A NEW *AGLYPTORHYNCHUS* (PERCIFORMES: SCOMBROIDEI) FROM THE LINCOLN CREEK FORMATION (LATE OLIGOCENE, WASHINGTON, U.S.A.)

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ABSTRACT—A partial rostrum with an attached lower jaw, a posterior neurocranium, and a proximal hyomandibular from the Lincoln Creek Formation (late Oligocene, Washington) are described and identified as *Aglyptorhynchus columbianus* sp. nov. In addition, ten articulated anterior caudal vertebrae presumably from the Lincoln Creek Formation are described and identified as *Aglyptorhynchus* sp. This is a second record of an *Aglyptorhynchus* from a deposit bordering the Pacific Ocean. The specimens are compared with other billfishes (Perciformes: Scombroidei), both extant and extinct. Unusual features include a tripartite celous occipital condyle composed equally of the basioccipital and exoccipitals, a lower jaw that is nearly twice as deep as the corresponding section of the rostrum, a subtemporal fossa, an oval-shaped fossa in the parasphenoid, two sphenotic ridges separated by a fossa, a bifurcated pterotic ridge, and a hyomandibular with a laterally curved posterior margin. With the exception of the deep lower jaw, these features have never been recorded before in extinct or extant scombroid fish. Heretofore, a tripartite occipital condyle was unknown in a non-beryciform percomorph fish. *Aglyptorhynchus* is placed in the Scombroidei, family incertae sedis, because of the paucity of shared characters with other scombroid taxa.

INTRODUCTION

The term billfish refers to those perciform fishes (Suborder Scombroidei) with their premaxillaries elongated into a non-protrusible rostrum or bill. Billfishes include the families Blochiidae (*Blochius* Volta, 1796), Hemingwayidae (*Hemingwaya* Sytchevskaya and Prokofiev, 2002), Istiophoridae (*Istiophorus* Lacépède, 1801; *Makaira* Lacépède, 1802; *Tetrapturus* Rafinesque, 1810), Palaeorhynchidae (*Homorhynchus* Van Beneden, 1873; *Palaeorhynchus* Blainville, 1818; *Pseudotetrapturus* Danil'chenko, 1960), and Xiphiidae (*Xiphias* Linnaeus, 1758; *Xiphiorhynchus* Van Beneden, 1871) (Carpenter et al., 1995; Fierstine and Monsch, 2002; Sytchevskaya and Prokofiev, 2002). Extinct billfishes inhabited the Tethys and Parathethys Seas and the Atlantic and Pacific Oceans from the Paleocene to the Oligocene (Bannikov, 1993; Fierstine and Monsch, 2002; Sytchevskaya and Prokofiev, 2002), whereas the extant billfishes inhabited all temperate and tropical seas from the Miocene to the Recent (Nakamura, 1983; Sorbini, 1988; Fierstine, 2001). There are several genera of putative billfishes (*Aglyptorhynchus* Casier, 1966; *Congorhynchus* Darteville and Casier, 1949; *Cylindracanthus* Leidy, 1856; *Enniskillenius* Casier, 1966; *Hemirhabdorrhynchus* Casier, 1946) that are known primarily by fragments of rostra and a few other elements (Casier, 1966; Schultz, 1987; Monsch, 2000), but there is much disagreement on the relationship of these latter genera to billfishes (Casier, 1966; Weems, 1999; Fierstine and Monsch, 2002). For example, *Aglyptorhynchus* has been placed in the Xiphiidae (Casier, 1966), Tetrapturidae (Schultz, 1987), and most recently in the ?Blochiidae (Fierstine, 2001; Fierstine and Monsch, 2002).

The discovery of four specimens of *Aglyptorhynchus*, a partial rostrum and lower jaw, and a posterior neurocranium with an attached hyomandibular, both from the Lincoln Creek Formation, late Oligocene, Washington, and ten articulated vertebrae presumably from the Lincoln Creek Formation, adds greatly to our morphological knowledge of the genus. This marks a second record of an *Aglyptorhynchus* from a deposit bordering the Pacific Ocean (Fierstine, 2001). The specimens are compared with fossil and Recent specimens (see material listed below) and published accounts of extant and extinct billfishes (see references in Schultz, 1987; Monsch, 2000; Fierstine and Monsch, 2002). A

phylogenetic analysis was not undertaken because Fierstine and Weems (2004) plan to include a cladistic analysis of *Aglyptorhynchus* in their study of the numerous billfish remains from the Ashley and Chandler Bridge Formations, mid-Oligocene, South Carolina, U.S.A.

