

## A NEW †AGLYPTORHYNCHUS (PERCIFORMES: SCOMBROIDEI: †?BLOCHIIDAE) FROM THE LATE OLIGOCENE OF OREGON

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**ABSTRACT**—A partial fish skull with a nearly complete rostrum, a cup-shaped sclerotic bone, and cycloid scales (UCMP 123170) from the Yaquina Formation (late Oligocene, Oregon) is described and identified as †*Aglyptorhynchus maxillaris*, sp. nov. Unusual features of the rostrum include a fused premaxillary segment with a low dorsal keel, and a maxilla with both a flat flange on its postero-ventral margin and a large condyle that presumably allowed dorso-ventral movement of the rostrum to increase the gape. The Yaquina Formation was estimated to have been deposited at a water depth of over 100 m and a sea surface temperature of at least 20°C, conditions that are similar to the preferred habitats of extant billfish and postulated paleoenvironments of blochiids from the Ashley River Formation, Belgian Basin, London Clay, and Monte Bolca. This is the first record of a blochiid from a deposit bordering the Pacific Ocean. It is hypothesized that †*A. maxillaris* or its ancestor emigrated from the warm Gulf Stream of the Atlantic into the Pacific via the Panama Seaway.

### INTRODUCTION

The Istiophoridae, Xiphiidae, and †Xiphiorhynchidae (Perciformes: Scombroidei) are known collectively as billfishes because of their elongate rostrum or bill (Fierstine, 1990). The fossil fish species discussed below are often considered billfishes, although their relationship to the Scombroidei is poorly understood or questionable.

†*Aglyptorhynchus* (nine species, early Eocene–late Oligocene) and three other supposedly related genera, †*Congorhynchus* (three species, late Cretaceous–late Eocene), †*Cylindracanthus* (nine species, late Cretaceous–late Eocene), and †*Hemirhabdorhynchus* (four species, early Eocene–middle Eocene), are known primarily from fragments of cylindrical, longitudinally striated structures that have been found in marine deposits of Africa, Europe, and the U.S.A. (Schultz, 1987). The incompleteness of the specimens has led to equivocal understanding of their morphology and systematics. After Carter (1927) demonstrated that a specimen of †*Cylindracanthus rectus* (Agassiz) was similar histologically to the rostrum of †*Blochius longirostris* Volta, a species known from complete skeletons from the middle Eocene of Italy, most workers have considered the remains to be fragments of rostra (see references in Schultz, 1987), although others have considered them fish spines (Casier, 1966; Fierstine, 1974).

There is general disagreement on the higher systematics of all five genera including †*Blochius*. Casier (1966) divided them into two distantly related families (†Blochiidae and Xiphiidae) and assigned the blochiids to a non-perciform order and the xiphiids (in which he included †*Aglyptorhynchus*) to the perciform suborder Scombroidei (=Xiphioidei). Schultz (1987) divided them into two closely related families (†Blochiidae and Tetrapturidae) and assigned both to the Scombroidei (=Xiphioidei). He included †*Aglyptorhynchus* in the Tetrapturidae along with †*Hemirhabdorhynchus* and the extant *Tetrapturus*. Patterson (1993a) followed Schultz (1987), except that he assigned the family †Blochiidae to Acanthomorpha incertae sedis and suggested (Patterson, 1993b) that blochiids are probably not even perciforms. Fierstine and Voigt (1996) pointed out that the primary character Schultz (1987) used to define the Tetrapturidae (presence of an edentulous zone on the ventral surface of the rostrum) was too variable in extant istiophorids for defining families.

A partial skull of a new species of †*Aglyptorhynchus* discov-

ered in the Yaquina Formation, late Oligocene, Oregon (Fig. 1), is the most complete blochiid known other than †*Blochius* and the first blochiid discovered in a deposit bordering the Pacific Ocean. Interpretation of the specimen resolves some of the morphological and few of the systematic uncertainties associated with †*Aglyptorhynchus*. Paleocological and paleogeographical implications are discussed.

### MATERIALS AND METHODS

I use the common and scientific names of Robins et al. (1991) for Recent species of fish and the classification system of Carpenter et al. (1995) so that the Suborder Scombroidei includes the extant families Sphyracidae, Gempylidae, Scombridae, Istiophoridae, and Xiphiidae. I follow the time scales of Gradstein et al. (1995) for the Cretaceous and Berggren et al. (1995) for the Tertiary.

### Comparative Materials

†**Blochiidae**—†*Blochius longirostris* Volta, 1796, holotype, MNHN 10868–10869; BMNH 19940; CMNH 4312, 4520; MCSNV 23183, VIII B31, T66; MNHN 10865, 10873; middle Eocene, Monte Bolca, Italy.

†**Blochiidae**—†*Aglyptorhynchus bruxelliensis* (Leriche, 1926), holotype, IRSNB P574, middle Eocene, Belgium. †*A. compressus* (Leriche, 1936, holotype, IRSNB EFP300 and 301, early Eocene, Belgium; IRSNB P587 middle Eocene, Belgium; IRSNB 1400 and 1401, middle Eocene, Belgium. †*A. denticulatus* (Leriche, 1909), holotype, two specimens, IRSNB 882b, early Oligocene, Belgium. †*A. robustus* (Leidy, 1860), holotype, AMNH 3087, late Oligocene, South Carolina. †*A. (=Glyptorhynchus) sulcatus* (Casier, 1946) holotype, IRSNB P315, early Eocene, Belgium. †*A. venablesi* Casier, 1966, holotype, BMNH P26157, early Eocene, England. †*Cylindracanthus octocostatus* Casier, 1946, two specimens, IRSNB P1454, 1455, late Cretaceous, Belgium. †*Hemirhabdorhynchus costatus* (Leriche, 1926), four specimens, IRSNB P575–577, P1398, middle Eocene, Belgium. †*H. depressus* Casier, 1946, two specimens, IRSNB P302, 303, early Eocene, Belgium. †*H. yprensiensis* Casier, 1946, holotype, IRSNB P304, early Eocene, Belgium.

