Bulletin of the Southern California Academy of Sciences

Volume 107 | Issue 2 Article 1

2008

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Bull. Southern California Acad. Sci.
107(2), 2008, pp. 45–56

A Fossil Skull of the Extant Blue Marlin (*Makaira nigricans* Lacepède, 1802) from the Late Miocene of Orange County, California

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Abstract.—A nearly complete fossil skull, including the rostrum, of blue marlin, *Makaira nigricans* Lacepède, 1802 (Perciformes: Xiphioidei: Istiophoridae), was collected from the Oso Member (latest Miocene) of the Capistrano Formation, Mission Viejo, Orange County, California. The specimen is compared with extant and fossil istiophorids, and 19 of its 20 morphological variables are within the range of values observed for extant *M. nigricans*, whereas only 13 or less variables are within the observed range of other extant istiophorids. Because extant *M. nigricans* usually inhabits a water column with a height of about 200 m or more and is the most tropical of all xiphioid species, its presence supports the hypotheses that the Oso Member was deposited at upper bathyal depths or greater and that the coastal paleoclimate of southern California was warmer during the late Miocene than at present.

The extant blue marlin, *Makaira nigricans* Lacepède 1802, (Perciformes: Xiphioidei: Istiophoridae) is an important commercial and recreational fish species that inhabits the tropical and temperate Atlantic, Indian, and Pacific oceans, various strata within a water column of about 200 m or more and average sea surface temperatures of approximately 24°C (Nakamura 1985). The blue marlin is rarely observed off the coast of southern California (Eschmeyer et al. 1983).

According to Fierstine (2006), the blue marlin or blue marlin-like xiphioids (*M*. cf. *M. nigricans*) are the most common fossils of the Family Istiophoridae. The earliest records are from the late Miocene where *M. nigricans* was identified in two rock units in southern California, the Monterey and San Mateo formations (Fierstine and Applegate 1968; Fierstine and Welton 1988; Fierstine 1998, 2001), and *M*. cf. *M. nigricans* was identified in three late Miocene rock units, the Eastover Formation, Virginia, U.S.A. (Fierstine 1998), Gatún Formation, Panama (Fierstine 1999), and Pietra leccese, Italy (Carnevale et al. 2002). In addition, blue marlin and blue marlin-like specimens also were described from the Trinidad Formation, Baja California Sur, Mexico, but because the age of the deposit ranges from late Miocene to late Pliocene (Fierstine et al. 2001), the specimens may or may not rank among the earliest known records of *M. nigricans*. The specimens from the two southern California localities were originally identified only to genus (*Makaira* sp.) (Fierstine and Applegate 1968; Fierstine and Welton 1988), but were re-identified by Fierstine (1998, 2001) after more comparative material became available.

In 1980, Hugh Wagner, during a paleomitigation project for the Mission Viejo Company, collected a nearly complete skull of *M. nigricans*, OCPC 31001 (Orange

County Paleontology Collection), from the Oso Member (latest Miocene) of the Capistrano Formation near the current northern city limit of Mission Viejo, Orange County, California (Fig. 1). According to Barnes and Raschke (1991), the Oso Member is correlative with all but the latest Hemphillian North American Land Mammal Age [4.6 to 9.0 Ma (Woodburne and Swisher 1995)]. Although the specimen is the third record of a blue marlin in late Miocene deposits of southern California (Fierstine 2006), it is the only one with a skull and rostrum, and warrants description.

Materials and Methods

Approximately 160 whole and partial skeletons of extant (= Recent or Holocene) specimens, representing seven species of the family Istiophoridae, were examined and used for comparison with the fossil skull. The scientific and common names of Nelson et al. (2004) are used for Recent istiophorids with the exception that I follow Orrell et al. (2006) and place the istiophorids in the suborder Xiphioidei, and Collette et al. (2006) who recognize only one species of blue marlin (*M. nigricans*) instead of two species [*M. nigricans* and *M. mazara* (Jordan and Snyder 1901)]. A combination of the osteological terminology of Arratia (1997), Davie (1990), Gregory and Conrad (1937), Gudger (1940), Rojo (1991), and Schultz (1987) is used.

