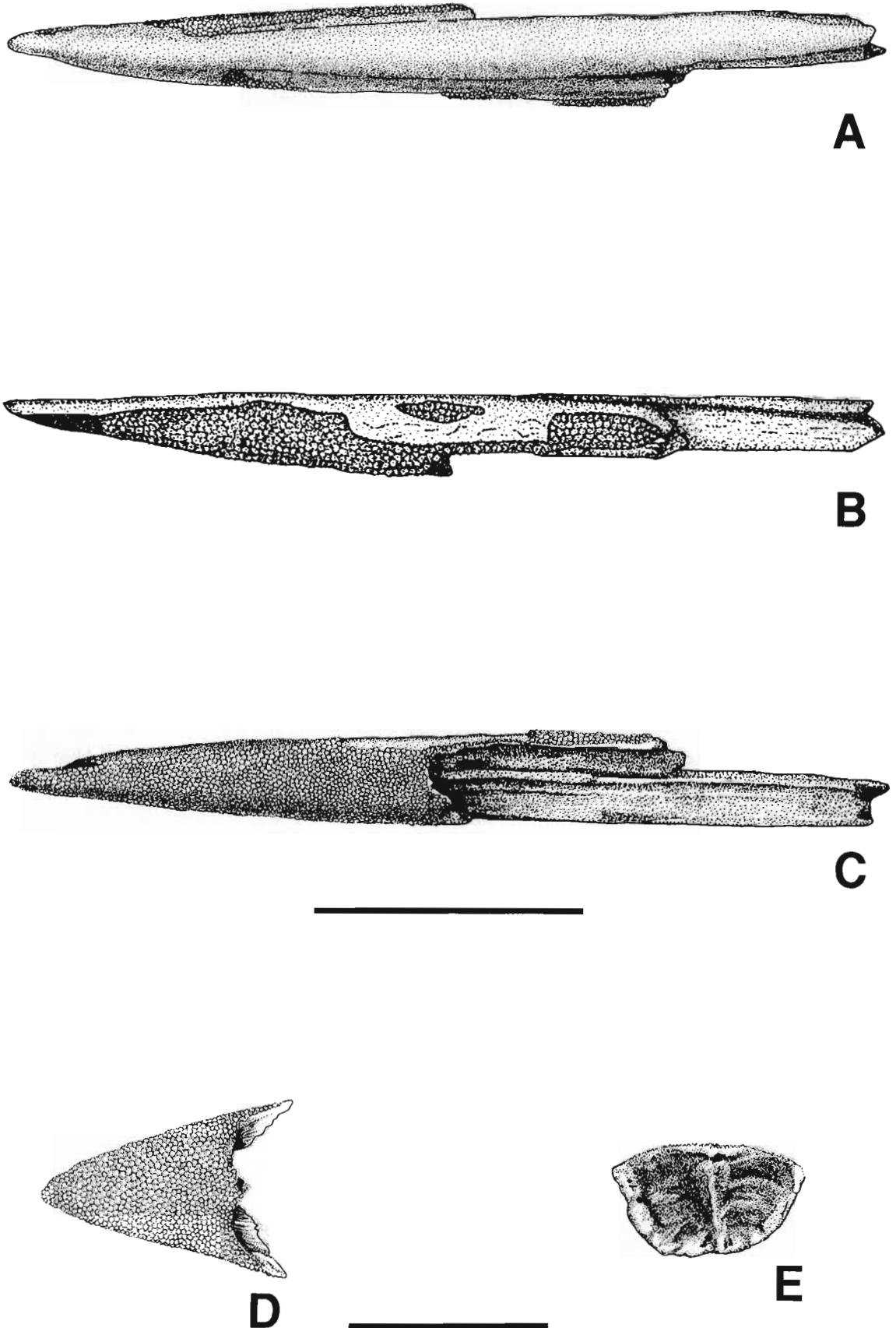
FIGURE 4. *Makaira* sp., cf. *M. nigricans* (USNM 375733), Eastover Formation (late Miocene), Virginia. **A**, distal rostrum, dorsal view. **B**, distal rostrum, lateral view. **C**, distal rostrum, ventral view. **D**, predentary, dorsal view. **E**, predentary, posterior view. **A–C**, scale bar = 10 cm. **D**, **E**, scale bar = 5 cm.

TABLE 1. Selected measurements of the partial head skeleton of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 375733), Eastover Formation (early late Miocene), Virginia. Abbreviations of measurements are defined in Methods section of text and Figures 1–3. All measurements are in mm except for Parasphenoidal Angle (α) that is in degrees (°). Values indicated by an asterisk (*) were taken from computer tomography (CT) scans and not directly from the specimen.

Bone or Region of Skull	Measurements
Neurocranium	
Greatest Length	320.0
Greatest Width	158.0
Greatest Depth	117.0
Occipital Region	
MBO	74.9
NWB	26.0
TD	37.3
Parasphenoid	
Greatest length	216.0
PAD	11.4
PAFW	21.5
PAW	15.0
Parasphenoidal Angle or α (°)	16.0
Right articular	
Greatest Length	259.0
Greatest Depth	73.5
AAL	12.0
AL	20.4
AW	15.8
ASM	25.9
ATW	24.0
Right Maxilla	
Greatest Length	450.0
MH	29.7
ML	46.2
MOL	268.0
MVH	13.4
MVW	17.0
MW	36.7
Right Metapterygoid	
Greatest Length (antero-posterior)	80.5
Greatest Height (dorso-ventral)	93.0
Rostrum	
Greatest Length	313.0
D2	*22.6
W2	*32.1
DD2	*10.6
H2	*4.0
P	185.0
Predentary	
PD	23.6
PL	45.3
PW	33.6

surface (DZ) and position of the prenasal bone from the distal tip of the rostrum (P).

Species Identification

Using a variation of the methods of Fierstine (in press), identification was accomplished by converting length and width measurements of individual bones (characters) to ratios (proportions), treating ratios as variables, and comparing them to ratios computed from a series of bones from Recent istiophorid species or to ratios computed from other istiophorid fossils. If a ratio fell within the range of one or more Recent species, then it was scored for each species that contained the ratio. The identification protocol is as follows: The Eastover specimen

would be identified as the Recent species with the most scores, unless: 1) its overall score overlapped two or more species of the same genus; 2) its overall score overlapped two or more genera; or 3) some of its scores fell outside the observed range of Recent species. In the first two cases, the Eastover specimen would be identified only to genus or family, respectively. In the third case, the Eastover specimen would be identified as a known fossil species, a variant of a Recent or fossil species, or a new species, depending on how it differed from the fossil or Recent species.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII (sensu Nelson, 1994)
Division TELEOSTEI (sensu Nelson, 1994)
Order PERCIFORMES (sensu Johnson and Patterson, 1993)
Suborder SCOMBROIDEI (sensu Carpenter et al., 1995)
Family ISTIOPHORIDAE (sensu Robins and deSylva, 1960)
Genus *Makaira* Lacépède, 1802

MAKAIRA sp., cf. *M. NIGRICANS* Lacépède, 1802
Figures 4–8A

Specimen—Incomplete, partially disarticulated skull (USNM 375733) including neurocranium, predentary, distal rostrum, right maxillary, right articular, and right metapterygoid.