**Istiophoridae**—*Makaira nigricans* Lacépède, 1802, LACM 46023-1, female, 2720 mm LJFL, Indian Ocean. *Tetrapturus albidus* Poey, 1860, LACM 25505, male, 1530 mm LJFL, 19.2

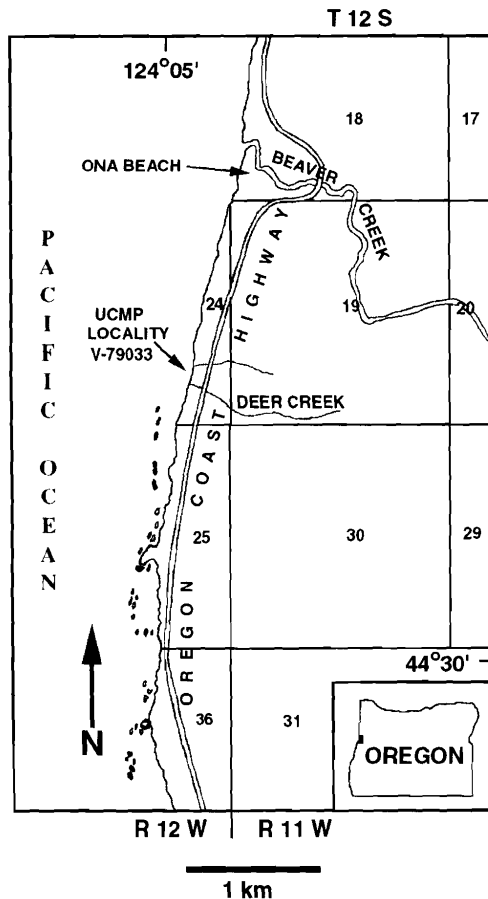


FIGURE 1. Map of coastal Oregon indicating collection site (UCMP locality V-79033) of †*Aglyptorhynchus maxillaris*, sp. nov. (UCMP 123170), holotype, late Oligocene, Yaquina Formation.

Kg, Pensacola, Florida. *T. angustirostris* Tanaka, 1915, LACM 25421, male, 1486 mm LJFL, Kailua-Kona, Hawaii; LACM 25422, sex and size unknown, Kailua-Kona, Hawaii; LACM 25499, female, 1619 mm LJFL, 15.9 kg, Kailua-Kona, Hawaii. *T. pfluegeri* Robins and de Sylva, 1960, LACM 25461, female, 1690 mm LJFL, off Venezuela; LACM 25462, male, 1740 mm LJFL, off Venezuela.

**Preparation**

Standard mechanical techniques (Leiggi and May, 1994) were used to remove the holotype of †*Aglyptorhynchus* from the matrix. Whole and partial scales that were exposed on the surface of the matrix were removed with a flexshaft grinder with a carbide burr. Each scale was kept intact during removal by leaving abundant matrix around the unexposed side of the scale. The surface of the exposed side was cemented to a glass microscope slide with methacrylate gel by putting a generous amount of cement on both slide and scale, and then pressing the two together until firmly attached (about one minute). Gel was chosen over liquid methacrylate cement to fill the cup-shaped surface of the scale in order to make a strong bond between scale and glass slide. The remainder of the matrix was removed from each scale using the flexshaft grinder and needles under magnification.

The rostrum of the new species of †*Aglyptorhynchus* was opaque to computer tomography (CT) scanning. A scan value of 140 kv, 200 mA, and 3.0 s yielded the best results, but the

images remained opaque. Apparently the bone is mineralized with heavy metallic compounds.

**Abbreviations**

**Anatomical**—A, alveoli; C, condyle of maxilla; D, depth of rostrum; EG, edentulous groove; F, point where premaxillae fuse into a single element; FL, flange of maxilla; K, dorsal keel of fused premaxillae; LJFL, length from lower jaw to fork of caudal fin; LR, longitudinal ridge of premaxilla; M, maxilla; NC, nutrient canal; PM, premaxilla; SS, sagittal suture; TL, total length (tip of bill to tip of caudal fin); W, width of rostrum; X.S., cross-section; †, extinct taxon.

**Institutional**—AMNH, American Museum of Natural History, New York, New York; BMNH, The Natural History Museum, London, England; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; MCSNV, Museo Civico di Storia Naturale, Verona, Italy; MNHN, Muséum national d'Histoire naturelle, Paris, France; NJSM, New Jersey State Museum, Trenton, New Jersey; UCMP, University of California Museum of Paleontology, University of California, Berkeley, California; UWBM, University of Washington, Thomas Burke Memorial Washington State Museum, Seattle, Washington; YPM, Peabody Museum, Yale University, New Haven, Connecticut.

**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? †BLOCHIIDAE (Bleeker, 1859)
- †AGLYPTORHYNCHUS Casier, 1966

**Type Species**—†*Cylindracanthus (Glyptorhynchus) denticulatus* Leriche, 1909

**Revised Generic Diagnosis**—Most species of †*Aglyptorhynchus* are only known by anterior rostral fragments, therefore only features of the anterior rostrum are used in this diagnosis. Rostrum composed of paired premaxillae that fuse anteriorly into a single structure that gradually tapers to a point; longitudinal ridges and sulci cover the dorsal and lateral surfaces of the premaxillae; ventral surface of each premaxilla bears a band of villiform denticles (or their alveoli), approximately two-to-ten denticles wide, that join anteriorly onto the fused segment except for a narrow edentulous area between the two bands; as seen in cross-section or in radiographs, the posterior portion of the fused premaxillae contains one-to-two pairs of large diameter longitudinal canals and up to five small diameter canals that gradually taper anteriorly to unite into one pair of canals near the tip.