Anatomical abbreviations are:**a-a**, angular-articular; **bo**, basioccipital; **de**, dentary; **fr**, frontal; **fv**, facet on maxilla for articulation with vomer; **ipr**, internal (anterior) process of the maxilla; **le**, lateral ethmoid; **mpr**, maxillary (posterior) process of the maxilla; **mx**, maxilla(e); **na**, nasal; **nc**, nutrient canal; **pa**, parasphenoid; **pd**, predentary; **pmx**, premaxilla(e); **pn**, prenasal; **pop**, preopercle; **pt**, pterygoid; **qu**, quadrate; **sph**, sphenotic; **tr**, triangular region of maxilla; **vo**, vomer.

Institutional abbreviations are: **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; **MAUL**, Museo dell'Ambiente, Lecce University, Puglia, Italy; **OCPC**, Orange County Paleontology Collection, Santa Ana, California, U.S.A.; **UCMP**, University of California Museum of Paleontology, University of California, Berkeley, California, U.S.A.; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Characters and their definition for each bone or structure were taken liberally from Fierstine (1998, 2001) and are as follows:

Rostrum.—Rostra were measured according to the methods of Fierstine and Voigt (1996). Two regions were emphasized: 0.5 L, or one-half the distance between the distal tip and the orbital margin of the lateral ethmoid, and 0.25 L, or one-fourth the distance between the distal tip and the orbital margin of the lateral ethmoid. Cross-sections were obtained at 0.5 L and 0.25 L using computer tomography (CT) at scan values of 120 kv, 100 mA, and 2.0 sec. Characters studied in each region (.05 L and 0.25 L, respectively) were depth (D_1, D_2) and width (W_1, W_2) of the rostrum, height (H_1, H_2) and width (N_1, N_2) of the left nutrient canal (as seen in cross-section), and distance (DD_1, DD_2) of the left nutrient canal from the dorsal surface of the rostrum (as viewed in cross-section). Characters studied without reference to region were distribution of denticles on the dorsal (DZ) and ventral (DVS) surfaces of the rostrum (both measured from the distal tip), length (P) from the distal tip of the rostrum to the distal extremity of the prenasal bone, presence or absence of denticles on the prenasal bone, and length from the tip along the ventral surface where the fused premaxillae divide (VSPM) into separate bones.

Predentary.—Three morphometric characters were studied: length along the ventral mid-line (PL); width across the widest expanse of the toothed surface (PW); and depth