Locality—According to Frank C. Whitmore, Jr. (letter dated January 5, 1988, U.S. Geological Survey, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560), "the billfish was collected at the Grove, the estate of George Edmond Massie, Caroline County, Virginia, . . .in an unnamed tributary of the Pamunkey R., 1 km north of the northernmost bend of the Pamunkey R., USGS Hanover, VA, 7.5' quadrangle. It was found in blue clay . . . , probably part of the Claremont Manor member of the Eastover Formation (L.W. Ward, written communication, August 1984)." The specimen was collected in the same creek bank as a partial skull and articulated vertebrae of an undescribed large delphinoid cetacean (USNM 256746), family Kentriodontidae (Whitmore, 1984).

Age—According to Ward and Blackwelder (1980), the Claremont Manor member is probably of early Tortonian Age (early late Miocene) and was deposited in an open, marine environment. The precise age of the base of the Eastover (Claremont Manor Member) is not well constrained (Whitmore, 1994), but probably is somewhere around 11 Ma (Ward and Blackwelder, 1980), whereas the age of the top of the Claremont Manor Member is 8.9 ± 0.4 Ma (Blackwelder, 1981).

DESCRIPTION AND COMPARISON WITH EXTANT ISTIOPHORID SPECIES

Except for the neurocranium, the head skeleton of USNM 375733 consists of 15 separate pieces (Figs. 4–8). Selected measurements from six of the more complete elements are given in Table 1. Ratios (variables) computed from most measurements are listed in Table 2 along with the mean, observed range, and number of bones examined for the same variable in eight extant species of the family Istiophoridae.

Rostrum (Figs. 4, 8A)

Because the rostrum is a distal segment with many of its denticles worn away, only three variables were analyzed (Table 2). Variable D2/W2 (0.70) is within the observed range of *I. platypterus, M. indica,* and *M. nigricans;* H2/D2 (0.18) is within the observed ranges of *I. platypterus* and *M. nigricans;* DD2/D2 (0.47) falls within or is close to the observed range of all istiophorids studied except for two species of *Tetrapturus.*
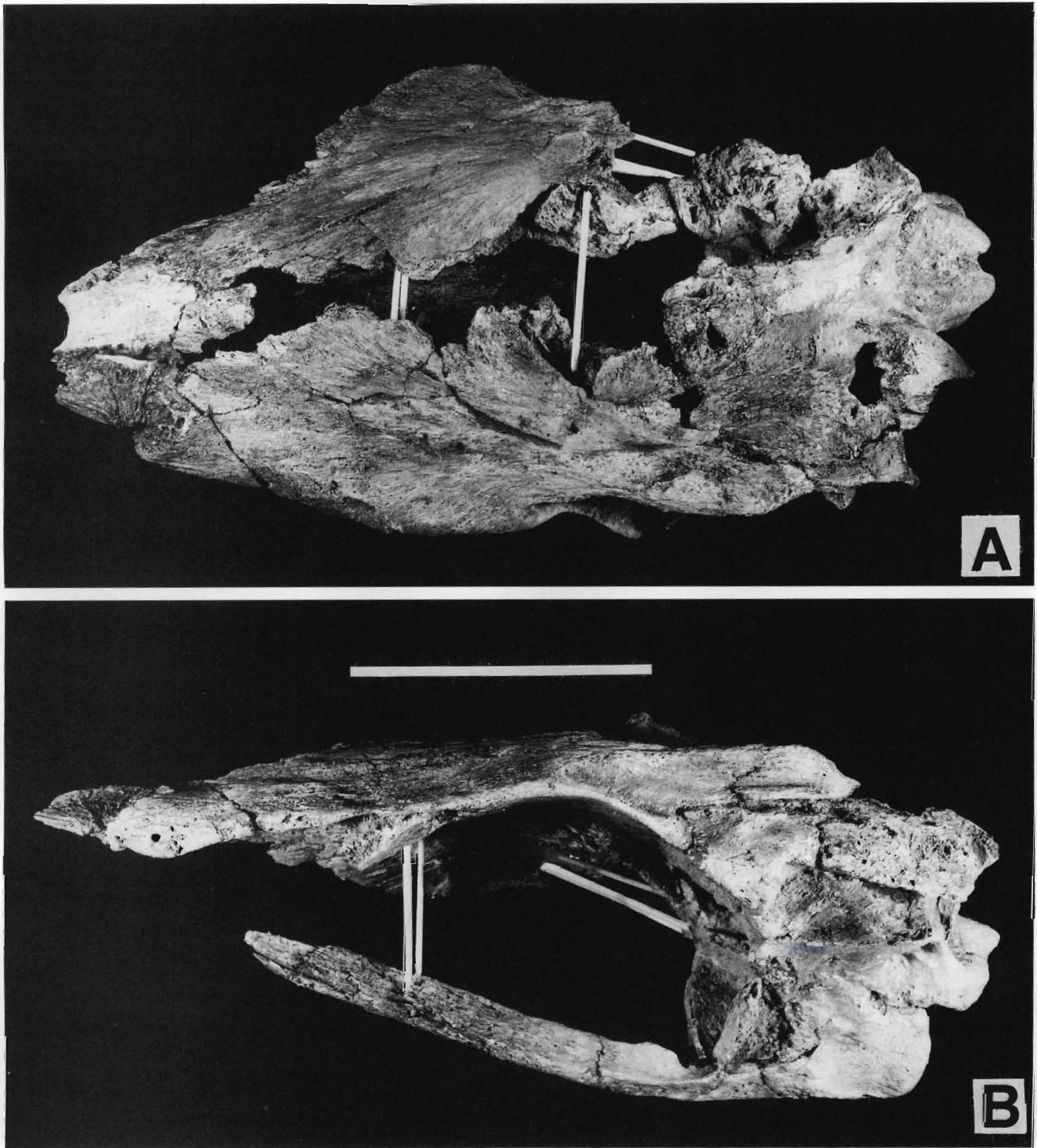
FIGURE 5. *Makaira* sp., cf. *M. nigricans* neurocranium (USNM 375733), Eastover Formation (late Miocene), Virginia. **A**, dorsal view. **B**, left lateral view. Support structures are visible. Scale bar = 10 cm.