†AGLYPTORHYNCHUS MAXILLARIS, sp. nov.  
(Figs. 2–4; Tables 1–3)

**Holotype**—UCMP 123170, a partial head skeleton consisting of the following associated elements: a nearly complete rostrum, a sclerotic bone, and numerous scales.

**Type Locality and Age**—UCMP locality V-79033, Yaquina Formation, latest Oligocene, Ona Beach, Lincoln County, Oregon; Sec. 24, T12S, R12W, Yaquina Quadrangle, 15-minute Series, U.S.G.S., 1957 (Fig. 1). Specimen was collected approximately 30 m offshore in a sandstone concretion that was exposed at low tide. The Yaquina Formation in the vicinity of Ona Beach has produced a rich fauna of pinnipeds, desmostylians, and cetaceans, and a land mammal (Emlong, 1966;

Domning et al., 1986; Barnes et al., 1995). Most of the Yaquina Formation is usually assigned to the upper Zemorrian benthic foraminiferal stage (Chattian, late Oligocene) with only the uppermost part referred to the lower Saucian benthic foraminiferal stage (Aquitian, early Miocene) (Armentrout et al., 1983: chart; Domning et al., 1986). However, D. Prothero (pers. comm.) believes there is no Miocene component in the Yaquina Formation and its age is no younger than 28 Ma (late Oligocene). He bases his decision on unpublished paleomagnetic data and that McKeel and Lipps (1972) reported zone P22 planktonic foraminifera in the overlying Nye Formation. Barnes et al. (1995) considered UCMP V-79013, a locality geographically near but stratigraphically below UCMP V-79033, to be near the top of the Yaquina Formation and assigned it to the latest Oligocene. L. G. Barnes (pers. comm.) believes the cetaceans and pinnipeds in the Yaquina Formation are more primitive than those found in any early Miocene deposit. The presence of †*Aglyptorhynchus maxillaris* sp. nov. in the late Oligocene rather than in the early Miocene is consistent with the cetacean and pinniped data.

**Etymology**—Named for its large expanded maxilla.

**Diagnosis**—Rostral characters are the same as in the generic diagnosis except for the following: rostrum is composed of both paired premaxillae and maxillae; the fused premaxillary segment has a horseshoe-shaped cross-section that is round dorsally and flat ventrally, except for a low keel on the dorsal margin of the mid-anterior region; rostrum tapers rapidly from the keel presumably to a point anteriorly; a band of alveoli that presumably held villiform denticles (6–11 denticles wide) extends the entire length of the ventral surface of each premaxilla; the two bands of denticles in the fused segment are separated by a narrow, shallow, edentulous groove; the fused segment has two pairs of longitudinal nutrient canals posteriorly that taper and reduce to one pair anteriorly; maxilla is smooth (without ridges and sulci) and edentulous with a large postero-ventral flange that extends ventro-lateral to the band of teeth on the premaxilla and with a well-developed condyle on its postero-dorsal margin presumably for articulation with the lateral ethmoid or mesethmoid. Large, round-to-oval cycloid scales. Well-developed sclerotic bone.

#### DESCRIPTION AND COMPARISON WITH OTHER BLOCHIIIDS AND EXTANT SCOMBROID FISHES

##### Rostrum

Measurements of †*A. maxillaris* and morphological comparisons with other blochiids are given in Tables 1–3. The rostrum (Figs. 2, 4) is apparently composed of only the premaxillae and maxillae, a condition found in the Xiphiidae. There is no indication that the prenasal bone of istiophorid billfish (Fierstine and Voigt, 1996) is present, however, the bill is poorly preserved in the region where prenasals might be located. Maxillae have not been described in other blochiids, but I believe they were once present. Perhaps the maxillae were slender and fragile similar to maxillae of †*B. longirostris* (H. Fierstine, unpubl. obs.) and lost when the rostrum broke away from the neurocranium before preservation.

The rostrum is nearly complete, except for the following: absence of approximately 32 mm from the distal tip, a short dorsal section of the fused premaxillae, posterior tooth band of the right premaxilla, postero-dorsal region of the left premaxilla, and right maxillary. There is some distortion. The anterior half is preserved in its normal symmetrical state, but the posterior half is rotated so that the right premaxilla is dorsal to the left premaxilla when viewed anteriorly.

The paired premaxillae fuse anteriorly into a single structure 110 mm from the broken distal tip (F). Although most of the dorsal surface of the fused section is round, the anterior dorsal

TABLE 1. Selected counts and measurements of the rostrum and sclerotic of †*Aglyptorhynchus maxillaris*, sp. nov., holotype (UCMP 123170), Yaquina Formation (late Oligocene), Oregon. Measurements in mm. Counts indicated by an asterisk (\*).