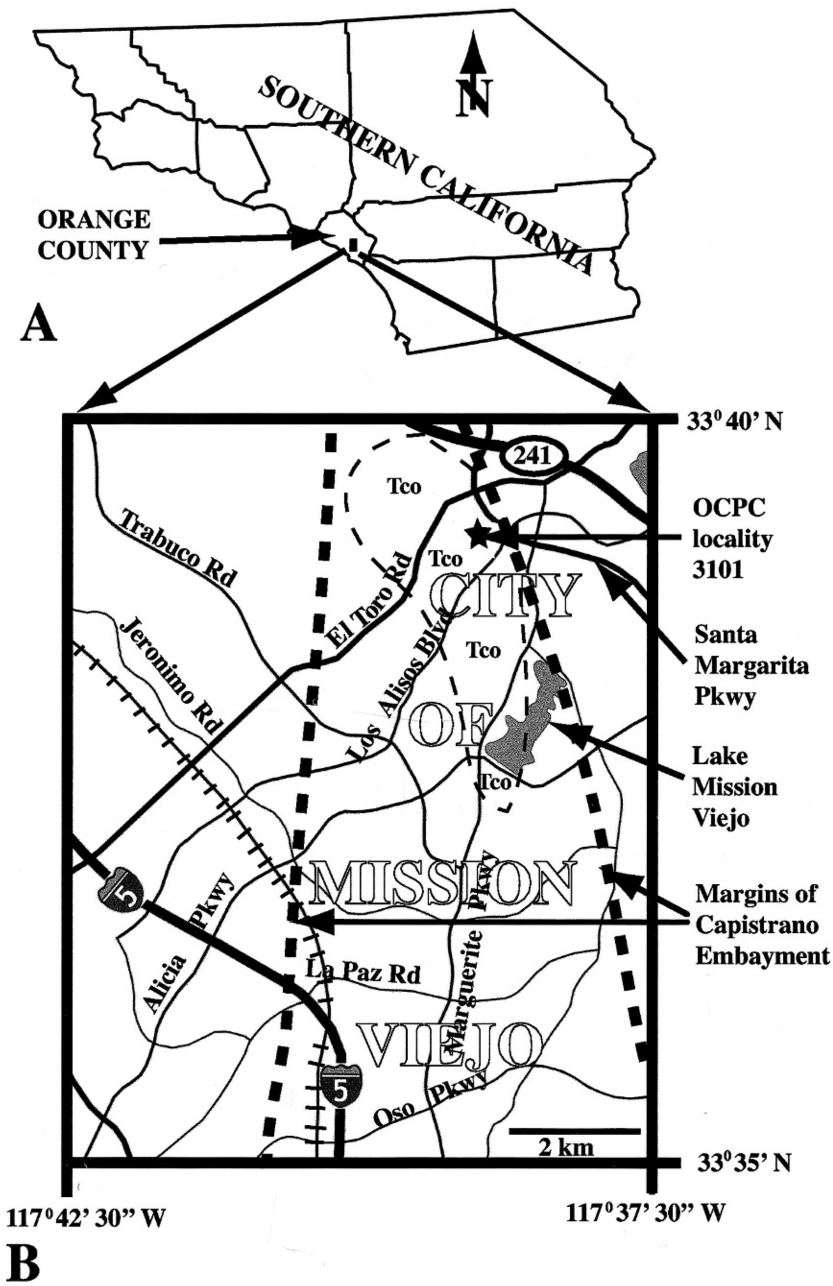

Fig. 1. Map of the collection site (OCPC locality 3101) of the skull of *Makaira nigricans* Lacepède 1802 (OCPC 31001), late Miocene, Oso Member, Capistrano Formation. **A**. Orange County in relation to other counties in southern California; **B**. Road map of area around Mission Viejo, Orange County, California with the collection site indicated by a star. Thick dotted lines represent the approximate margins of the northern extension of the Capistrano Embayment and thinner dotted lines within the Capistrano Embayment represent the generalized outcrop of the Oso Member (Tco). [modified from Ehlig (1979) and Morton et al. (2004)].

perpendicular to the long axis from the widest expanse of the toothed surface to the ventral surface of the bone (PD).

Quadrate.—Five characters were measured: greatest height from the condyle for articulation with angulo-articular to the tip of the dorsal process (QH); height from the condyle to the notch for the symplectic bone (QHS); greatest width (medial to lateral) in the region of the condyle (QAW); width of the condyle (QMW); and length of the condyle (QML).

Maxilla.—Six morphometric characters were studied, five in the triangular region (tr) that articulates with the nasal, premaxillae, 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 width (MVW) of the facet. The sixth character is the length of the posterior limb from the anterior tip of the triangle to the posterior tip of the maxillary process (mpr) at the gape (MOL).

Neurocranium.—Because the neurocranium is badly crushed dorso-ventrally, only the presence or absence of its bony constituents is noted.

Systematic Paleontology

Class Actinopterygii Cope 1887

Division Teleostei Müller 1844

Order Perciformes Bleeker 1859

Suborder Xiphioidei Swainson 1839

Family Istiophoridae sensu Robins and de Sylva 1960

Genus *Makaira* Lacepède 1802

Makaira nigricans Lacepède 1802

Figures 2, 3; Tables 1, 2

Material.—OCPC 31001, partial skull, including the skull roof, rostrum, lower jaws and quadrate.

Locality.—OCPC locality 3101 (= MV19), a reddish brown, pebble conglomerate to coarse sand unit of the Oso Member (latest Miocene) of the Capistrano Formation, in a roadcut facing Los Alisos Boulevard approximately 3.5 km northeast of the junction of Los Alisos Boulevard and Trabuco Road, Mission Viejo, Orange County, California, NW 1/4, NE 1/4, Sec. 18, T. 6 S., R. & W., El Toro, California quadrangle, U.S.G.S., 1968 (photorevised 1982), 1:24,000 scale (Fig. 1).

Remarks.—The specimen mostly consists of the rostrum, lower jaws, and a dorso-ventrally crushed neurocranium (Figs. 2,3). The ventral and lateral skull region (basisphenoid, myodome, most of the otic bones and vomer), all the opercular bones (except for part of the preopercule), most of the lateral ethmoids, and suspensoria are missing. Measurements of the specimen are listed in Table 1.