Predentary (Fig. 4D, E)

The predentary is well preserved except for some wear at its distal tip. Variable PW/PL (0.74) is only within the observed range of *M. nigricans*; PD/PL (0.52) falls within the observed range of values for *M. nigricans* and *T. angustirostris*, although it is near to that of *T. belone*. Variable PD/PW (0.70) falls

within the observed range of *I. platypterus, M. indica,* and *T. audax.*

Partial Neurocranium (Figs. 5–6)

The neurocranium consists mostly of the otico-occipital region, skull roof, and parasphenoid. The basisphenoid, most of

TABLE 2. Variables (ratios and parasphenoidal angle) of *Makaira* sp., cf. *M. nigricans* (USNM 375733), Eastover Formation, late Miocene, Virginia, compared with the mean ($\bar{x}$), observed range (OR), and number of bones examined (N) for the same variables of eight Recent species of the family Istiophoridae. Abbreviations of variables (ratios) are defined in Methods section of text and Figures 1–3.

Ratios or Angle	USNM 375733	*I. platypterus* $\bar{x}$(OR)N	*M. indica* $\bar{x}$(OR)N	*M. nigricans* $\bar{x}$(OR)N	*T. albidus* $\bar{x}$(OR)N	*T. angustirostris* $\bar{x}$(OR)N
			Articular			
AL/ASM	0.79	0.70 (0.59–0.80) 22	0.90 (0.85–0.94) 2	0.80 (0.66–0.93) 23	0.71 (0.58–0.91) 15	—
AW/AL	0.77	0.74 (0.53–0.94) 22	0.70 (0.69–0.70) 2	0.84 (0.68–1.1) 23	0.91 (0.65–1.3) 15	—
AAL/AL	0.59	0.74 (0.59–0.92) 22	0.59 (0.59–0.60) 2	0.68 (0.47–0.91) 23	0.70 (0.54–0.97) 15	—
ATW/AL	1.2	1.1 (0.91–1.4) 21	0.94 (0.94–0.95) 2	1.2 (0.98–1.6) 22	1.3 (0.96–1.9) 15	—
AW/ATW	0.66	0.67 (0.54–0.78) 26	0.74 (0.74–0.74) 2	0.71 (0.55–0.78) 22	0.71 (0.57–0.86) 15	—
			Maxilla			
ML/MOL	0.17	0.31 (0.23–0.35) 9	—	0.20 (0.17–0.23) 14	0.26 (0.23–0.29) 10	—
MW/MOL	0.14	0.12 (0.08–0.14) 9	—	0.13 (0.13–0.13) 5	0.13 (0.12–0.13) 8	—
MW/ML	0.79	0.39 (0.25–0.57) 14	—	0.64 (0.60–0.70) 5	0.47 (0.44–0.51) 8	—
MH/ML	0.64	0.33 (0.26–0.47) 14	—	0.43 (0.38–0.49) 14	0.38 (0.34–0.45) 10	—
MVW/MVH	1.3	1.4 (0.95–2.4) 9	—	1.2 (1.1–1.3) 3	1.2 (0.80–1.8) 3	—
MVW/ML	0.37	0.22 (0.17–0.36) 9	—	0.36 (0.35–0.37) 3	0.20 (0.18–0.24) 3	—
MVW/MW	0.46	0.55 (0.48–0.63) 9	—	0.56 (0.53–0.60) 3	0.44 (0.40–0.48) 3	—
MVW/MH	0.57	0.64 (0.59–0.75) 9	—	0.90 (0.81–0.96) 3	0.54 (0.50–0.58) 3	—
			Parasphenoid			
PAD/PAFW	0.53	1.1 (0.74–1.4) 9	(0.59) 1	0.63 (0.55–0.79) 8	0.86 (0.73–0.98) 9	—
PAW/PAFW	0.70	0.70 (0.62–0.86) 9	(0.85) 1	0.84 (0.67–1.0) 8	0.53 (0.41–0.73) 9	—
PAD/PAW	0.76	1.6 (1.2–2.2) 9	(0.70) 1	0.77 (0.62–0.97) 8	1.7 (1.0–2.1) 9	—
Angle (°)	16	31 (26–37) 14	18 (15–23) 3	22 (16–30) 15	28 (20–33) 13	23 (23) 1
			Neurocranium (Occipital Region)			
TD/MBO	0.50	0.52 (0.45–0.61) 10	0.54 (0.50–0.57) 3	0.55 (0.33–0.64) 17	0.47 (0.42–0.52) 14	—
NWB/TD	0.70	0.35 (0.21–0.51) 12	0.50 (0.43–0.59) 3	0.51 (0.34–0.67) 15	0.26 (0.23–0.35) 13	—
			Predentary			
PW/PL	0.74	0.50 (0.23–0.63) 21	0.54 (0.48–0.62) 5	0.65 (0.45–1.1) 23	0.41 (0.34–0.57) 15	0.60 (0.54–0.69) 4
PD/PL	0.52	0.27 (0.20–0.37) 21	0.38 (0.30–0.41) 5	0.36 (0.26–0.58) 23	0.24 (0.20–0.33) 15	0.59 (0.52–0.69) 4
PD/PW	0.70	0.56 (0.48–1.0) 21	0.70 (0.63–0.81) 5	0.56 (0.48–0.61) 23	0.59 (0.53–0.65) 15	0.99 (0.97–1.0) 4
			Rostrum			
D2/W2	0.70	0.64 (0.55–0.75) 30	0.68 (0.58–0.77) 10	0.64 (0.54–0.83) 41	0.53 (0.47–0.61) 14	0.61 (0.58–0.64) 3
H2/D2	0.18	0.18 (0.11–0.26) 28	0.10 (0.08–0.12) 9	0.12 (0.06–0.21) 32	0.12 (0.09–0.14) 7	0.11 (0.07–0.14) 2
DD2/D2	0.47	0.38 (0.28–0.46) 28	0.46 (0.38–0.51) 9	0.47 (0.22–0.64) 32	0.40 (0.32–0.43) 7	0.63 (0.62–0.63) 2

the dermethmoid and both lateral ethmoids, right otic area, skull roof over the pineal organ, all of the proximal rostrum except for a partial left prenasal bone, and most of the vomer are missing. The TD/MBO ratio (0.50) falls within the range of values of most other istiophorids; however, the NWB/TD ratio (0.70) is outside the range of values of all extant istiophorids, although near the upper limit of *M. nigricans* (Table 2).

The parasphenoid is complete except for the lateral extensions of its anterior process and the area surrounding each carotid foramen. The PAW/PAFW variable (0.70) is within the observed range of values of *I. platypterus*, *M. nigricans*, and *T. albidus*; the parasphenoidal angle (16°) is within the observed range of *M. indica* and *M. nigricans*; the PAD/PAW variable (0.76) falls only within the observed range of values for *M. nigricans*; and the PAD/PAFW ratio (0.53) is outside the range of values of all extant istiophorids, although near to that of *M. nigricans*.

Right Articular (Fig. 7B)

The right articular is complete. All five of its variables fall within the observed range of values of most extant istiophorid species listed in Table 2.

Right Maxilla (Fig. 7A)

The right maxilla is complete except for a reconstructed region near the junction of its internal process and triangle. Six ratios (MW/MOL, MW/ML, MVW/MVH, MVW/ML, MVW/MW, and MVW/MH) were omitted from my comparison with *M. nigricans* because the sample size was too small (five or

fewer). Variable ML/MOL (0.17) falls only within the observed range of values for *M. nigricans* and variable MH/ML (0.64) is outside the observed range of values for all extant istiophorids measured.

