**MAKAIRA SP., CF. *M. NIGRICANS* LACÉPÈDE, 1802
(TELEOSTEI: PERCIFORMES: ISTIOPHORIDAE) FROM THE LATE MIOCENE, PANAMA, AND
ITS PROBABLE USE OF THE PANAMA SEAWAY**

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ABSTRACT—A nearly complete rostrum (USNM 358534) similar in morphology to the extant blue marlin, *Makaira nigricans* Lacépède 1802, is identified from the Gatún Formation (late Miocene, Panama). Identification is based on comparison with a large series of Recent istiophorid species and with fossil species of the genus *Makaira*. The Gatún specimen and additional examples from other fossil vertebrates provide evidence that the ancient Panama Seaway probably was a travel route between the Atlantic and Indo-Pacific for large marine vertebrates during the middle Miocene to earliest Pliocene. This is the first record of an istiophorid billfish from the Gatún Formation and the second record of a fossil marlin from Panama.

INTRODUCTION

The blue marlin, *Makaira nigricans* Lacépède 1802, is an important commercial and recreational fish species that inhabits the tropical and temperate Atlantic, Indian, and Pacific Oceans favoring depths of over 100 m and temperatures around 24°C (Nakamura, 1983, 1985). Movement between the Atlantic and Indo-Pacific populations of blue marlin occurs via the Cape of Good Hope (National Marine Fisheries Service, 1994). Fossil remains of the blue marlin are rare, generally poorly preserved, and chronologically and geographically scattered from the middle Miocene of Belgium, to the late Miocene of southern California, USA, and to the early Pliocene of North Carolina, USA (Fierstine, 1998, in press).

The following is a description of a nearly complete rostrum referred to *Makaira* sp., cf. *M. nigricans* from the Gatún Formation (late Miocene), Panama (Fig. 1), and a discussion of the Panama (Central American) Seaway and Cape of Good Hope as travel routes between the Atlantic and Indo-Pacific for blue marlin and other large marine vertebrates. This is the first record of an istiophorid billfish from the Gatún Formation and the second record of a fossil marlin from Panama (Fierstine, 1978).

Institutional Abbreviations—**IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **MNHN**, Museum National d'Histoire Naturelle, Paris; **USNM**, United States National Museum of Natural History, Washington, D.C.

Anatomical Abbreviations—**LE**, lateral ethmoid; **M**, Maxillary; **N**, nasal; **NC**, nutrient canal; **PM**, premaxillary; **PN**, prenasal; † denotes extinct taxa.

MATERIALS AND METHODS

The materials and methods used in this study have been described fully in Fierstine and Voigt (1996) and Fierstine (1998, in press), but some of it is repeated for convenience. I use the scientific and common names of Robins et al. (1991:66) for Recent species of fishes. Approximately 160 whole and partial skeletons of Recent specimens representing seven species of the family Istiophoridae were examined. The museum number, geological age, and locality are given in Table 3 for each fossil rostrum that was used as comparative material. The rationale for the identification of each comparative specimen is given in Fierstine (1998, in press).

Measurements

Linear measurements were made with dial calipers or metric rule. Characters and their definitions for each bone or structure are as follows and are taken liberally from Fierstine (1998, in press):

Rostrum—Rostral length (L) is from the distal tip of the bill to the orbital margin of the lateral ethmoid. Two regions were emphasized along this length: 0.5L, or one-half rostral length, and 0.25L, or one-fourth rostral length measured from the distal tip. Six morphometric characters were studied in each region: depth (D) and width (W) of the rostrum; height (H) and width (N) of the left nutrient canal (as seen in cross-section); distance (IC) between the right and left nutrient canals (as seen in cross-section); and distance (DD) of the left nutrient canal from the dorsal surface of the rostrum (as seen in cross-section). Characters studied without reference to region were: distribution of denticles on the dorsal surface of the rostrum measured from the distal tip (DZ); length from distal tip where denticles are absent from the ventral mid-line (DVS); length from the distal tip to the distal extremity of the prenasal (P); length from tip where fused premaxillaries divide into separate bones (VSPM); and presence or absence of denticles on the prenasal.