In dorsal view (Figs. 2A, 3A), the distal one half of the rostrum is well preserved, but the proximal half is incomplete and dorso-ventrally compressed (Fig. 2C). Denticles are restricted to the distal 22 mm of the rostrum. The left prenasal (pn) is complete, except for a middle segment, and the right pn is poorly preserved, except for its most distal extension onto the rostrum. The left nasal (na) is more complete than the right na, and its sutures with the frontal (fr) and pn are well-defined. Both fr are preserved. Most of the bones (supraoccipital, epitotic, pterotic, opisthotic, parietal, etc.) that compose the posterior part of the neurocranium are crushed beyond recognition. The right maxilla

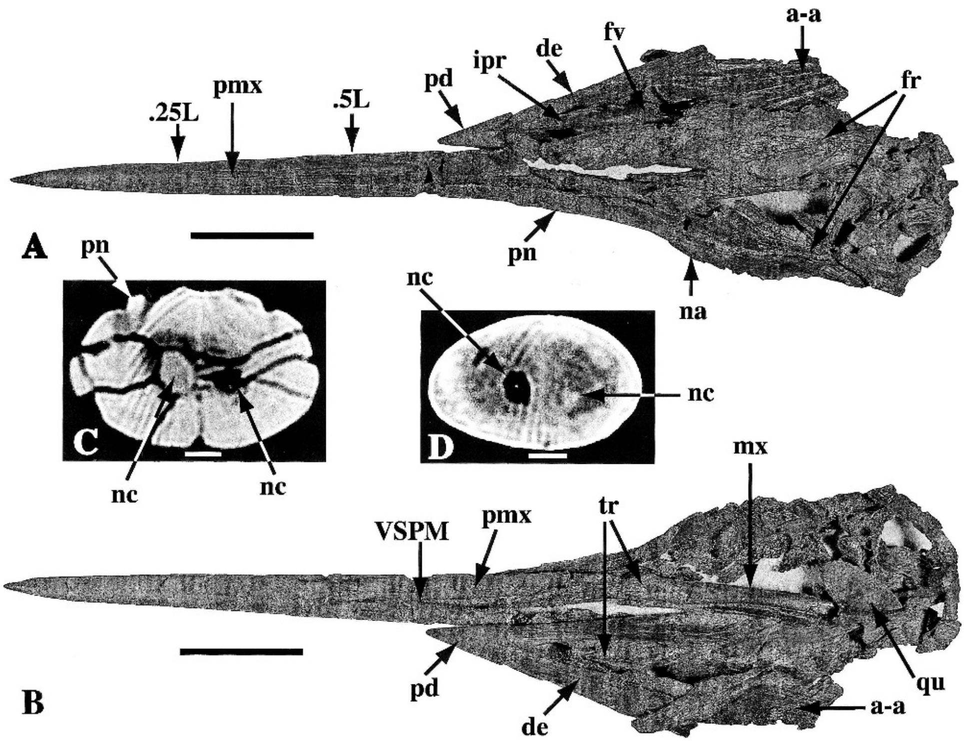

Fig. 2. Skull of *Makaira nigricans* Lacepède 1802 (OCPC 31001), Capistrano Formation, late Miocene, Orange County, California. **A**. Dorsal view; **B**. Ventral view; **C**. Cross section of rostrum at 0.5 L; **D**. Cross section of rostrum at 0.25 L. See text for definition of abbreviations. Scale bar equals 10 cm (A, B) and 5 mm (C, D).

(mx) is better preserved than its counterpart, with the former containing both the articulation for the vomer (fv) and the internal process (ipr). The right dentary (de) is well preserved, except for most of its denticles. The right angulo-articular (a-a) is incomplete posteriorly and is rotated clockwise with respect to the right de.

In ventral view (Figs. 2B, 3B), the distal segment of the rostrum is completely covered with denticles for approximately 261 mm (DZ) and then the denticles divide to form a narrow edentulous zone along the midline that terminates at the division (VSPM) of the right and left maxillae. Most of the right mx, including a large part of the maxillary (posterior) process, is visible. The rugose joint surface on the ventral margins of the left pn and na that articulates with the left mx (triangular region) is well preserved. The interior (ventral) surface of the left fr contains a fragment of the lateral ethmoid (le) and sphenotic (sph). The lateral surface of the left quadrate (qu) is complete; however, the entire element has undergone deformation that gives it a slightly melted appearance. The occipital condyle and ventral surface of the basioccipital (bo) are present. The lower jaw is complete from the distal tip of the predentary (pd) to the posterior part of the de. A small portion of the left a-a and most of the right a-a are visible, and both have been displaced and rotated from their normal anatomical position with respect to their dentaries. A large fragment of the left pterygoid (ecto- and entopterygoid) rests on the right lower jaw. Two flat elements, presumably the ventral surface of the parasphenoid (pa) and a small portion of the vomer (vo), are visible.