Bones or region of skull	Measurements/ counts
Rostrum	
Greatest (actual) length	320.0
Greatest length with tip reconstructed	352.0
Length of fused portion (F) from broken tip	110.0
Length of anterior margin of dorsal keel from broken tip	27.5
Length of dorsal keel	est. 38.9
Length from broken tip to anterior border of maxilla	259.0
Length from broken tip to anterior border of maxillary flange	272.0
Length of maxillary flange	55.0
Height of maxillary flange	71.3
Length from broken tip to posterior edge of condyle for articulation with ethmoid	301.0
Width of rostrum at F	18.8
Height of rostrum at F	15.3
Width of left row of denticles at F	4.4
Number of denticles across left tooth row at F	9*
Width of denticle free space between rows at F	8.5
Cross-section of rostrum at 87.7 mm from broken tip	
Depth (D)	14.4
Width (W)	15.1
Height (length of long axis) of dorsal foramen (Hd)	4.0
Width (length of short axis) of dorsal foramen (Nd)	2.0
Distance of dorsal foramen from dorsum (DDd)	5.0
Distance between dorsal foramina (ICd)	2.5
Height of ventral foramen (Hv)	3.5
Width of ventral foramen (Nv)	2.5
Distance of ventral foramen from dorsum (DDv)	7.0
Distance between ventral foramina (ICv)	3.5
Width of left row of denticles	5.0
Number of denticles across left tooth row	8*
Width of denticle free space between rows	4.5
Sclerotic Bone	
Length of long axis	52.8
Length of short axis	46.4
Thickness	18.0

margin is formed into a low keel (Figs. 2, 4). A keel has not been described in other blochiids nor in the Istiophoridae or Xiphiidae (Fierstine and Voigt, 1996), except for a small abnormal keel on the distal tip of the rostrum of a *Makaira nigricans* from the Yorktown Formation, early Pliocene (Fierstine, in press). The dorsal and lateral surfaces of the premaxillae are covered with longitudinal ridges and sulci (Fig. 2). Ridges and sulci are found on the rostra of all blochiids (Table 2), but not on the rostra of istiophorid and xiphiid billfish (Fierstine and Voigt, 1996).

The ventral surface of each premaxilla bears a row of alveoli that presumably supported villiform teeth. The right and left bands of alveoli of †*A. maxillaris* remain separate throughout the length of the fused segment, with each band separated by a narrow edentulous groove (Fig. 2D). Two separate bands of teeth are found in nearly all specimens of †*Aglyptorhynchus*, and some specimens of †*Congorhynchus*, †*Cylindracanthus* and †*Hemirhabdorhynchus* (Tables 2, 3). Although denticles (alveoli) are absent in the holotype of †*A. sulcatus* (Table 3), Casier (1966:304, pl. 51) described two bands of denticles in †*A. sulcatus* from the London Clay Formation (early Eocene). The tooth bands of †*Congorhynchus* and †*Cylindracanthus* when present, are each a single chain of denticles that are hidden within two grooves, unlike the broad, superficial bands of †*Aglyptorhynchus* and †*Hemirhabdorhynchus*. †*Blochioides longirostris* has teeth, but their arrangement in the rostrum is unknown (Table 3). Most istiophorids have the entire ventral sur-