Identification

All Recent istiophorid species, except *I. platypterus*, have too small of a sample size (n = 7 or fewer) in three or more variables (Table 2) to make a meaningful comparison with the Eastover marlin. Especially noteworthy is the small sample size (n = three or fewer) for *T. angustirostris*, *T. belone*, *T. pfluegeri*, and *T. georgei* Lowe, 1840. The latter species was omitted for the lack of morphological data relative to this study. Fortunately, insufficient data for the four species of *Tetrapturus* are probably not crucial because they are species of small size (maximum of 70 kg or less) with slender rostra (Nakamura, 1985; Fierstine and Voigt, 1996) quite unlike the Eastover marlin.

Only 19 of the 25 variables analyzed have an adequate sample size (n = 8 or more) in Recent *I. platypterus*, *M. nigricans*, and *T. albidus* for meaningful comparison with the Eastover marlin (Table 2). Fifteen of the 19 variables fall within the observed range of *M. nigricans*, ten within the range of *I. platypterus*, eight within the range of *T. audax*, seven within the range of *T. albidus*, six within the range of *M. indica*, and one within the range of *T. angustirostris*. Three variables fall only within the range of *M. nigricans* (ML/MOL, PAD/PAW, PW/PL). Three of the four variables that lie outside the observed range of *M. nigricans*, also fall outside the range of all Recent istiophorids. Two of these variables (NWB/TD, PAD/

TABLE 2. Extended.

Ratios or Angle	T. audax x̄(OR)N	T. belone x̄(OR)N	T. pfluegeri x̄(OR)N
Articular			
AL/ASM	0.78 (0.68–0.88) 9	—	(0.81) 1
AW/AL	0.71 (0.58–0.85) 9	—	(0.89) 1
AAL/AL	0.66 (0.55–0.79) 9	—	(0.29) 1
ATW/AL	1.1 (0.87–1.3) 9	—	(1.1) 1
AW/ATW	0.63 (0.58–0.70) 10	—	(0.81) 1
Maxilla			
ML/MOL	0.26 (0.25–0.27) 2	—	0.33 (0.33–0.33) 2
MW/MOL	0.12 (0.12) 2	—	0.08 (0.08–0.08) 2
MW/ML	0.47 (0.45–0.49) 2	—	0.24 (0.23–0.24) 2
MH/ML	0.37 (0.36–0.37) 2	—	0.33 (0.31–0.34) 2
MVW/MVH	1.2 (0.96–1.5) 2	—	—
MVW/ML	0.28 (0.25–0.31) 2	—	—
MVW/MW	0.60 (0.51–0.69) 2	—	—
MVW/MH	0.77 (0.68–0.85) 2	—	—
Parasphenoid			
PAD/PAFW	1.1 (1.1–1.1) 2	—	(1.3) 1
PAW/PAFW	0.58 (0.47–0.68) 2	—	(0.89) 1
PAD/PAW	2.0 (1.6–2.4) 2	—	(1.5) 1
Angle (°)	26 (22–30) 8	—	32 (32) 1
Neurocranium (Occipital Region)			
TD/MBO	0.49 (0.37–0.54) 7	—	0.43 (0.43) 1
NWB/TD	0.33 (0.25–0.42) 7	—	0.17 (0.17) 1
Predentary			
PW/PL	0.42 (0.33–0.51) 13	(0.59) 1	(0.65) 1
PD/PL	0.26 (0.22–0.30) 13	(0.53) 1	(0.60) 1
PD/PW	0.60 (0.53–0.72) 13	(0.90) 1	(0.92) 1
Rostrum			
D2/W2	0.61 (0.52–0.67) 13	—	0.65 (0.65) 2
H2/D2	0.12 (0.09–0.14) 8	—	(0.15) 1
DD2/D2	0.46 (0.41–0.55) 8	—	0.49 (0.48–0.50) 2

PAFW) are less than 5% different from *M. nigricans*, but far outside the range of other istiophorids. A third variable (MH/ML) falls far outside the range of all Recent istiophorids (triangle region of the maxilla is 23.4% shorter and thicker); however, this includes the region of the maxillary that was reconstructed. A fourth variable (PD/PW) demonstrates that the predentary is considerably more round (15%) than Recent *M. nigricans*.

There is enough taxonomic uncertainty in the above information that I identify the Eastover specimen as *Makaira* sp., cf. *M. nigricans*. Although the Eastover specimen is similar to extant *M. nigricans* in 15 of the 19 morphometric variables, it is dissimilar in four, three of which are outside the observed range of all istiophorids. Larger sample sizes of some of the comparative material, especially *M. indica*, may or may not have made the identification more certain.

COMPARISON WITH FOSSIL ISTIOPHORIDS OF THE GENUS *MAKAIRA*

The following discussion is based on a review of fossil billfish by Fierstine (in press) in the study of billfish from Lee Creek Mine (early Pliocene, Yorktown Formation). Only fossil specimens with a direct relevance to the Eastover marlin (USNM 375733) are discussed here (Tables 3 and 4).

†*Makaira belgicus* (Leriche, 1926) (IRSNB P1117, holotype, middle Miocene, Anvers, Belgium) is a distal rostral fragment. All three ratios listed for the specimen in Table 4 fall within the range of *M. nigricans*, two within or just outside the range of *I. platypterus* and *T. albidus*, and one within or just outside the range of *T. angustirostris*, *T. audax*, and *T. pfluegeri* (Table 2). Two of the ratios fall within the range of values of *M. nigricans* from Lee Creek Mine and none are with the observed range of other fossil istiophorid species, except for *M. nigricans* (LACM 17693) from the late Miocene of California (Table 4). Based on the above evidence, †Makaira *belgicus* is synonymous with *M. nigricans*.