In cross section at 0.5 L (Fig. 2C), the rostrum is crushed dorso-ventrally and the exact width and depth of the rostrum were only estimated. The left nutrient canal is abnormally

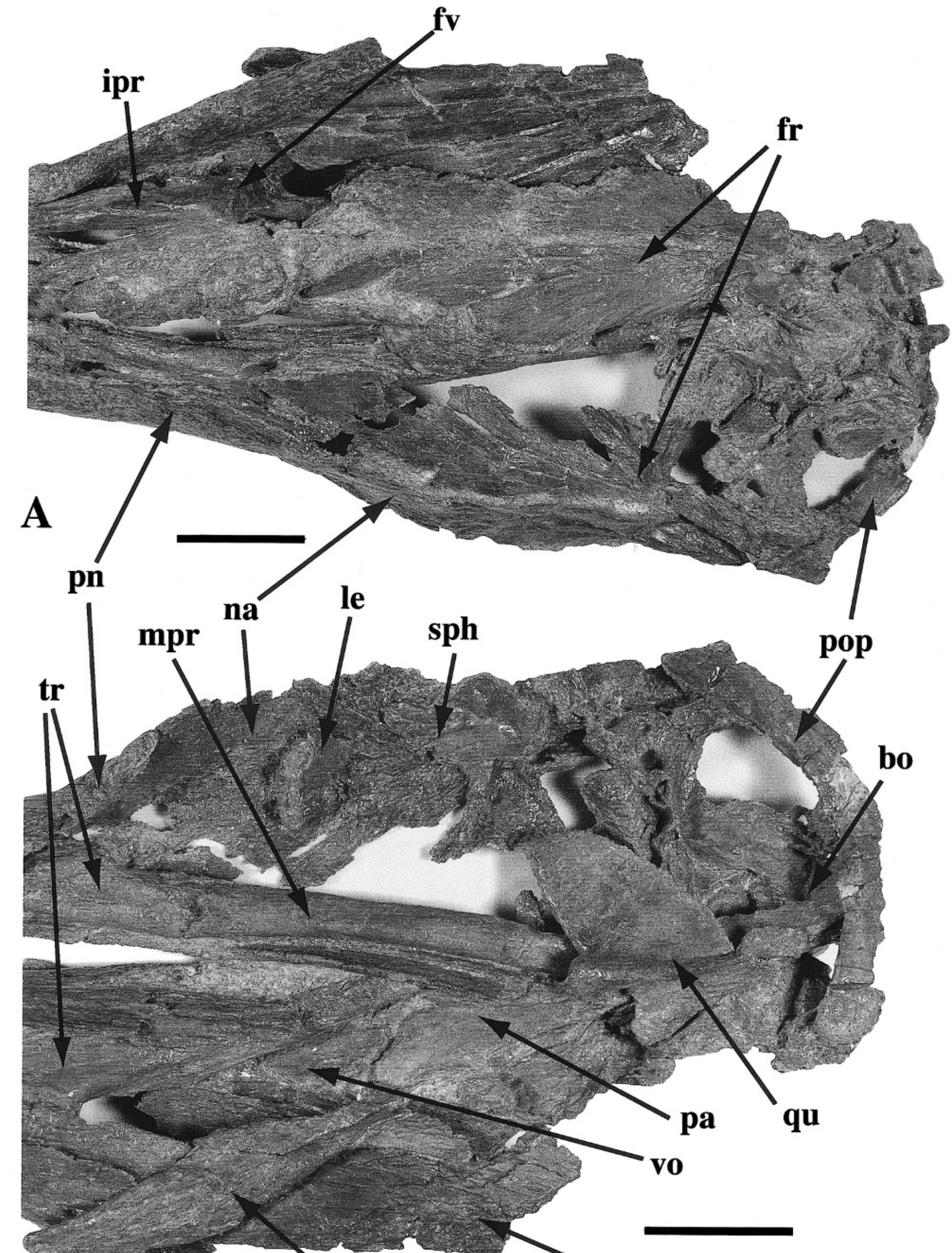

Fig. 3. Posterior skull of *Makaira nigricans* Lacepède 1802 (OCPC 31001), Capistrano Formation, late Miocene, Orange County, California. **A**. Dorsal view; **B**. Ventral view. See text for definition of abbreviations. Scale bar equals 5 cm (A, B).