Species Identification—Using the methods of Fierstine (1998), 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, it was scored for each species that contained the ratio. The identification protocol is as follows: The fossil unknown 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 unknown would be identified only to genus or family, respectively. In the third case, the unknown 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.

FIGURE 1. Map of Panama indicating collection site of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 358534), late Miocene, Gatún Formation.

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 deSilva, 1960)

Genus *MAKAIRA* Lacépède, 1802
MAKAIRA sp., cf. *M. nigricans* Lacépède, 1802
 (Fig. 2)

Specimen—Nearly complete rostrum (USNM 358534).

Locality and Age—There is some confusion as to the exact location in the Gatún Formation, Panama, where the specimen was found. F. C. Whitmore, Jr. writes (letter dated January 18, 1985) that the specimen “came from 2 km southwest of Coco Solo Hospital, just north of the back road to Fort Gulick.” R. H. Stewart, the collector of the specimen, writes (letter dated February 22, 1985) that his original guess at the locality was in error and that the true location was 6.8 km NNE by E of the Coco Solo outcrop or 9°21'N + 675 m, 79°48'W +1,600 m (Fig. 1). He also states that this location is about 15.0 m higher in the section than another locality about 1 km south near the police station at Sabanita. Presumably the Sabanita locality is the one reported by Gillette (1984) who believed his collection site to be in Woodring’s basal or oldest subdivision of the Gatún Formation. The Gatún Formation was originally thought to be middle Miocene (Woodring, 1957–1982:575; Stewart and Stewart, 1980; Gillette, 1984:173), but is now considered late Miocene (based on the presence of the nannofossil *Discogaster quinquerramus* [zone NN11] that Berggren et al. [1985] had assigned a time interval of 5.6–8.2 Ma), and that Whittaker and Hodgkinson (in Woodring, 1957–1982:575) had correlated the lower part of the Gatún Formation as midzone N16 (early late Miocene or younger) based on planktonic forams (Coates et al., 1992:825). More recently Berggren et al. (1995:162, 196) assigned zone NN11 to a time interval of 5.6–8.6 Ma and zone N16 to an interval of 8.3–10.9 Ma. Duque-Caro (1990:220)

FIGURE 2. Nearly complete rostrum of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 358534), late Miocene, Gatún Formation, Panama. A, left lateral view; B, dorsal view; C, cross-section approximately at 0.25L (one-fourth bill length); D, cross-section approximately at 0.5L (one-half bill length). Denticles are denoted by stipples; missing bone filled with plaster is denoted by cross-hatch. Scale bar equals 1 cm (A, B); 2 cm (C, D).

TABLE 1. Selected measurements of the rostrum of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 358534), Gatún Formation, late Miocene, Panama. See text for definition of abbreviations. Forty-five mm are considered missing from the distal tip and have been added to measurements indicated by asterisk (*).

Characters	Measurements (mm)
L	794.0*
D1	30.2
W1	40.4
H1	6.0
N1	3.5
DD1	15.0
IC1	2.0
D2	23.6
W2	31.8
H2	3.6
N2	2.5
DD2	11.7
IC2	2.9
DZ	72.0*
DVS	359.0*
P	230.0*
VSPM	483.0*

correlated the Gatún Formation with the late Miocene to early Pliocene Munguido Formation of northwest Colombia while Vokes (1992:41) considered the Gatún Formation to be early Pliocene based on gastropods. I find the evidence presented by Coates et al. (1992) more compelling and consider the Gatún Formation as late Miocene.

DESCRIPTION

The rostrum is nearly complete and consists of the prenasal and premaxillary bones and a partial left nasal (Fig. 2). The overall length is 749 mm from the posterior edge of the left nasal to the incomplete distal tip and 716 mm from the proximal border of the right prenasal to the incomplete distal tip (Table 1). Approximately 45 mm are missing from the distal tip of the rostrum; therefore the overall length of the specimen is estimated to be 794 mm. At the proximal end, the width is 114.9 mm and depth is 38.1 mm.