TABLE 3. Variables (ratios and parasphenoidal angle), excluding rostrum, of *Makaira* sp., cf. *M. nigricans* (USNM 375733), Eastover Formation, late Miocene, Virginia, compared with the same variables of four fossil istiophorid taxa. The mean (x̄), observed range (OR), and number of bones examined (N) are given for specimens from Lee Creek Mine. Abbreviations of variables [ratios and parasphenoidal angle (α)] are defined in Methods section of text and Figures 1, 2.

| Ratios or Angle (α)	USNM 375733	Makaira indica Yorktown Fm. Lee Creek Mine E. Pliocene x̄ (OR) N	Makaira nigricans Yorktown Fm. Lee Creek Mine E. Pliocene x̄ (OR) N	Makaira sp., cf. M. nigricans Yorktown Fm. Lee Creek Mine E. Pliocene x̄ (OR) N	Makaira nigricans UCMP 117559 San Mateo Fm. L. Miocene	†Makaira panamensis Holotype USNM 181710 Chagres S.S. L. Miocene/ E. Pliocene
Articular						
AL/ASM	0.79	—	—	—	—	—
AW/AL	0.77	—	—	—	0.91	—
AAL/AL	0.59	—	—	—	—	—
ATW/AL	1.2	—	—	—	1.2	—
AW/ATW	0.66	—	—	—	0.76	—
Parasphenoid						
PAD/PAFW	0.53	—	(0.71) 1	0.65 (0.61–0.69) 2	—	—
PAW/PAFW	0.70	—	(0.87) 1	(0.72) 1	—	—
PAD/PAW	0.76	—	0.83 (0.73–0.94) 7	0.92 (0.87–0.96) 2	—	—
α (°)	16.0	—	—	—	—	20
Neurocranium (Occipital Region)						
TD/MBO	0.50	—	—	—	—	0.58
NWB/TD	0.70	—	—	—	—	0.50
Predentary						
PW/PL	0.74	0.62 (0.57–0.63) 4	0.76 (0.64–1.1) 13	—	—	—
PD/PL	0.52	0.40 (0.38–0.41) 4	0.47 (0.40–0.61) 13	—	—	—
PD/PW	0.70	0.65 (0.64–0.67) 4	0.62 (0.58–0.74) 13	—	—	—
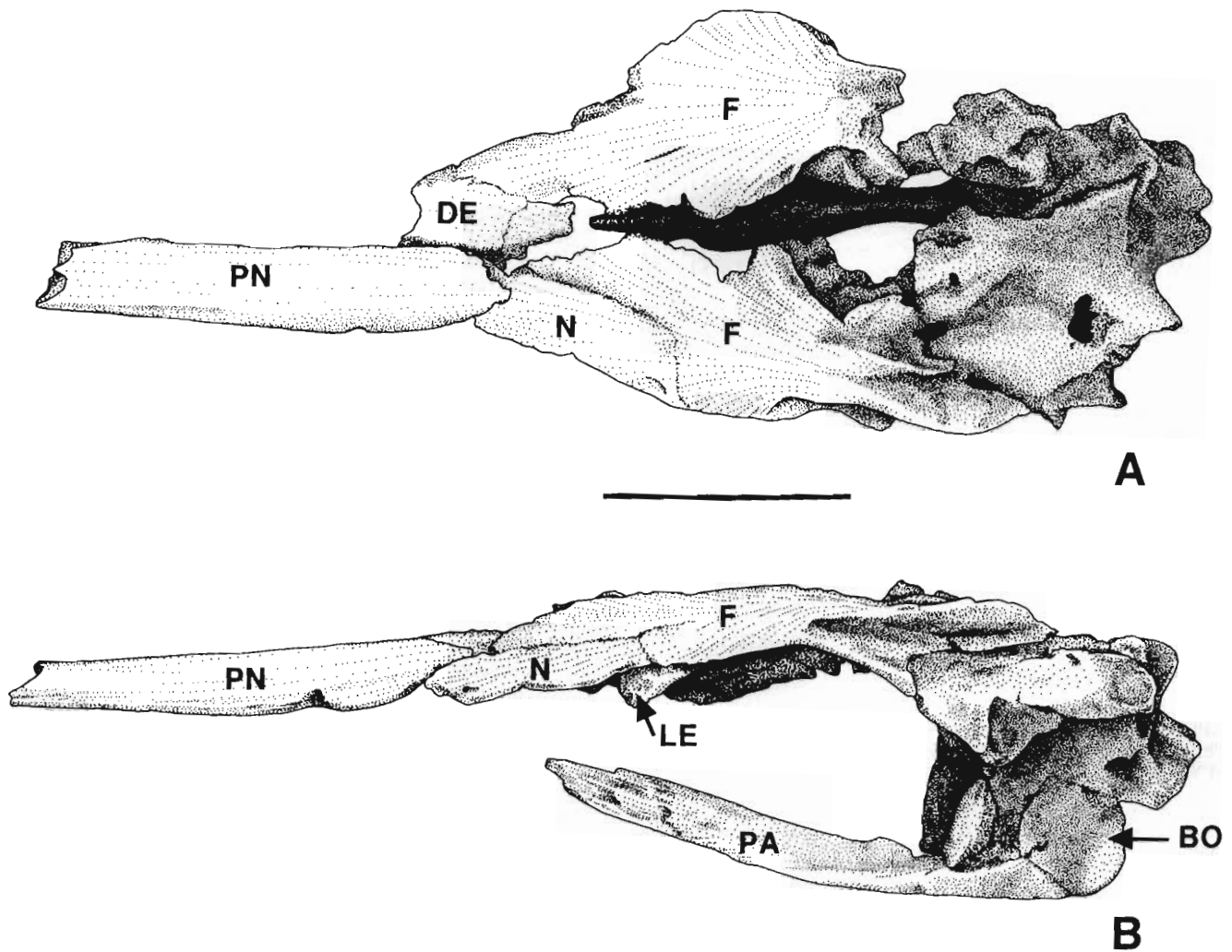
FIGURE 6.   Drawing of *Makaira* sp., cf. *M. nigricans* neurocranium (USNM 375733), Eastover Formation (late Miocene), Virginia. **A**, dorsal view. **B**, left lateral view. Same as Figure 5 except left prenasal is present. Scale bar = 10 cm.

TABLE 4.   Variables (ratios) of the rostrum of *Makaira* sp., cf. *M. nigricans* (USNM 375733) and †*Istiophorus calvertensis* holotype (USNM 9344), Eastover Formation, late Miocene, Virginia, compared with the same variables of eight fossil istiophorid taxa. The mean ($\bar{x}$), observed range (OR), and number of bones examined (N) are given for specimens from Lee Creek Mine. Abbreviations of variables (ratios) are defined in Methods section of text and Figure 3.