Table 1. Selected measurements of the skull of *Makaira nigricans* Lacepède 1802, OCPC 31001, Oso Member, Capistrano Formation, late Miocene, Orange County, California. See text for definition of abbreviations. Measurements that were distorted during fossilization are given as estimates (est.), and those characters affected by abnormal development of the nutrient canals are noted as questionable (?). Values indicated by an asterisk (*) were taken from computer tomography (CT) scans and not directly from the specimen.

Bone or region of skull	Measurements (mm)
Overall length of specimen	780.0
Rostrum	
Length (L)	570.0
D_1	23.5
W_1	est. 35.1
H_1	?5.7*
N_1	?4.1*
DD_1	?8.7*
IC_1	?2.6*
D_2	17.3
W_2	26.3
H_2	?4.3*
N_2	?2.8*
DD_2	?6.5*
IC_2	–
DZ	22.0
DVS	261.0
P	231.0
VSPM	324.0
Left maxilla	
MH	est. 24.8
ML	51.5
MOL	est. 200.0
MVH	15.5
MVW	14.5
MW	est. 26.5
Left quadrate	
QH	est. 65.7
QHS	est. 52.2
QAW	est. 17.0
QMW	12.0
QML	14.4
QW	74.4
Predentary	
PD	18.2
PL	61.0
PW	30.2

larger than the right, thus the size of the canals (H_1, N_1) and their position with respect to the dorsal surface (DD_1) and to one another (IC_1) were considered too uncertain for comparison with other istiophorids. In cross section at 0.25 L (Fig. 2D), the rostrum is preserved with no evidence of dorso-ventral compression. However, the left nutrient canal is abnormally larger than the right canal also, thus measurements of the size and position of the canals were not used for comparison with other istiophorids.

Table 2. Variables (ratios) of *Makaira nigricans* Lacepède1802, OCPC 31001, Oso Member, Capistrano Formation, late Miocene, California, compared with the mean ($\bar{x}$), observed range (or), and number of bones examined (n) for the same variables of eight extant species of the family Istiophoridae. Abbreviations for variables are explained in the Materials and Methods section of text. Only variables of normally developed characters (without question marks [?] in Table 1) are listed.