The rostrum is compared to other specimens on the assumption that 45 mm are absent from the distal tip and that the incomplete posterior edge of the left nasal is in the same transverse plane as the lateral ethmoid in more complete specimens (Fig. 3). Therefore, rostrum length (L) of the Gatún specimen

is 794 mm and equals the overall length of the specimen. Table 1 lists all the variables studied and their measurements.

The specimen was collected in several pieces. In most cases, each piece was a well-preserved, complete segment that was studied in cross-section prior to restoration. The two cross-sections shown in Figure 2 approximate 0.5L (Fig. 2C) and 0.25L (Fig. 2D). Denticles cover the entire ventral surface of the rostrum from the broken tip to the expanded proximal extensions of the premaxillaries.

COMPARISON WITH ISTIOPHORIDS OF THE GENUS *MAKAIRA*

Most morphometric ratios of the Gatún rostrum fall within the range of values of two Recent species of the genus *Makaira* (Table 2), 15 of 18 ratios fall within the range of values of *M. indica* (Cuvier), and 16 of 18 ratios fall within the range of *M. nigricans*. Two ratios (DD1/D1, H2/D2) are within the range of *M. nigricans*, but not *M. indica*, and two ratios (DZ/P, DZ/W2) are within the range of *M. indica*, but not *M. nigricans*. One ratio (DD1/D1) falls solely within the range of *M. nigricans*.

Of the 18 morphometric ratios listed in Tables 2 and 3 for the Gatún rostrum, only 12 have been measured in other fossil istiophorids of the genus *Makaira* (Table 3). With the exception of specimens from the Yorktown Formation (early Pliocene, North Carolina), fossil discoveries are represented by a single individual. The Gatún specimen has few ratios within the observed range of values of other istiophorids: four ratios in common with *M. nigricans* from the Yorktown Formation and one each in common with *M. nigricans* from the middle Miocene of Belgium (=†*M. belgicus* Leriche), and *Makaira* sp., cf. *M. nigricans* from the Yorktown Formation.

There is enough taxonomic uncertainty in the above morphological comparisons that I identify the Gatún specimen as *Makaira* sp., cf. *M. nigricans*. Although ratios DZ/P and DZ/W2 are within the range of Recent *M. indica* and not Recent *M. nigricans*, I give less systematic importance to these because fossil *M. nigricans* has DZ/P and DZ/W2 values within the observed range of Recent *M. indica*. (Table 2).

Fierstine and Voigt (1996:156–157, Table 1) included the ratio cross-sectional area of nutrient canal/cross-sectional area of bill at 0.5L, (H1*N1)/(D1*W1), in the identification key that separated Recent *M. nigricans* from Recent *M. indica*. Their data were reanalyzed to include some additional specimens of *M. indica* and were found to contain a mathematical error. The recomputed ratio (H*N1)/(D1*W1), as well as cross-sectional

FIGURE 3. Skull of *Makaira nigricans* Lacépède, left lateral view. Drawing is a composite of two Recent specimens (LACM 25491 and 46023-1). Scale bar equals 10 cm.

TABLE 2. Morphometric ratios of the rostrum of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 358534), Gatún Formation, late Miocene, Panama, compared with the mean ($\bar{x}$), observed range (OR), and number of specimens examined (N) for each of the same variables of seven Recent species of the family Istiophoridae. Abbreviations for ratios are explained in the text.