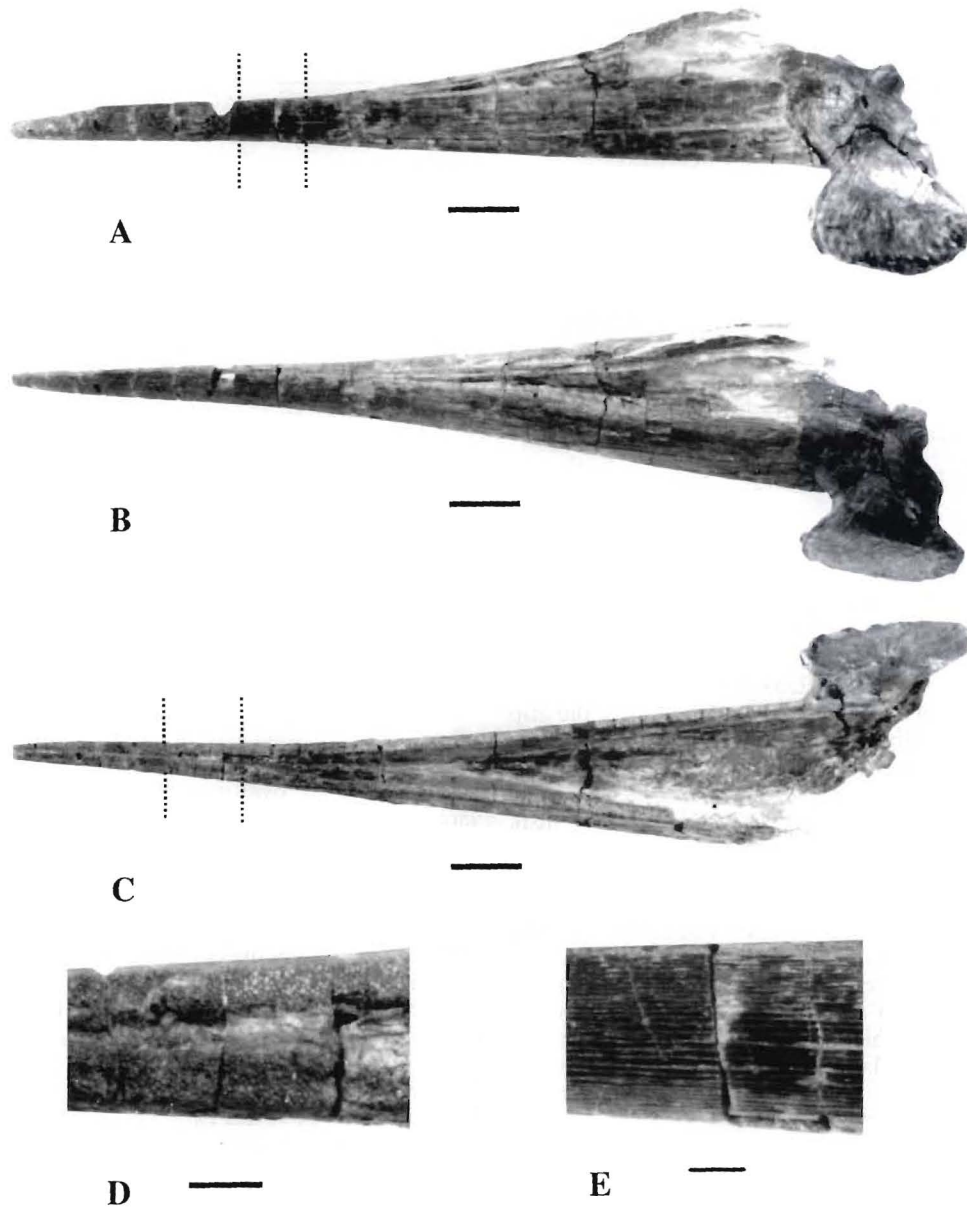


FIGURE 2. Partial rostrum of †*Aglyptorhynchus maxillaris*, sp. nov. (UCMP 123170), holotype, late Oligocene, Yaquina Formation, Oregon. **A**, left lateral view; **B**, dorsal view; **C**, ventral view; **D**, magnified section of fused premaxillae (indicated by dotted lines in C), ventral view; **E** magnified section of fused premaxillae (indicated by dotted lines in A), lateral view. Scale equals 25 mm (**A–C**), 5.0 mm (**D, E**).

face of the rostrum covered with denticles, but the extant spearfishes, *Tetrapturus angustirostris*, *T. belone*, and *T. pfluegeri*, sometimes have a narrow edentulous area along the ventral mid-line of the rostrum. The alveolar bands are widest (~5 mm and approximately 11 denticles across) in the middle of the fused section of the rostrum (Fig. 2D), tapering in width (~2 mm and approximately six denticles across) both anteriorly and posteriorly. The tooth bands are flat in the fused section and rounded posteriorly. The number of denticles/mm in each band is fairly uniform (approximately three denticles/mm) throughout the length of the rostrum.

The following morphology is visible in a cross-section of the fused premaxillae taken 87.7 mm from the broken tip (Figs. 3A, 4B, Table 1). The shape is similar to a horseshoe, i.e., round dorsally, slightly rounded sides, and flat ventrally. The depth (D)/ width (W) ratio is 0.95. Two pairs of oval-shaped longitudinal nutrient canals of approximately the same size, each

with their long axis oriented dorso-medially to ventro-laterally, are located in the middle third of rostral depth (0.33D–0.67D). The sagittal suture is well-developed and there is no central canal. The longitudinal ridges and sulci are not just superficial ornamentation, but each sulcus penetrates into the cross-section a few mm to delineate a petal-shaped ridge (Fig. 4B), a condition seen in †*Cylindracanthus rectus* (Carter, 1927:pl. 1), but not in †*A. venablesi* (Casier, 1966:pl. 61). I assume this infolding acts to strengthen the slender rostrum. The number and shape of the longitudinal canals in the rostrum of other blochiids is highly variable even within the same species. Perhaps some of these differences are due to the position of the cross-section within the rostrum. For example, Fierstine and Voigt (1996) showed that rostra of extant istiophorids have one pair of canals that taper in diameter from large posteriorly to small anteriorly, and that one canal may terminate anteriorly before the other.

TABLE 2. Comparison of rostral morphology, stratigraphic range, and geographic distribution of the five genera that are usually included in the Blochiidae (mostly from Schultz, 1987).

	† <i>Aglyptorhynchus</i>	† <i>Blochius</i>	† <i>Congorhynchus</i>	† <i>Cylindracanthus</i>	† <i>Hemirhabdorhynchus</i>
Rostrum:					
shape of longitudinal ridges	Round	Round	Angular	Round	Round
shape of X.S.	Round dorsally, flat ventrally	Round	Round	Round	Round
denticles (alveoli)	2 rows on flat ventral surface; each row 2–11 alveoli wide	Present, but unable to determine if they are in rows or evenly distributed	Usually none; some species with 2 rows; each row 1 alveolus wide and located in a ventrolateral groove	Usually none; some specimens with 2 rows on ventral surface; each row 1 alveolus wide and located in a groove	2 rows generally; some specimens without alveoli
canals	1–7	72	2–4	numerous large and small	2
Stratigraphic Range	early Eocene-late Oligocene	middle Eocene	late Cretaceous-late Eocene	late Cretaceous-late Eocene	early-middle Eocene
Geographic Distribution	Europe, U.S.A.	Italy	Congo, U.K., ?U.S.A.	Africa, Europe, U.S.A., Mid East	W. Africa, Belgium

An edentulous maxilla (Figs. 2, 4) forms the posterior part of the rostrum. Its lateral surface lacks longitudinal ridges and sulci, but has a fibrous texture. Unlike the maxillary of other teleosts (see figures in Gregory, 1933), it is enlarged postero-ventrally into a large flange that looks superficially like the grip of a pistol. Postero-dorsally there is a well-developed condyle presumably for articulation with the lateral ethmoid or mesethmoid.

There are no published accounts of jaw kinematics in billfish, with the exception that istiophorids and xiphiids are known to impale a variety of objects or use their rostra during feeding (Nakamura, 1983; Frazier et al., 1994). I have manipulated the jaws of several freshly caught *M. nigricans* and found that their rostra were immobile and unable to rotate dorsally with respect to the neurocranium. In contrast, the rostrum of †*A. maxillaris* probably rotated dorsally in order to increase the gape when the mouth was opened. This movement would explain the unique condyle on its maxilla, a feature unknown in other extinct or extant billfishes (Gregory and Conrad, 1937; Schultz, 1987; Fierstine and Voigt, 1996).

The distance from the ethmoid articulation of the maxilla to the reconstructed anterior tip of †*A. maxillaris* (Table 1) is approximately equivalent to bill length of istiophorids as defined by Fierstine and Voigt (1996). Based on this assumption, the rostrum of †*A. maxillaris* is approximately the same length as measured in two extant specimens of *T. pfluegeri* (LACM 25461, 25462) with bill lengths of 391 mm and 357 mm, and LJFL of 1690 mm and 1740 mm, respectively.