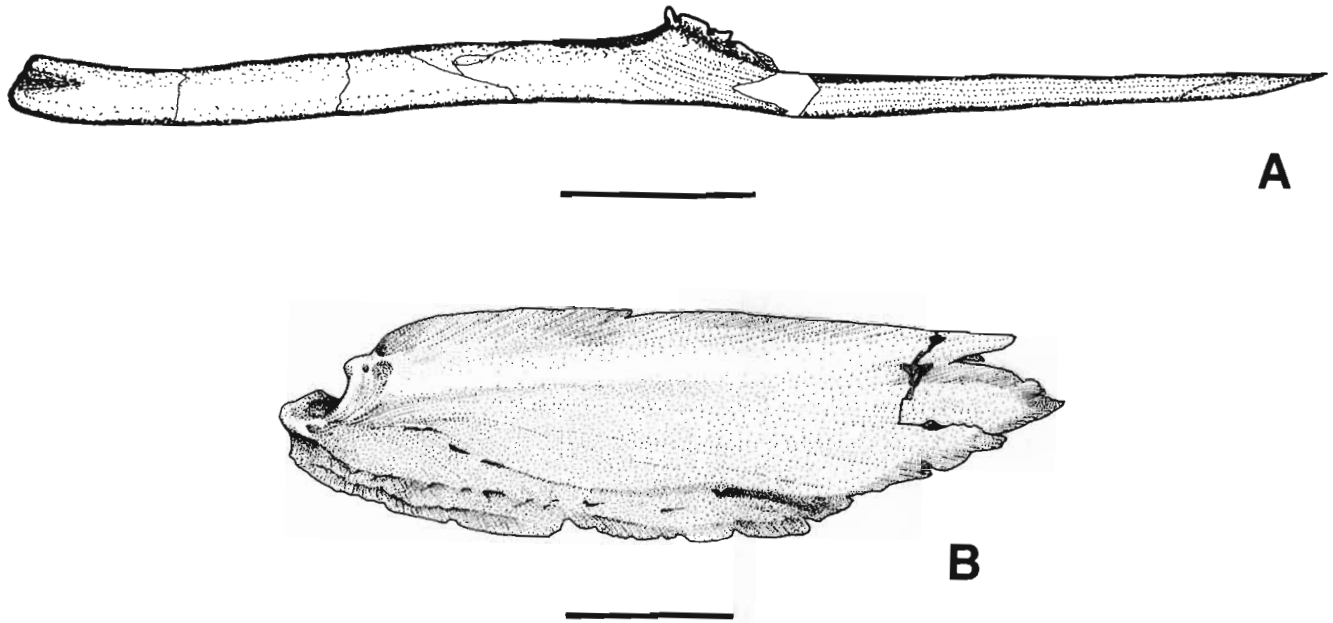| Ratios	USNM 375733	USNM 9344	*Istiophorus platypterus* Yorktown Fm. Lee Creek Mine E. Pliocene $\bar{x}$ (OR) N	*Istiophorus* sp., cf. *platypterus* Yorktown Fm. Lee Creek Mine E. Pliocene $\bar{x}$ (OR) N	†*Makaira belgicus* Holotype IRSNB P1117 M. Miocene	†*Makaira courcelli* Holotype MNHN 250 E. Pliocene	*Makaira nigricans* Yorktown Fm. Lee Creek Mine E. Pliocene $\bar{x}$ (OR) N	*Makaira nigricans* LACM 17693 Monterey Fm. L. Miocene	†*Makaira panamensis* Holotype USNM 181710 Chagres S.S. L. Miocene/E. Pliocene	†*Makaira tereti-rostris* Holotype ?M. Miocene
D1/W1	—	0.72	0.73 (0.72–0.75) 3	—	—	0.67	0.79 (0.77–0.80) 3	—	—	0.87
H1/D1	—	0.27	0.21 (0.19–0.23) 4	—	—	—	0.15 (0.09–0.19) 14	—	—	0.10
DD1/D1	—	0.43	0.41 (0.35–0.50) 4	—	—	—	0.52 (0.41–0.59) 14	—	—	0.58
D2/W2	0.70	0.69	0.71 (0.69–0.72) 2	(0.75) 1	0.80	0.66	0.76 (0.66–0.83) 36	0.76	0.76	0.84
H2/D2	0.18	0.27	(0.25) 1	(0.27) 1	0.15	—	0.15 (0.06–0.22) 16	0.17	0.27	0.11
DD2/D2	0.47	0.39	(0.45) 1	(0.39) 1	0.34	—	0.52 (0.40–0.62) 16	0.56	—	0.56
DZ/P	—	0.34	(0.50) 1	—	—	—	0.49 (0.38–0.59) 3	—	—	—

FIGURE 7.   *Makaira* sp., cf. *M. nigricans* (USNM 375733), Eastover Formation (late Miocene), Virginia. **A**, right maxilla, lateral view. **B**, right articular, lateral view. A, scale bar = 6 cm; B, scale bar = 5 cm.

†*Makaira courcelli* (Arambourg, 1927) (MNHN 250), holotype, lower Pliocene, Algeria) consists of two rostra and several fragments. Arambourg originally placed the specimens in †*Xiphiorhynchus* but Schultz (1987) correctly placed the specimens in *Makaira*. Fierstine (in press) states that the lack of cross-sectional data (size and position of nutrient canals) in †*M. courcelli* made comparison with other fossil and extant istiophorids nearly impossible. This conclusion holds for comparison with the Eastover marlin (Table 4).

Makaira indica (Cuvier, 1832), an extant species, was identified from four predentaries (Table 3) and two scapulas collected in the Yorktown Formation (early Pliocene) at Lee Creek Mine (Fierstine, in press). The predentaries are rounder (PD/PW > 0.61) than those of Recent *M. nigricans,* within the range of *M. nigricans* from Lee Creek, and more oval (less round) than the predentary of the Eastover marlin. The scapulas have a narrow, flat articular surface for the first pectoral ray that is diagnostic for *M. indica.*

Makaira indica was also identified from a partial head skeleton (including pectoral and pelvic girdles and rays) from the early Pleistocene, ?Cabatuan Formation, Luzon, Philippines (Fierstine and Welton, 1983). Other than the parasphenoidal angle (15°), the Philippine specimen does not have the same variables preserved as the Eastover marlin. In general, the specimen resembles both *M. indica* and *M. nigricans* except that it has a rigid pectoral fin and a scapula with a flat articular surface for the first pectoral ray (diagnostic features of extant *M. indica*).

Makaira nigricans Lacépède, 1802 was identified from approximately 500 separate bones collected in the Yorktown Formation (early Pliocene) at Lee Creek Mine, North Carolina (Fierstine, in press). Tables 3 and 4 list ratios from four elements of the Lee Creek *M. nigricans* that were found as part of the Eastover marlin. All ratios of the Eastover marlin are within the range of values of Lee Creek *M. nigricans,* except for the PAD/PAFW ratio (0.53), a much smaller value than computed for the parasphenoid (0.71) identified as *M. nigricans* from Lee Creek Mine.

Makaira nigricans also was identified from several bones of a single individual (UCMP 118559), late Miocene, San Mateo

Formation, San Diego County, California (Fierstine and Welton, 1988), but an articular is the only element in common with *M. nigricans* from the Eastover Formation. Variables AW/AL (0.91) and AW/ATW (0.76) are larger values and ATW/AL (1.2) is identical to those measured in the Eastover marlin (Table 3). All three values are within the observed range measured in Recent *M. nigricans* (Table 2).

A large predentary (LACM 16074, late Miocene, Capistrano Formation, Orange County, California) was originally identified as *Makaira* sp. (Fierstine and Applegate, 1968), but recently reidentified as Istiophoridae genus and species indeterminate (Fierstine, in press). The specimen has ratios (PW/PL = 0.62; PD/PL = 0.37; PD/PW = 0.60) that are within the observed range of both Recent *I. platypterus* and Recent *M. nigricans.* Two of its ratios (PW/PL and PD/PW) fall outside the range of values for *M. nigricans* from Lee Creek Mine and none of its ratios are really close to those observed in the Eastover marlin.