Ratios	USNM 358534	<i>I. platypterus</i> $\bar{x}$ (OR)N	<i>M. indica</i> $\bar{x}$ (OR)N	<i>M. nigricans</i> $\bar{x}$ (OR)N	<i>T. albidus</i> $\bar{x}$ (OR)N	<i>T. angustirostris</i> $\bar{x}$ (OR)N	<i>T. audax</i> $\bar{x}$ (OR)N	<i>T. pfluegeri</i> $\bar{x}$ (OR)N
D1/W1	0.75	0.68 (0.58–0.78)31	0.72 (0.66–0.78)10	0.70 (0.59–0.80)41	0.62 (0.56–0.66)13	0.64 (0.57–0.70)3	0.68 (0.59–0.80)13	0.62 (0.59–0.64)2
H1/D1	0.20	0.24 (0.15–0.35)28	0.16 (0.13–0.20)9	0.14 (0.07–0.20)36	0.13 (0.09–0.15)7	—	0.14 (0.10–0.17)8	—
DD1/D1	0.50	0.32 (0.21–0.41)28	0.43 (0.38–0.49)9	0.46 (0.33–0.62)36	0.40 (0.35–0.45)7	—	0.11 (0.08–0.14)7	—
IC1/W1	0.05	0.03 (0.01–0.07)26	0.07 (0.04–0.10)7	0.05 (0.01–0.13)29	0.04 (0.02–0.07)7	—	0.07 (0.04–0.08)7	—
(H1*N1)/(D1*W1)	0.02	0.03 (0.01–0.05)28	0.02 (0.01–0.02)9	0.01 (0.00–0.02)35	0.01 (0.01–0.02)7	—	0.01 (0.01–0.02)8	—
D2/W2	0.74	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	0.61 (0.52–0.67)13	0.65 (0.65)2
H2/D2	0.15	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	0.12 (0.09–0.14)8	0.15 (0.15)1
DD2/D2	0.50	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	0.46 (0.41–0.55)8	0.49 (0.48–0.50)2
IC2/W2	0.09	0.14 (0.06–0.21)27	0.13 (0.11–0.16)7	0.12 (0.04–0.25)32	0.16 (0.13–0.20)7	0.43 (0.40–0.45)2	0.18 (0.13–0.25)8	0.24 (0.24)1
(H2*N2)/(D2*W2)	0.01	0.02 (0.01–0.04)27	0.01 (0.00–0.01)9	0.01 (0.00–0.02)32	0.01 (0.00–0.01)7	0.00 (0.00–0.01)2	0.01 (0.00–0.01)8	0.01 (0.01)1
D2/VSPM	0.05	0.03 (0.03–0.04)25	0.06 (0.05–0.08)8	0.04 (0.04–0.05)35	0.04 (0.03–0.05)12	0.15 (0.13–0.19)3	0.04 (0.03–0.05)12	0.05 (0.05–0.06)2
W2/VSPM	0.07	0.05 (0.04–0.06)24	0.09 (0.07–0.10)8	0.07 (0.05–0.08)35	0.07 (0.06–0.09)12	0.24 (0.20–0.30)3	0.06 (0.05–0.08)12	0.08 (0.07–0.09)2
DVS/VSPM	0.74	0.72 (0.48–0.97)23	0.72 (0.48–0.94)8	0.86 (0.54–1.0)34	0.80 (0.66–0.95)9	0.31 (0–0.52)3	0.76 (0.64–0.94)10	0.02 (0–0.04)2
P/VSPM	0.48	0.58 (0.45–0.83)17	0.53 (0.48–0.60)8	0.51 (0.38–0.87)33	0.53 (0.42–0.66)11	0.39 (0.30–0.45)3	0.48 (0.38–0.57)12	0.55 (0.55–0.56)2
P/D2	9.8	18.8 (13.0–23.2)18	9.0 (7.3–10.5)10	11.9 (8.9–20.2)41	14.2 (10.9–21.3)12	2.7 (2.3–3.3)3	12.9 (10.8–16.1)11	10.6 (9.8–11.3)2
P/W2	7.2	11.6 (8.7–14.0)17	6.1 (5.1–7.3)10	7.6 (5.9–12.3)41	7.6 (5.7–10.3)12	1.6 (1.3–2.1)3	7.8 (6.7–9.5)11	6.9 (6.4–7.4)2
DZ/P	0.31	1.4 (0.76–2.5)18	0.30 (0.10–0.50)9	0.04 (0–0.11)37	2.4 (1.5–3.3)9	0 (0)3	0.93 (0.30–2.0)9	0 (0)2
DZ/W2	2.3	19.5 (9.9–29.1)30	1.8 (0.71–3.0)9	0.30 (0.00–0.85)37	18.6 (14.6–21.7)10	0 (0)3	5.8 (2.5–9.5)8	0 (0)2
		(Yes/No)N	(Yes/No)N	(Yes/No)N	(Yes/No)N	(Yes/No)N	(Yes/No)N	(Yes/No)N
Denticles on prenasal	No	(8/23)31	(0/10)10	(1/36)37	(9/1)10	(0/3)3	(2/8)10	(0/2)2

TABLE 3. Morphometric ratios for the rostrum of *Makaira* sp., cf. *M. nigricans* Lacépède (USNM 358534), Gatún Formation, late Miocene, Panama, compared with the same variables of eight fossil istiophorid assemblages of the genus *Makaira*. The mean ($\bar{x}$), observed range (OR), and number of bones examined (N) are given for specimens from Lee Creek Mine. Abbreviations of ratios are same as in Table 2.