Ratios	OCPC 31001	*I. platypterus* (Shaw and Nodder 1792) $\bar{x}$ (or) n	*M. indica* (Cuvier 1832) $\bar{x}$ (or) n	*M. nigricans* Lacepède 1802 $\bar{x}$ (or) n	*T. albidus* Poey 1860 $\bar{x}$ (or) n	*T. angust-irostris* Tanaka 1915 $\bar{x}$ (or) n	*T. audax* Philippi 1887 $\bar{x}$ (or) n	*T. pfluegeri* Robins & de Sylva 1963 $\bar{x}$ (or) n
				Rostrum				
D1/W1	.67	.68(.58–.78)31	.72(.66–.78)10	.70(.59–.80)41	.62(.56–.66)13	.64(.57–.70)3	.68(.59–.80)13	.62(.59–.64)2
D2/W2	.66	.64(.55–.75)30	.68(.58–.77)10	.64(.54–.83)41	.53(.47–.61)14	.61(.58–.64)3	.61(.52–.67)13	.65(.65)2
D2/VSPM	.05	.03(.03–.04)25	.06(0.5–.08)8	.04(.04–.05)35	.04(.03–.05)12	.15(.13–.19)3	.04(.03–.05)12	.05(.05–.06)2
W2/VSPM	.08	.05(.04–.06)24	.09(.07–.10)8	.07(.05–.08)35	.07(.06–.09)12	.24(.20–.30)3	.06(.05–.08)12	.08(.07–.09)2
DVS/VSPM	.81	.72(.48–.97)23	.72(.48–.94)8	.86(.54–1.0)34	.80(.66–.95)9	.31(0–.52)3	.76(.64–.94)10	.02(0–.04)2
P/VSPM	.71	.58(.45–.83)17	.53(.48–.60)8	.51(.38–.87)33	.53(.42–.66)11	.39(.30–.45)3	.48(.38–.57)12	.55(.55–.56)2
P/D2	13.4	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)12	10.6(9.8–11.3)2
P/W2	8.8	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	.10	1.4(.76–2.5)18	.30(.10–.50)9	.04(0–.11)37	2.4(1.5–3.3)9	0(0)3	.93(.30–2.0)9	0(0)2
DZ/W2	.84	19.5(9.9–29.1)30	1.8(.71–3.0)9	.30(.00–.85)37	18.6(14.6–21.7)10	0(0)3	5.8(2.5–9.5)11	0(0)2
				Maxilla				
ML/MOL	.26	.31(.23–.35)9	—	.20(.17–.23)14	.26(.23–.29)10	—	.26(.25–.27)2	.33(.33–.33)2
MW/MOL	.13	.12(.08–.14)9	—	.13(.13–.13)5	.13(.12–.13)8	—	.12(.12)2	.08(.08–.08)2
MW/ML	.51	.39(.25–.57)14	—	.64(.60–.70)5	.47(.44–.51)8	—	.47(.45–.49)2	.24(.23–.24)2
MH/ML	.48	.33(.26–.47)14	—	.43(.38–.49)14	.38(.34–.45)10	—	.37(.36–.37)2	.33(.31–.34)2
MVW/MVH	.94	1.4(.95–2.4)9	—	1.2(1.1–1.3)3	1.2(.80–1.8)3	—	1.2(.96–1.5)2	—
MVW/ML	.31	.22(.17–.36)9	—	.36(.35–.37)3	.20(.18–.24)3	—	.28(.25–.31)2	—
MVW/MW	.55	.55(.48–.63)9	—	.56(.53–.60)3	.44(.40–.48)3	—	.60(.51–.69)2	—
MVW/MH	.53	.64(.59–.75)9	—	.90(.81–.96)3	.54(.50–.58)3	—	.77(.68–.85)2	—
				Predentary				
PW/PL	.50	.50(.23–.63)21	.54(.48–.62)5	.65(.45–1.1)23	.41(.34–.57)15	.60(.54–.69)4	.42(.33–.51)13	(.65)1
PD/PL	.30	.27(.20–.37)21	.38(.30–.41)5	.36(.26–.58)23	.24(.20–.33)15	.59(.52–.69)4	.26(.22–.30)13	(.60)1
PD/PW	.61	.56(.48–1.0)21	.70(.63–.81)5	.56(.48–.61)23	.59(.53–.65)15	.99(.97–1.0)4	.60(.53–.72)13	(.92)1
				Quadrate				
QAW/QH	.26	.17(.15–.20)11	.29(.28–.31)2	.23(.19–.27)22	.21(.18–.24)17	(.16)1	.21(.20–.22)4	(.17)1
QMW/QAW	.71	.68(.58–.81)11	.85(.83–.88)2	.77(.57–.92)22	.73(.48–.88)18	(.65)1	.71(.67–.77)4	(.62)1
QAW/QHS	.33	.29(.24–.39)11	.44(.44–.45)2	.36(.30–.43)21	.35(.30–.40)18	—	.38(.37–.39)2	(.30)1
QMW/QHS	.23	.19(.17–.23)11	.38(.38–.38)2	.27(.22–.35)21	.25(.19–.30)18	—	.28(.27–.28)2	(.18)1
QMW/QML	.83	.73(.62–.80)11	1.1(1.1–1.1)2	.86(.63–1.0)22	.83(.53–1.0)18	(.56)1	.79(.65–1.0)4	(.71)1

Discussion and Conclusions

Only 20 of the 26 variables (ratios) listed in Table 2 for OCPC 31001 are considered to have an adequate sample size (n ≥ 7) in three or more species of recent istiophorids to warrant interspecies comparison. Nineteen of the 20 variables are within the range of values observed for *M. nigricans*, with other species having 13 or less variables within their observed range. One variable (ML/MOL) is within the observed range of three extant istiophorids, but not *M. nigricans*. However, the measurement of MOL is an estimate, and perhaps the variable would be within the observed range of *M. nigricans* if it could be more accurately determined. This evidence indicates OCPC 31001 is *M. nigricans*.