MATERIALS AND METHODS

I use the classification systems of Carpenter et al. (1995) for extant Scombroidei and Fierstine and Monsch (2002) for extinct Scombroidei, except for the addition of Hemingwayidae, which was recently described by Sytchevskaya and Prokofiev (2002). I follow the time scales of Berggren et al. (1995) for the Tertiary, and supplement the osteological terminology of Rojo (1991) with the nomenclature of Collette and Russo (1984), Davie (1990), and Fierstine (2001) for structures that are characteristic of scombroids, especially billfishes.

Comparative Materials

Institutional abbreviations are explained below. Authors and dates of first publication of Recent taxa are not given or cited for the sake of brevity (except for those genera in the Introduction).

Blochiidae—*Blochius longirostris* Volta, 1796, holotype, MNHN 10868–10869, middle Eocene, Monte Bolca, Italy.

Family incertae sedis—*Aglyptorhynchus bruxellensis* (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. maxillaris* Fierstine, 2001, holotype, UCMP 123170, late Oligocene, Oregon, U.S.A. *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. *Aglyptorhynchus* sp., ChM GPV685, PV4751, PV4752, PV5990, PV6930, PV6942, PV6944, PV6948, PV6951, PV6958, PV6989, PV6990, PV6995, mid-Oligocene, South Carolina.

Carangidae—*Caranx hippos*, LACM 37975-1, skeleton, Gulf of Mexico, off Florida.

Chirocentridae—*Chirocentrus nudus*, LACM 38292-22, skeleton, fish market, Karachi, Pakistan.

Holocentridae—*Holocentrus rufus*, LACM 38030-1, skeleton, western North Atlantic Ocean, off Florida. *Holocentrus suborbitalis*, LACM 37801-5, skeleton, Gulf of California, Mexico.

Istiophoridae—*Istiophorus platypterus*, LACM 37998-1, skeleton, Gulf of Mexico, off Destin, Florida. *Tetrapturus angustirostris*, LACM 25499, skeleton, female, 1619 mm LJFL, 15.9 kg, Kailua-Kona, Hawaii.

Scombridae—*Acanthocybium solandri*, CAS-SU 112754, head skeleton, off Hawaii; LACM 37930-3, skeleton, Gulf of Mexico, off Destin, Florida. *Scomber japonicus*, LACM42074-1, skeleton, Eastern Pacific Ocean, off Santa Monica. *Rastrelliger* sp., LACM 38118-68, skeleton, fish market, Karachi, Pakistan.

Sphyracidae—*Sphyracna argentea*, CAS-SU 112472, disarticulated skeleton, off San Francisco, California. *Sphyracna* sp., LACM 35732-18, skeleton, fish market, Guayamas, Mexico.

Xiphiidae—*Xiphias gladius*, LACM 44458-1, skeleton, 2033 TL, no other data; CAS 25818, partial skeleton, no other data. *Xiphiorhynchus kimblalocki* Fierstine and Applegate, 1974, holotype, LACM 25575.1-25575.6, late Eocene, Mississippi.

Preparation

The holotype (LACM 143980) was studied without preparation in order to avoid the destruction of denticles. Standard mechanical techniques (Leiggi and May, 1994) were used to remove the neurocranium and hyomandibular (UWBM 29536) from the matrix. The articulated vertebrae (UWBM 40763) were removed from the matrix by immersion in dilute formic acid. Computer tomography (CT) images of the rostrum and lower jaw and neurocranium were scanned at a value of 120 kv, 300 mA, and 3.0 s.

Abbreviations

Anatomical—**a**, alveolus(i); **asr**, anterior sphenotic ridge; **Ba**, basisphenoid; **Bo**, basioccipital; **cc**, central canal; **cpm**, curved posterior margin of hyomandibular; **erc**, cranial cavity; **D**, depth of rostrum; **De**, dentary; **dent**, denticle(s); **df**, depth of rostrum at f (see below for definition of f); **dif**, dilatator fossa; **dpoz**, dorsal postzygapophysis; **dprz**, dorsal prezygapophysis; **Eo**, exoccipital; **Ep**, epiotic; **f**, point where premaxillae fuse into single structure; **fo**, fossa(ae); **fm**, foramen magnum; **Fr**, frontal; **hs**, hemal spine; **Ic**, intercalar; **icf**, internal carotid artery foramen; **LJFL** length from lower jaw to fork of caudal fin; **lr**, longitudinal ridge of either premaxilla or dentary; **m**, posterior myodome; **nc**, nutrient canal; **ns**, neural spine; **oc**, occipital condyle; **Pa**, parietal; **Pas**, parasphenoid; **pasf**, parasphenoid fossa; **Pm**, premaxilla; **pof**, posttemporal fossa; **Pr**, prootic; **psr**, posterior sphenotic ridge; **Pt**, pterotic; **ptc**, pterotic condyle; **Pte**, pterosphenoid; **ptf**, pterotic fossa; **ptr**, pterotic ridge; **ri**, rib; **sc**, supraoccipital crest; **So**, supraoccipital; **Sp**, sphenotic; **spc**, sphenotic condyle; **spf**, sphenotic fossa; **subf**, subtemporal fossa; **suf**, supratemporal fossa; **tef**, temporal fossa; **ter**, temporal ridge; **TL**, length from tip of rostrum to tip of caudal fin; **vprz**, ventral prezygapophysis; **W**, width of rostrum; **wf**, width of rostrum at f; **X.S.**, cross-section of rostrum.