Ratios	USNM 358534	† <i>Makaira cour-</i> <i>celli</i> (Arambourg, 1927) Holotype MNHN 250 Algeria E. Pliocene	<i>M. nigricans</i> [=† <i>M. belgicus</i> (Leriche, 1926)] Holotype IRSNB P1117 Belgium M. Miocene	<i>M. nigricans</i> Yorktown Fm. Lee Creek Mine North Carolina, USA E. Pliocene $\bar{x}$ (OR)N	<i>M. nigricans</i> LACM 17693 Monterey Fm. California, USA L. Miocene	<i>Makaira</i> sp., cf. <i>M.</i> <i>nigricans</i> Yorktown Fm. Lee Creek Mine North Carolina, USA E. Pliocene $\bar{x}$ (OR)N	<i>Makaira</i> sp., cf. <i>M. nigricans</i> USNM 375733 Eastover Fm. Virginia, USA L. Miocene	† <i>M. panamensis</i> Fierstine, 1978 Holotype USNM 181710 Chagres S.S. Panama L. Miocene/ E. Pliocene	† <i>M. teretirostris</i> (Van Beneden, 1871) Holotype Belgium ?M. Miocene
D1/W1	0.75	0.67	—	0.79 (0.77–0.80)3	—	0.86 (0.86)1	—	—	0.87
H1/D1	0.20	—	—	0.15 (0.09–0.19)14	—	0.14 (0.11–0.19)3	—	—	0.10
DD1/D1	0.50	—	—	0.52 (0.41–0.59)14	—	0.59 (0.47–0.80)3	—	—	0.58
IC1/W1 (H1*N1)/ (D1*W1)	0.05 0.02	— —	— —	— —	— —	— —	— —	— —	— —
D2/W2	0.74	0.66	0.80	0.76 (0.66–0.83)36	0.76	0.90 (0.86–1.0)4	0.70	0.76	0.84
H2/D2	0.15	—	0.15	0.15 (0.06–0.22)16	0.17	0.09 (0.06–0.12)2	0.18	0.27	0.11
DD2/D2	0.50	—	0.34	0.52 (0.40–0.62)16	0.56	0.57 (0.57)1	0.47	—	0.56
IC2/W2 (H2*N2)/ (D2*W2)	0.09 0.01	— —	— —	— —	— —	— —	0.10 0.02	— —	0.15 —
D2/VSPM	0.05	—	—	—	—	—	—	—	—
W2/VSPM	0.07	—	—	—	—	—	—	—	—
DVS/VSPM	0.74	—	—	—	—	—	—	—	—
P/VSPM	0.48	—	—	—	—	—	—	—	—
P/D2	9.8	10.0	—	4.4 (2.9–6.3)11	—	2.8 (2.7–2.9)3	8.2	—	—
P/W2	7.2	6.6	—	3.4 (2.3–5.1)11	—	2.5 (2.3–2.7)3	5.8	—	—
DZ/P	0.31	—	—	0.49 (0.38–0.59)3	—	0.81 (0.81)1	—	—	—
DZ/W2	2.3	—	—	1.2 (0.43–1.9)7	—	2.0 (2.0)1	—	—	—

area of nutrient canal/ cross-sectional area of bill at $0.25L$, $(H2 \cdot N2)/(D2 \cdot W2)$, are included in Table 2. Except for the sailfish, *Istiophorus platypterus* (Shaw and Nodder), all istiophorids, including the Gatún marlin, have nearly identical range of values. Unfortunately, ratios with cross-sectional data are not useful in distinguishing *M. nigricans* from *M. indica*.