### Sclerotic

The sclerotic bone is an oval, cup-shaped structure that apparently enclosed the entire eye (Fig. 3B, Table 1). It is complete, except that most of its medial wall is missing and it is slightly crushed medio-laterally. Because the sclerotic was not found in place within an orbit, I was unable to determine whether it is a right or left element. In addition I could not determine if it is composed of two or more moities. It appears similar in morphology to sclerotics of the Scombridae (Conrad, 1938:6, fig. 3; Collette and Russo, 1984), Istiophoridae (Davie, 1990:3, fig. 1), Xiphiidae (Gregory and Conrad, 1937:17, fig. 3), and †Xiphiorhynchidae (Casier, 1966:pl. 65). I assume that the sclerotic was oriented with its long axis directed antero-posteriorly and its short axis directed dorso-ventrally as in extant istiophorids (Davie, 1990). For comparison, the element is slightly smaller (Table 1) than one from an extant *T. pfluegeri* (LACM 25461) that measures 52.9 mm (long axis), 50.1 mm (short

axis), and with a thickness of 32.1 mm. The differences in thickness between the sclerotics of LACM 25461 and UCMP 123170 are probably because the thin medial wall was not preserved in the fossil specimen.

### Scales

The scales are oval or round, and cycloid (Fig. 3C–F). The largest examined was 17.0 mm × 13.3 mm with the focus located in the center of the scale and the smallest examined was 9.0 mm × 8.8 mm with the focus located 0.5 mm from one edge of the scale's long axis. Scales are known in only one other blochiid, †*B. longirostris*, but its scales are diamond-shaped and slightly overlapping, without any obvious spines or circuli, and there are two longitudinal rows of enlarged scales, one above the ventral margin and one below the dorsal margin of the fish (Woodward, 1901). Smaller diamond-shaped scales fill in above, below, and between the two rows of large scales.

According to Nakamura (1983, 1985) extant istiophorids have cycloid-like scales early in development, but they become elongate, flat, and multi-pointed in the adult. They apparently lack circuli at any stage. Even the so-called roundscale spearfish, *T. georgei*, has multi-pointed scales (Nakamura, 1985). The scales of the extant swordfish, *Xiphias gladius*, are morphologically different from both istiophorids and blochiids. They begin as spinoid scales (round base with numerous projecting spines) in the early larval stage (Roberts, 1993:85) and later become arranged in four longitudinal rows, two of which are located in approximately the same position as the longitudinal scale rows of †*B. longirostris* (Woodward, 1901). With further development the scales are lost and the adult is scaleless (Nakamura, 1985). Roberts (1993:112, appendix 1) notes that cycloid scales are present in the scombroidei, Sphyraenidae, Gempylidae, and Scombridae, and I believe he should have included the Istiophoridae as well.

### SYSTEMATIC DISCUSSION AND CONCLUSIONS

Although †*A. maxillaris*, sp. nov. is the most complete specimen of †*Aglyptorhynchus* known, it lacks much of the morphology (e.g., neurocranium, fins, vertebrae, branchial skeleton, etc.) that Johnson (1986) and Carpenter et al. (1995) used to define the character states for their cladistic analyses of extant Scombroidei and billfishes (Istiophoridae and Xiphiidae). Exceptions are the upper jaw complex which is non-protrusible in all scombroidei, and both the elongate premaxillary bill and villiform teeth which are synapomorphies of billfishes (Johnson,

TABLE 3. Morphological comparisons of rostrum of †*Aglyptorhynchus maxillaris*, sp. nov., holotype (UCMP 123170) with the holotypes of other species of †*Aglyptorhynchus*.

	† <i>A. maxillaris</i> , sp. nov. 123170 UCMP	† <i>A. bruxellienis</i> (Leriche, 1926) P574 IRSNB	† <i>A. casieri</i> Nolf, 1970 uncat. IRSNB	† <i>A. compressus</i> (Leriche, 1936) P300/301 IRSNB	† <i>A. denticulatus</i> (Leriche, 1909) 882b IRSNB	† <i>A. parvulus</i> (Marsh, 1870) 529 YPM	† <i>A. robustus</i> (Leidy, 1860) 3087 AMNH	† <i>A. sulcatus</i> (Casier, 1946) P315 IRSNB	† <i>A. venablesi</i> Casier, 1966 P.26157 BMNH
Premaxillae (Fused Region)									
Shape of X.S.	Horseshoe-shape, flat ventrally; dorsal keel mid-anteriorly; D/W $\approx$ 1 ex- cept for region of keel where D/W > 1	Round to slightly oval; D/W $\approx$ 1	D/W < 1	D/W > 1; Flat sides	D/W $\approx$ 1	?D/W > 1	Horseshoe- shaped, flat ventrally; D/W < 1 posterior- ly; D/W > 1 anteriorly	D/W > 1; Deep groove along mid-dorsal margin	D/W $\approx$ 1; Slight groove mid- dorsally
Denticles (alveoli)	2 rows, each ~6- 11 alveoli wide; shallow, groove between rows	2 rows, each ~10 alveoli wide; shallow groove between rows	2 rows, each 4 al- veoli wide; shallow groove between rows	2 rows, each 2-4 alveoli wide; ridge or space (no groove) be- tween rows	2 rows, each ~2- 10 alveoli wide; shallow groove between rows	2 rows, each ??? alveoli wide; ? between rows	2 rows, each 10- 18 alveoli wide; groove (proximally) or narrow space (distally) be- tween rows	None	2 rows, each ~6 alveoli wide; shallow groove between rows
Canals	No central; two pairs of equal sized canals proximally, one pair distally	Central may be divided in two; small pair dor- sal and small pair ventral to central canal	No central; large pair dorsal and small pair ven- tral to central canal	Central; one pair of small canals	No central; one pair of small canals	?	No central; 9 un- equal-sized ca- nals not ar- ranged into pairs	Central partially divided in two: two small pairs of canals dorsal and one small pair ventral to central canal	Proximally: paired central, one pair of smaller canals below and three canals above central; Distally: single canal
Unusual feature(s)	Keel on distal dorsum of ros- trum; maxillary with a tuberosi- ty and flange	Two rows of fo- ramina on dor- so-lateral sur- face			Only one pair of canals		Wide rows of al- veoli	No alveoli; deep mid-dorsal groove	
Formation or Lo- cality/Age	Yaquina Fm, OR/ late Oligocene	Belgian Basin/ middle Eocene	Belgian Basin/ early Eocene	Belgian Basin/ middle Eocene	Belgian Basin/ early Oligocene	Manasquan Fm, NJ/early Eo- cene	Ashley River Fm, SC/late Oligo- cene	Belgian Basin/ early Eocene	London Clay Fm, England/early Eocene