Institutional—**AMNH**, American Museum of Natural History, New York, New York; **BMNH**, The Natural History Museum, London, England; **CAS**, California Academy of Sciences, San Francisco, California; **CAS-SU**, Stanford University Collection of the California Academy of Sciences, San Francisco, California; **ChM**, Charleston Museum, Charleston, South Carolina; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **MNH**, Muséum national d'Histoire naturelle, Paris, France; **UCMP**, University of Cali-

fornia Museum of Paleontology, University of California, Berkeley, California; **UWBM**, University of Washington, Burke Museum of Natural History and Culture, Seattle, Washington.

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, and Fierstine and Monsch, 2002

Family incertae sedis

AGLYPTORHYNCHUS Casier, 1966

1909 *Cylindracanthus* (*Glyptorhynchus*): Leriche, p. 381.

1910 *Glyptorhynchus*: Leriche, p. 339.

1917 *Xiphias*?: Eastman, p. 298.

1966 *Aglyptorhynchus*: Casier, p. 393.

1991 *Glyptorhynchus*: Pharissat, p. 71.

2001 *Hemirhabdorrhynchus*: Purdy et al., p. 184.

2001 *Aglyptorhynchus*: Fierstine, p. 25.

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

Emended Generic Diagnosis—The genus *Aglyptorhynchus* differs from other scombroid fishes by having a tripartite occipital condyle, a maxilla with a large, expanded ventral flange, a pterotic ridge that is bifurcated posteriorly, an oval-shaped fossa in the parasphenoid, two sphenotic ridges that are separated by a fossa, and a well-developed subtemporal fossa. The premaxillae fuse anteriorly into an elongated rostrum that contains (as seen in cross-section) one to two pairs of large-diameter lateral nutrient canals, up to five small-diameter canals, and usually an unpaired central canal; all paired canals gradually taper anteriorly to unite into a single pair near the distal tip; the central canal may be absent near the distal tip. The lower jaw is deeper than the corresponding section of the rostrum, especially posteriorly. Longitudinal ridges and sulci cover the dorsal and lateral surfaces of the premaxillae and the dorsal surface of the dentaries. The ventral surface of each premaxilla and the dorsal surface of each dentary bear a band of villiform denticles (or their alveoli) approximately 2–20 denticles wide; the two bands of denticles on the fused segment of the rostrum nearly join together, except for a narrow edentulous area.

AGLYPTORHYNCHUS COLUMBIANUS, sp. nov.

(Figs. 1, 3–5; Tables 1, 2)

Holotype—LACM 143980, a partial rostrum and lower jaw.

Type Locality and Age—The collection site (LACM 4510) of the holotype is on the N shore of the Columbia River, in the northern part of the bay between Grays Point and Knappton, section 9, T9N, R9W, Knappton quadrangle (USGS), 7.5 minute, 1949 (photorevised 1984), Pacific County, Washington (Fig. 2). It is one of several sites along the shore of the Columbia River that has yielded a diverse and well-studied invertebrate fauna (Moore, 1984b; Goedert and Squires, 1993) and numerous vertebrates (Moore, 1984b:2), including the referred specimens described below. Most specimens are found in concretions from the upper part of the Lincoln Creek Formation that have been transported downslope in modern landslides and deposited on the beach terrace (Moore, 1984b). Based on mollusks, as well as other lines of evidence, Squires and Goedert (1994) concluded that the upper part of the Lincoln Creek Formation at Knappton is of late Oligocene age. Moore (1984a, b), however, assigned the Knappton localities to the earliest Miocene and suggested (Moore, 1984b) that deposition took place at depths between 100 and 350 m based on mollusks, and 1000 m or greater based on

FIGURE 1. Partial rostrum and lower jaw of *Aglyptorhynchus columbianus*, sp. nov., holotype (LACM 143980), late Oligocene, Lincoln Creek Formation, Pacific County, Washington. **A**, rostrum and lower jaw, right lateral view. **B**, close-up of tooth row of rostrum and lower jaw, right lateral view. Scale equals 10 mm (A), 1 mm (B). Abbreviations defined in text.

foraminifers. Sea surface temperatures may have reached 22° to 24° C (Moore, 1984a).