Morphological variation of the rostrum through time is not known for the black marlin and is only poorly known for blue marlin. Fierstine (in press) noted that rostra of *M. nigricans* from the Yorktown Formation (early Pliocene), in comparison with rostra of Recent blue marlin, have rounder cross-sections throughout their length ($D1/W1$, $D2/W2$), have smaller nutrient canals distally ($H2/D2$) that are more ventrally placed ($DD1/D1$, $DD2/D2$), and a distal dorsal surface that is covered with more denticles (DZ/P , $DZ/W2$). Except for the increase in denticles, the ratios of the Gatún marlin are within the observed range of ratios for Recent blue marlin (Table 2).

GENERAL DISCUSSION AND CONCLUSIONS

Discovery of *Makaira* sp., cf. *M. nigricans* in the Gatún Formation is evidence that blue marlin (or at least their closest known relative) inhabited the Caribbean (north) side of the Panama Seaway and probably used it for travel between the Atlantic Ocean and Pacific Ocean during the late Miocene. Assuming that fossil blue marlin had similar ecological preferences as Recent blue marlin (Fierstine, 1998:41), the environment in the region of the seaway probably was not suitable habitat for blue marlin throughout the year. Duque-Caro (1990:223) concluded that water depths and temperatures in the seaway area ranged from greater than 150 m and cool in the late middle to early late Miocene (11.8–7.0 Ma), to less than 150 m and cold in the late Miocene (7.0–6.3 Ma), to less than 50 m and warm in the latest Miocene to early Pliocene (6.3–3.7 Ma). Complete emergence of the Isthmus of Panama occurred about 3.5 Ma (Coates et al., 1992:827). Recent blue marlin prefer water depths greater than 100 m and sea surface temperatures 22–31°C (Nakamura, 1983, 1985). If the habitat requirements of the Gatún specimen were the same as the Recent blue marlin, then, cool and cold water in the middle and late Miocene (Duque-Caro did not give specific temperatures) would have prevented *Makaira* sp., cf. *M. nigricans* from using the seaway except during summer and fall when water temperatures were warmer, or during years of anomalously high sea surface temperatures. This supposition is based on observations that Recent blue marlin makes seasonal north–south migrations following warm ocean currents in both the western North Atlantic and central North Pacific (Nakamura, 1983, 1985). Although there is insufficient data on north–south migration of Recent blue marlin in the eastern North Pacific Ocean, it is generally more abundant off western Mexico during the summer and early fall (Eldridge and Wares, 1974:90). Occasionally blue marlin is observed off southern California, but only during periods of anomalously high sea surface temperatures (National Marine Fisheries Service [The Southwest Fisheries Science Center's 1996 Billfish Newsletter], unpublished).

Makaira nigricans has been identified in the upper part of the Monterey Formation, late Miocene, southern California (Fierstine and Applegate, 1968; Fierstine, 1998). The upper Monterey Formation is a possible chronostratigraphic and ecological correlative of the Gatún Formation (Duque-Caro, 1990:217; Coates et al., 1992), and conditions (temperature and stratification) in the photic zone (upper 100 m) of the Monterey Formation were probably similar to conditions off southern California today (Schoell et al., 1994:1124). *Makaira nigricans* has been identified in two other late Miocene deposits in southern California (Capistrano Formation [Fierstine, personal observ.]; San Mateo Formation [Fierstine and Welton, 1988]). These

three discoveries are further evidence that the blue marlin was at least a seasonal visitor in the eastern North Pacific Ocean during the late Miocene and a potential candidate to use the Panama Seaway.