A distal rostrum (LACM 17693) from the late Miocene, Monterey Formation, Orange County, California, was originally identified to genus (*Makaira* sp.) because of insufficient comparative material (Fierstine and Applegate, 1968), but later reidentified as *M. nigricans* when more comparative skeletal material became available (Fierstine, in press). The variables (ratios) of the specimen fall within the range of values observed for Recent and Lee Creek *M. nigricans* and are similar to those observed for the Eastover marlin (Table 4).

Schultz (1996) identified two rostral fragments from the lower Pliocene of El Alquian, Spain, as *Makaira* sp. The poor preservation of the specimens and differences in Schultz's and my methods of making measurements preclude direct comparison with other fossil and Recent istiophorids.

†*Makaira panamensis* Fierstine, 1978 (USNM 181710, late Miocene or early Pliocene, Chagres Sandstone, Atlantic Coast of Panama) is the only fossil neurocranium with features well enough preserved to compare with the Eastover marlin. The parasphenoidal angle (20°) and TD/MBO ratio are slightly larger values and NWB/TD ratio is a smaller value than in the Eastover specimen (Table 3), but all three values are within the observed range of *M. nigricans* (Table 2). †*Makaira panamen-*
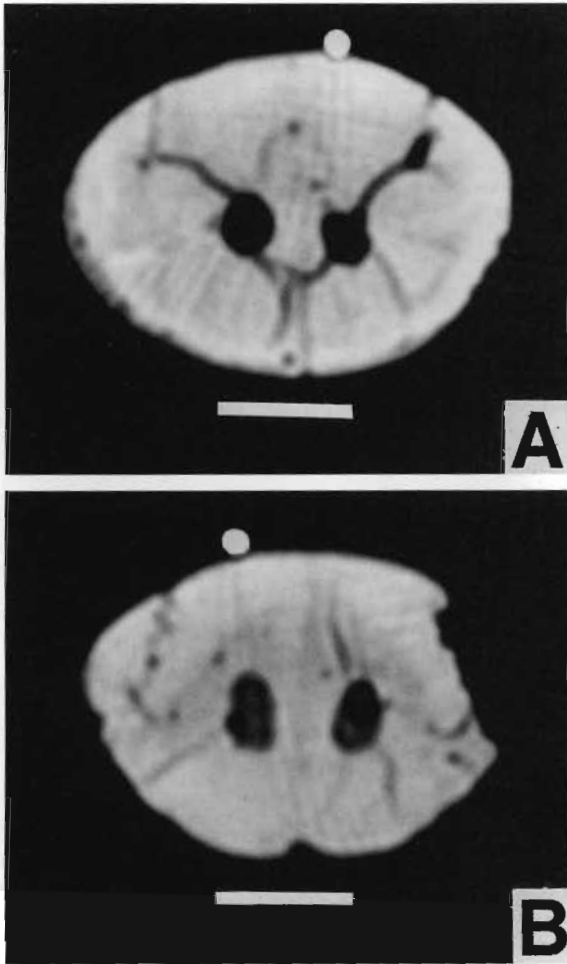
FIGURE 8.   Computer tomography images of rostra at 0.25L (one-fourth the distance from tip of rostrum to orbital border of lateral ethmoid). **A**, *Makaira* sp., cf. *M. nigricans* (USNM 375733), Eastover Formation (late Miocene), Virginia. **B**, †*Istiophorus calvertensis* Berry, 1917 (USNM 9344, holotype, late Miocene, Eastover Formation, Virginia). An opaque marker (artifact) is on the dorsal surface of each image. Scale bar = 10 mm.

sis has a larger myodome and longer orbit than other members of the genus *Makaira* (Fierstine, 1978), features not preserved in the Eastover marlin. The rostrum (Table 4) has nutrient canals at 0.25L (H2/D2 = 0.27) that are relatively larger than those of any other fossil or Recent istiophorid, except a single specimen from Lee Creek Mine identified as *Istiophorus* sp., cf. *I. platypterus*. Fierstine (1978) believed the Chagres Sand-

stone was late Miocene in age, but its age is now considered late Miocene or early Pliocene (Woodring, 1982) or Pliocene (Coates et al., 1992).

†*Makaira teretirostris* (Van Beneden, 1871) (?middle Miocene, Belgium, exact locality unknown) is based on a large, distal rostral fragment. Disposition of the type is unknown. Schultz (1987) synonymized the specimen with †*M. belgicus* and gave the type locality as southern France and age as Pliocene. Fierstine (in press:table 6) made measurements and computed ratios from the drawing in Van Beneden (1871). Because ratios D1/W1 and D2/W2 (Table 4) are larger (indicating a slightly rounder rostrum) and fall outside the range of values of Recent *M. nigricans* and *M. nigricans* from Lee Creek Mine, I continue to recognize †*M. teretirostris* as a valid species. †*Makaira teretirostris* has a rounder rostrum, relatively smaller nutrient canals, and more ventrally placed nutrient canals than the Eastover marlin (Table 4).

REEXAMINATION OF †*ISTIOPHORUS CALVERTENSIS* BERRY, 1917

†*Istiophorus calvertensis* Berry, 1917 (USNM 9344, holotype, late Miocene, Eastover Formation, Tar Bay, James River, Virginia) is a distal rostral segment, 310 mm long (Figs. 8B, 9). Berry (1917) originally thought the specimen was collected in the Calvert Formation, but it was probably collected in the Claremont Manor Member of the Eastover Formation (early late Miocene) (Kimmel and Purdy, 1984; Fierstine, in press) that is well represented at Tar Bay (Ward and Blackwelder, 1980). Since the original description of the collection site of †*I. calvertensis* was vague, the stratigraphy of the type locality and age of the specimen will remain controversial. As mentioned in Fierstine (in press), the rostrum could have been collected in the Yorktown Formation, although it is unlikely due to the Yorktown's minor presence at Tar Bay.