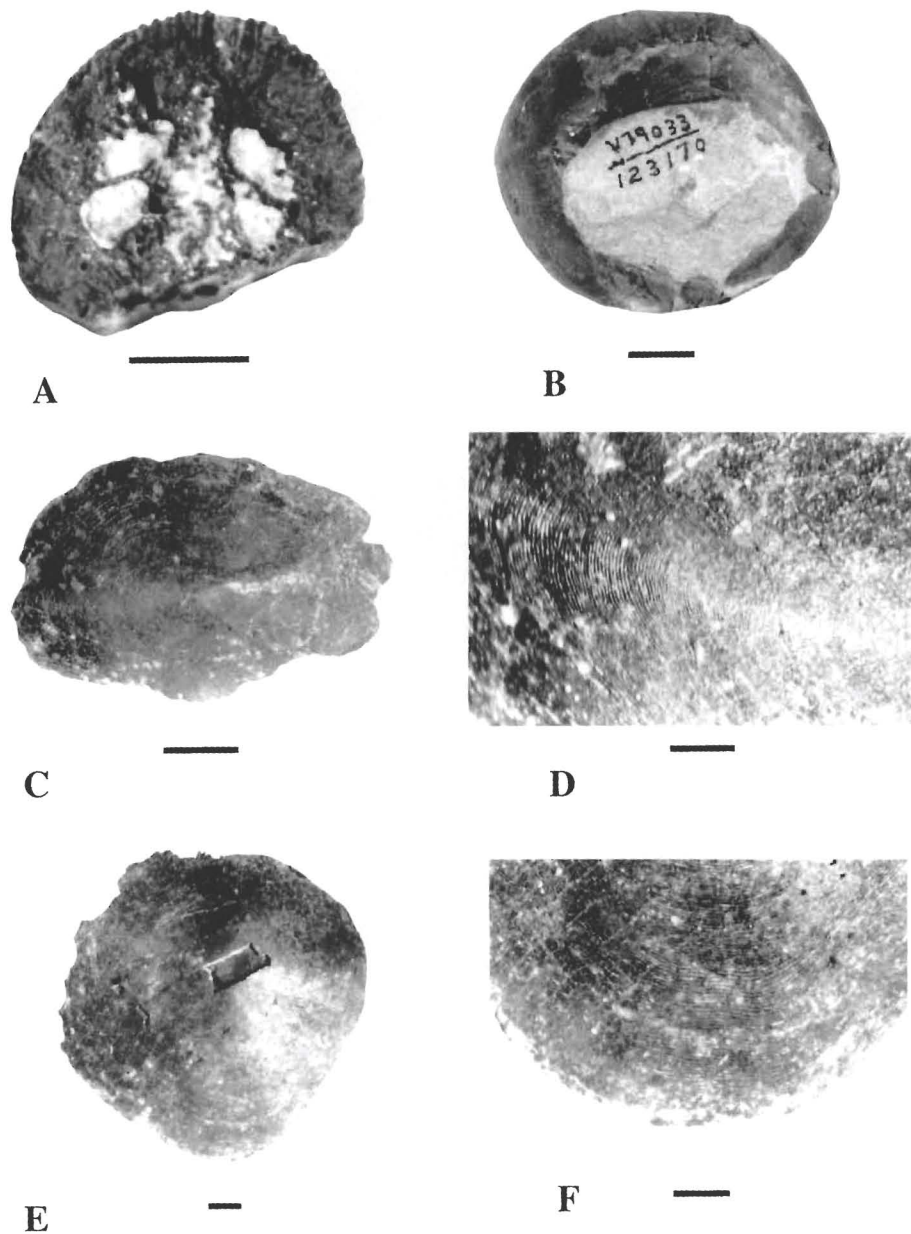


FIGURE 3. Rostral cross-section, sclerotic, and bony scales of †*Aglyptorhynchus maxillaris*, sp. nov. (UCMP 123170), holotype, late Oligocene, Yaquina Formation, Oregon. **A**, rostral cross-section at 87.7 mm from broken tip; **B**, sclerotic, lateral view; **C**, ovoid bony scale, low magnification; **D**, left field of **C**, but higher magnification; **E**, round bony scale, low magnification, rectangular hole in center of scale is an artifact made during preparation; **F**, lower left field of **E**, but higher magnification. Scale equals 5.0 mm (**A**); 10 mm (**B**); 2.0 mm (**C**, **E**); 0.5 mm (**D**, **F**).

1986). Although a cup-shaped sclerotic bone and cycloid scales are found in many scombroids, they are plesiomorphic features and not useful in defining the Scombroidei. The enlarged maxilla is unique to †*A. maxillaris*, sp. nov. Based on the limited information presented above, I conclude that †*A. maxillaris*, sp. nov. is a scombroid.