There are two examples of other istiophorids possibly using the seaway for east–west movement. The black marlin, *M. indica*, has been identified in the Yorktown Formation (early Pliocene) at Lee Creek Mine, North Carolina (Fierstine, in press). Because the black marlin is not found in the North Atlantic Ocean today, Fierstine postulated that *M. indica* entered the Atlantic from the Pacific via the Panama Seaway during or prior to the early Pliocene. Although there are many similarities in the ecological requirements of *M. indica* and *M. nigricans*, *M. indica* usually inhabits surface waters close to land masses, whereas *M. nigricans* is not usually seen near landmasses or islands, unless there is a deep drop-off (Nakamura, 1985). Because shallowing (Duque-Caro, 1990:223; Coates et al., 1992:814, 827) and island formation (Whitmore and Stewart, 1965:181; Marshall et al., 1982:1351; Duque-Caro, 1990:223) preceded formation of the Isthmus, *M. indica* may have used the seaway up to the time of closure, whereas *Makaira* sp., cf. *M. nigricans* avoided using the seaway during the latest Miocene and early Pliocene when depths were too shallow (<100 m). In addition there is the presence of †*M. panamensis* Fierstine in the Chagres S.S., late Miocene/early Pliocene, Panama (Fierstine, 1978). Although †*M. panamensis* is unknown outside Panama and its ecological requirements are unknown as well, it not only inhabited the seaway, but probably used it for travel between the Atlantic and Indo-Pacific. Because the Chagres S.S. overlies the Gatún Formation, we can assume the seaway was inhabited by istiophorids throughout “Gatúnian” deposition and for some time later.

The Panama Seaway was probably a passage between the Caribbean Sea and eastern Pacific Ocean for other large vertebrates during the mid-Neogene (Fierstine, in press). Gillette (1984) noted that an ichthyofauna (mainly selachians) from the Gatún Formation (Sabanita, Panama), was similar to the Miocene selachian faunas of Antilles, Ecuador, and Pungo River Formation of North Carolina. He included all four faunas in the Tertiary Caribbean Faunal Province of Woodring (1966, 1978), and postulated that the Panama Seaway was part of a continuous environment from the eastern Pacific off Ecuador to the Atlantic off the southeastern United States. Although the shark fauna Gillette studied has a much wider distribution than just the region of the Tertiary Caribbean Faunal Province (Purdy et al., in press; D. Long, pers. comm.), the selachians probably used the seaway for travel. The sirenian, †*Metaxytherium crataegense* (Simpson) (=†*M. calvertense* Kellogg), is known from both the middle Miocene Calvert Formation (Maryland) and the middle Miocene Monteria Formation of Peru (deMuizon and Domning, 1985:204–205; Aranda-Manteca et al., 1994:199). It would be difficult to explain the disjunct distribution of †*M. crataegense* without assuming the Panama Seaway was a travel route for the species (Domning and Furusawa, 1995:509).

In a study of mtDNA of several istiophorid fishes, Graves and McDowell (1995) hypothesized that blue marlin underwent the following sequence of events from some unspecified time in the past to the present: (1) a period of genetic interchange between the Atlantic and Indo-Pacific populations of *M. nigricans*; (2) a period of genetic (and physical) isolation; and (3) a second period of genetic interchange. They presumed that all east–west movement between the two populations occurred via the Cape of Good Hope. If both the Cape and Panama Seaway were travel routes during the early late Miocene, then gene flow between the two populations must have been at its maximum. Subsequently, when the seaway became too shallow for blue marlin and then closed (latest Miocene to present, circa 6.0

Ma), gene flow between the two populations decreased and physical interchange was limited to the Cape of Good Hope. However, the Cape may not always have been suitable habitat for blue marlin throughout the Neogene and Quaternary. Graves and McDowell (1995:202) suggested that the period of genetic isolation occurred during a time of tropical compression when water around the Cape was too cold for blue marlin, probably about one million years based on the estimated divergence time of the mtDNA clades of blue marlin (J. Graves, personal commun.). This supposition, although plausible, would be difficult to prove because Penrith and Cram (1974) were unable to explain why the Cape is currently a corridor for some large oceanic fishes, but not for others. They found no physical barrier and suggested that maybe the fishes had an innate behavior pattern that developed as a result of earlier hydrographic conditions. There is no fossil evidence, and without it, there is no way of knowing when the Cape was an east-west corridor or a barrier for istiophorid fishes. Except for one Recent *M. nigricans* that was tagged off Delaware, and recaptured in the Indian Ocean (National Marine Fisheries Service, 1994), there is no direct evidence that other blue marlins actually travel around the Cape of Good Hope today, although most ichthyologists tacitly assume they use this passage.

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