Comparing ratios of †*I. calvertensis* to ratios of Recent and other fossil istiophorids, Fierstine (in press) concluded †*I. calvertensis* was a valid species. However, examination of the 0.25L region (Fig. 8B) of †*I. calvertensis* with computer tomography (CT) yields two new variables (H2/D2 and DD2/D2) and based on the added information (Table 4), I now believe †*I. calvertensis* should be identified as *Istiophorus* sp., cf. *I. platypterus* for the following reasons: 1) ratios H1/D1 and H2/D2 of †*I. calvertensis* fall only within the observed range of Recent *I. platypterus* and just outside the range of *I. platypterus* from Lee Creek Mine; 2) ratio DD1/D1 is within the range of values of most Recent and Lee Creek istiophorids, but just outside the range of Recent *I. platypterus*; 3) ratios D1/W1, D2/W2, and DD2/D2 of †*I. calvertensis* fall within the range of values of most Recent and fossil istiophorids, including *I. platypterus*; 4) ratios H2/D2 and DD2/D2 are identical to *Istiophorus* cf. *I. platypterus* from Lee Creek Mine; and 5) ratio DZ/P is only within the range of values of Recent *M. indica*
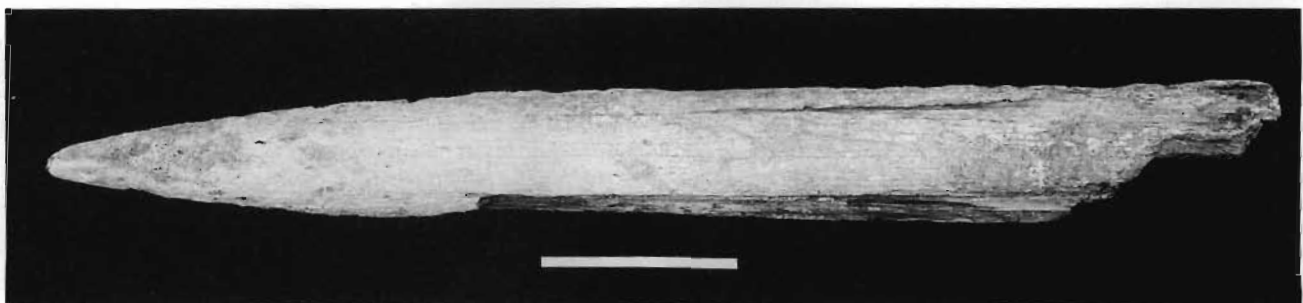

FIGURE 9.   Rostrum of †*Istiophorus calvertensis* Berry, 1917 (USNM 9344, holotype, late Miocene, Eastover Formation, Virginia), dorsal view. Scale bar = 5 cm.

and *Tetrapturus audax*. However, I think the distribution of denticles on the dorsal surface of the rostrum (DZ) is an unreliable feature in fossil specimens because denticles are often loosely attached on the dorsum of rostra of Recent *I. platypterus* and were probably not preserved.

There are two fossil records of *I. platypterus*: two maxillae and five rostra in the early Pliocene Yorktown Formation, North Carolina (Fierstine in press) and a partial trunk vertebra from the late Pliocene San Diego Formation, California (Gottfried, 1982). There are two fossil records of *Istiophorus* sp., cf. *I. platypterus*: the holotype of †*I. calvertensis* described above and one rostrum and one hypural from the early Pliocene Yorktown Formation, North Carolina (Fierstine, in press).

PALEOECOLOGY OF ISTIOPHORID BILLFISH IN THE EASTOVER FORMATION

Recent *I. platypterus* and *M. nigricans* inhabit tropical and temperate waters of the Atlantic, Indian, and Pacific oceans, with *M. nigricans* favoring blue water (depths > 100 m) with surface temperatures of 22–31°C, and *I. platypterus* often migrating to near-shore waters at temperatures of 21–28°C (Nakamura, 1983, 1985). In the western North Atlantic Ocean, both species migrate northward in an extension of warm water during the summer and migrate southward with the onset of cold weather. Fierstine (in press) hypothesized that istiophorid billfish during Yorktown time (early Pliocene) from Lee Creek Mine had similar ecological preferences and distribution patterns as extant billfish. Is it possible the same patterns and preferances were established by Eastover time (late Miocene)?

The answer is a qualified yes. Significant changes in body temperature pose a serious challenge to the maintenance of integrated physiological function (Hazel, 1993). Istiophorid billfish gain some thermal independence by having regional endothermy (brain and eye heater), but they usually remain above the thermocline (Block, 1991) in water temperatures between 21 and 31°C. In the absence of evidence to the contrary, one can assume that fossil and living billfish of the same species have identical thermal preferences. Although one can not assume identical thermal preferences of all species within a genus or all genera within a family, in the case of istiophorids, the thermal preferences of all species are similar (Nakamura, 1985). There is conflicting evidence whether the Claremont Manor Member of the Eastover Formation represents a near-shore, shallow, cool-temperate environment, based on bottom fish (Kimmel and Purdy, 1984), or an open, pelagic (Ward and Blackwelder, 1980), warm-temperate (Blackwelder, 1981) environment based on mollusks. The presence of istiophorids supports the hypothesis that an open, pelagic, warm-temperate environment existed. Because the Gulf Stream formed prior to the Miocene and strengthened (became deeper and stronger) during the Miocene (Riggs, 1984; Whitmore, 1994), istiophorids probably inhabited the Gulf Stream current during deposition of the Claremont Manor Member. Most likely, billfish were only summer visitors, because there is evidence for terrestrial and oceanic cooling during the latter part of the Miocene in the Chesapeake Bay region (Gottfried et al., 1994).

Makaira nigricans in the Atlantic Ocean reaches a total length (tip of bill to tip of tail) of approximately 4.0 m and a weight of 580 kg, whereas in the Pacific Ocean it reaches a total length of 4.5 m and a weight of 906 kg (Nakamura, 1983, 1985). Based on the width of the rostrum at 0.25L, the Eastover marlin is similar to LACM 25476, 226.7 cm body length (lower jaw to fork of tail), 178.6 kg, and female. Usually *M. nigricans* larger than 136 kg are female (Strasburg, 1969). The Eastover *Makaira* sp., cf. *M. nigricans* is within the expected size and weight range of *M. nigricans* in the Atlantic Ocean.

Istiophorus platypterus reaches around 3.2 m total length and 58 kg in the Atlantic Ocean, and around 3.4 m total length and 100 kg in the Indo-Pacific Ocean (Nakamura, 1983, 1985). Female *I. platypterus* are consistently larger than males of the same age, but, unlike *M. nigricans*, large fish can be either sex. Based on the width of the rostrum at 0.25L, the Eastover *Istiophorus* sp., cf. *I. platypterus* was probably twice the maximum size and weight of *I. platypterus* in the Atlantic Ocean, but was comparable to the maximum size and weight of *I. platypterus* in the Indo-Pacific Ocean.

CONCLUSION

The presence of *Makaira* sp., cf. *M. nigricans* and *Istiophorus* sp., cf. *I. platypterus* (= †*I. calvertensis*) in the early late Miocene, Eastover Formation, Virginia, marks the oldest record of both species in the western North Atlantic Ocean and the oldest fossil record of *Istiophorus* sp., cf. *I. platypterus* regardless of geographic locality. *Makaira nigricans* (= †*M. belgicus*) has inhabited the Atlantic Ocean since the middle Miocene and the Indo-Pacific Ocean since the late Miocene.

Based on ecological requirements of extant species, the presence of *Istiophorus* sp., cf. *I. platypterus* and *Makaira* sp., cf. *M. nigricans* indicates that deep, warm water probably existed at or near the collection sites for at least part of the year. *Istiophorus* sp., cf. *I. platypterus* from the Eastover Formation reached approximately twice the maximum body size of *I. platypterus* in the Atlantic Ocean today, but it was similar to the maximum body size of *I. platypterus* in the Indo-Pacific Ocean.

ACKNOWLEDGMENTS

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