With exception of its rostrum, specimen OCPC 31001 has few bones in common with other fossils of the genus *Makaira*. For example, two specimens of *M*. cf. *M. nigricans* (MAUL 917/1; USNM 375733) are the only other *Makaira* with a preserved maxilla (Fierstine 1998; Carnevale et al., 2002) and four specimens of *M*. cf. *M. nigricans* (MAUL 917/1; NCSM 6944; USNM 476372, 481903) are the only other ones with preserved quadrates (Fierstine 2001; Carnevale et al. 2002). Of the 26 variables (ratios) listed in Table 2 for the Capistrano Formation blue marlin, only 22 have been measured in other fossil istiophorids, and, with the exception of specimens from the Yorktown Formation and Pietra leccese, measurements were recorded from a single bone or structure that represents a single individual. It is not surprising then that only 14 variables of the Capistrano marlin are close to (± 25%) or within the observed range of other fossil istiophorids.

Paleoenvironment

The depth of deposition of the Oso Member has only been described in general terms. Based primarily on the stratigraphy of Vedder (1972), Barnes and Raschke (1991) interpreted the Oso Member as a nearshore (proximal) facies of the Capistrano Formation that has yielded remains of land mammals. Deméré and Berta (2005), based on the biostratigraphy of White (1956) and Ingle (1979), interpreted the Oso Member as probably being deposited at continental shelf depths (i.e., somewhere between 0 and 200 m). Ehlig (1979) concluded that the Oso Member in the northeastern part of the Capistrano Embayment (Fig. 1) was deposited at upper bathyal depths (i.e., 200 m or greater). Because all three studies differ in their interpretation of the depth of the deposit, perhaps the billfish skull can provide more precise bathymetric evidence for the Oso Member in the northeastern portion of the embayment.

Recent blue marlins are oceanic fishes (i.e. favor inhabiting a water column with a height greater than 200 m) and are rarely encountered in shallow, nearshore waters. They are not seen near landmasses or islands unless they are in the vicinity of a deep drop-off from the continental shelf (Nakamura 1985). If it is assumed that fossil istiophorids had ecological preferences similar to extant istiophorids (Fierstine 1998, 2001, 2006), then the presence of blue marlin remains in the Oso Member suggests that the stratum was deposited in at least 200 m of water. Unlike the carcasses of large marine mammals that often float after death and sometimes end up in more inshore waters (Berta et al. 2006), the carcasses of xiphioid fishes usually sink, based on pop-up satellite archival tags released from dead fish (E. Prince, NOAA, Miami, FL, pers. comm., October 29, 2007). Because the fossil skull (OCPC 31001) is fairly complete and shows no wear or breakage (e.g., the rostrum is articulated with the neurocranium), it is unlikely it was transported by ocean currents or wave action. Therefore, the billfish probably died in the vicinity of the water column where its skull became entombed.

Blue marlins inhabit temperate and tropical waters of the Atlantic and Indo-Pacific Oceans and are considered the most tropical of all istiophorid species (Nakamura 1983). They are generally found in water with an average sea surface temperature of approximately 24°C. As noted above, extant blue marlins are occasionally found off southern California (Eschmeyer et al. 1983), but only during periods of anomalously high sea surface temperatures (The Southwest Fisheries Science Center's 1996 Billfish Newsletter [unpublished]). Thus, the presence of *M. nigricans* in the Capistrano Formation offers further support that the coastal paleoclimate of southern California was warmer during the late Miocene than at present (Fierstine 2006).

Acknowledgments

I want to thank H. Wagner (SDNHM) for his collecting expertise, and allowing me to prepare and study the fossil marlin. J. Cooper (OCPC) and L. Babilonia (Los Coyotes Paleontology Museum) encouraged study of the specimen. J. Cooper (OCPC) and G. Takeuchi (LACM) generously provided pertinent literature and critically read various drafts of the manuscript. T. Deméré (San Diego Natural History Museum) furnished thoughtful criticisms of the submitted manuscript, and E. Prince (NOAA, Miami, FL) provided important literature and shared his extensive knowledge of tagging studies in billfishes.

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Accepted for publication 12 October 2007.