Determining the family affinity of †*A. maxillaris*, sp. nov. is more difficult. There are few choices. Either place it in an extant scombroid family, in the †Blochiidae, erect a new family, or conclude that the family affinity is unknown. Because †*A. maxillaris*, sp. nov. shares two character states with extant billfishes, it probably is a billfish, but the presence of an enlarged maxilla, a rostrum with numerous longitudinal nutrient foramina and external ridges and sulci, and large cycloid scales are features that are not found in adults of either of the extant

billfish families. Erecting a new family based on one partial specimen is scientifically imprudent and concluding that the family is unknown is not fully accurate. I am currently studying †*B. longirostris* and find that there are many morphological differences (and similarities) between †*A. maxillaris*, sp. nov. and †*Blochius*. Until I undertake a cladistic analysis and learn the systematic value of these characters, I assign †*A. maxillaris*, sp. nov. to the †Blochiidae, but show my uncertainty with a question mark (†?Blochiidae).

#### PALEOECOLOGICAL IMPLICATIONS

There is little information available on the paleoenvironment of the Yaquina Formation. Since the holotype of †*A. maxillaris* (UCMP 123170) was encased in a matrix of sandy silt, I assume

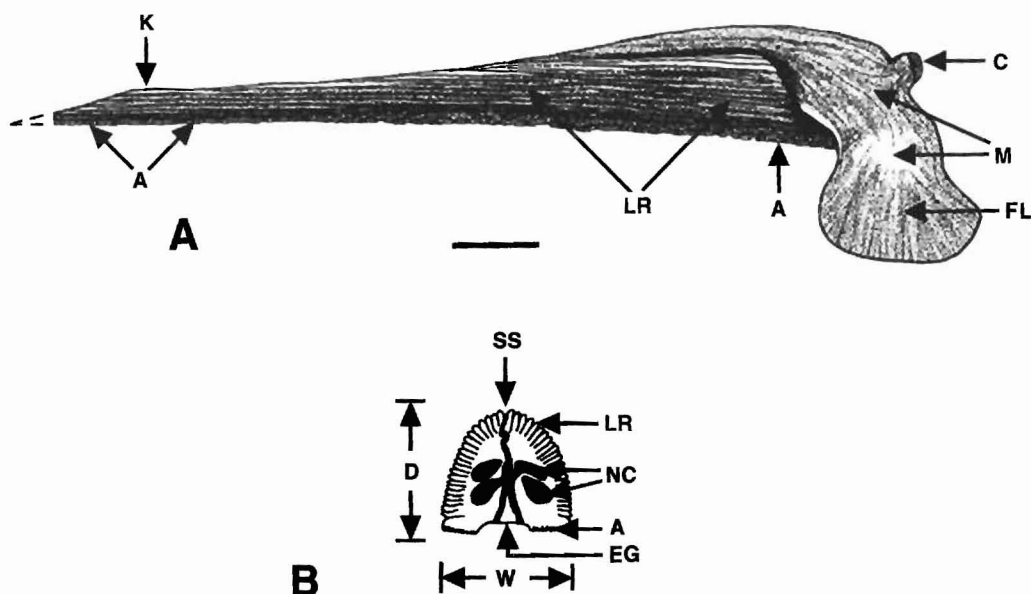


FIGURE 4. Labeled interpretative drawing of partial rostrum of †*Aglyptorhynchus maxillaris*, sp. nov. (UCMP 123170), holotype, late Oligocene, Yaquina Formation, Oregon. **A**, left lateral view; **B**, cross-section at 87.7 mm from broken tip. Scale equals 30 mm (**A**); 10 mm (**B**).

that it was buried in a low energy environment, but Armentrout et al. (1983) concluded that the Yaquina Formation is a high energy deltaic deposit. Information on the depth and temperature of the water is equivocal. Moore (1984) suggested that the presence of the gastropod *Liracassis apta* in the Yaquina Formation may indicate a sea surface temperature (SST) as high as 22–24°C and a water depth between 50 and 400 m. Domning et al. (1986) argued that the desmostylians in the Yaquina Formation probably inhabited bays and inlets to feed on nearby intertidal plants and may have hauled out onto nearby land.

Based on the above information, I estimate that the water depth was probably over 100 m and the SST was at least 20°C for part of the year. These environmental parameters are similar to the preferred habitats of extant billfish (Nakamura, 1983, 1985; Fierstine, in press) and postulated habitats of blochiids from the Ashley River Formation (R. Weems, pers. comm.), Belgian Basin (Casier, 1946), London Clay (Casier, 1966; Stinton, 1966; King, 1981), and Monte Bolca (Sorbin, 1983; Bellwood, 1998).

Of the nine recognized species of †*Aglyptorhynchus* (Table 3), six species are found in the Belgian and London Basins, two species inhabited the east coast of the United States, and only one species, †*A. maxillaris*, is found in a deposit bordering the Pacific Ocean. Most likely †*A. maxillaris* or its ancestor emigrated from the Atlantic Ocean into the Pacific Ocean via the Panama Seaway. The warm Gulf Stream was present during the late Oligocene (Aubry, 1992) and flowed into the Pacific through the Panama Seaway (Prothero, 1994:fig. 6.4). Because the cold California current flowed southward along the Washington, Oregon, and California coasts during the Oligocene (Aubry, 1992), †*A. maxillaris* probably was prevented from traveling northward into the eastern North Pacific, except during summer or fall when water temperatures were warmer. This supposition is based on observations of the extant striped marlin, *T. audax*, that makes seasonal north-south migrations in the eastern North Pacific (Nakamura, 1985), sometimes as far north as Oregon (Eschmeyer et al., 1983) during anomalously warm years.

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