Other Localities—UWBM 4284 is located adjacent to LACM 4510 (type locality) at 46° 17.09'N, 123° 48.1'W, Lincoln Creek Formation, late Oligocene, Pacific County, Washington (Fig. 2B).

Referred Material—From locality UWBM 4284: a posterior neurocranium and right proximal hyomandibular (UWBM 29536).

Etymology—The epithet *columbianus* refers to the proximity of the type locality (LACM 4510) to the Columbia River.

Species Diagnosis—Same as for genus, except rostrum round (D/W ≈ 1) from the point of fusion of the premaxillae (f) to distal broken tip; two pairs of large-diameter nutrient canals and a large diameter central canal; bands of alveoli (or denticles) in both rostrum and lower jaw are approximately 18 alveoli (or

denticles) wide; lower jaw approximately twice as deep as the corresponding section of the rostrum. The posterior margin of the hyomandibular is curved laterally (outward).

DESCRIPTION AND COMPARISON WITH OTHER EXTINCT AND EXTANT (MOSTLY SCOMBROID) FISHES

Rostrum and Lower Jaw

The holotype of *A. columbianus*, sp. nov., consists of middle segments of both the rostrum and lower jaw that were preserved in normal position of articulation (Fig. 1). The two elements were not removed from the matrix and each one will be described separately.

FIGURE 2. Map of southwestern Washington and northwestern Oregon indicating collection sites of *Aglyptorhynchus columbianus*, sp. nov., holotype (LACM 143980) and referred specimen (UWBM 29536), late Oligocene, Lincoln Creek Formation, Pacific County, Washington (localities LACM 4510 and UWBM 4284, respectively), and specimen of *Aglyptorhynchus* sp. (UWBM 40763) presumably collected from strata in the Lincoln Creek Formation (locality UWBM A8967). **A**, overall view (modified from Moore, 1984b). **B**, collection sites on the Columbia River, Pacific County, Washington (modified from Knappton Quadrangle, U.S.G.S. 1949). Scale as indicated.

The rostral segment (Figs. 1, 3; Table 1) is 134 mm long and composed of two premaxillary rami that are separated proximally, but fused together 21.5 mm from the distal broken end. The rostral segment is complete except for a large patch of superficial bone that is missing on the right mid-lateral side, several small patches missing on the left lateral side, and the absence of bone along the dorsal mid-line. The rostrum has a proximal width of 45.5 mm and depth of 38.2 mm. The fused portion is nearly round in cross-section with a width and estimated depth both measuring 22.6 mm at the distal end. The ventral surface of each premaxillary ramus has a wide tooth row that continues distally onto the fused segment (Fig. 1). The right and left tooth rows nearly unite into a single row across the mid-line, except for a narrow denticle-free space that measures 1.5 mm at the distal end. Counting transversely at the distal (anterior) end of the specimen, each tooth row contains approximately 18 villiform denticles (or their alveoli). The external surfaces of the premaxillae are covered with approximately 13 longitudinal ridges and sulci for each 10 mm of surface area.

Well-developed denticles (villiform teeth) cover the ventral and part of the dorsal surfaces of the rostra of most istiophorids and the ventral surface of the rostra of *Xiphiorhynchus*. The denticles are arranged in two rows on the ventral surface of the

TABLE 1. Selected counts and measurements of the rostrum and lower jaw of *Aglyptorhynchus columbianus*, sp. nov., holotype (LACM 143980), Lincoln Creek Formation, late Oligocene, Washington. Measurements in mm. Counts indicated by an asterisk (*). See text for definition of abbreviations.

Structures	Measurements/ counts
Rostrum	
Greatest (actual) length	134.0
Greatest depth at proximal (posterior) end	38.2
Greatest width at proximal end	45.5
Depth at distal (anterior) end	est. 22.6
Width at distal end	22.6
Length of fused portion from broken tip	21.5
wf (measured from CT image)	23.4
df (measured from CT image)	23.9
Width of right tooth row at distal end	10.0
Number of denticles or alveoli across right tooth row at distal end	circa 18*
Width of denticle free space between right and left tooth rows at distal end	1.5
Number of longitudinal ridges/10 mm on right side of rostrum	est. 13*
Lower jaw	
Greatest (actual) length of right ramus	126.0
Greatest depth of right ramus	47.8
Greatest width across both rami at distal end	28.6
Depth of right ramus at distal end	43.5
Length of tooth row of right ramus	125.0
Width of right tooth row at distal end	8.1
Number of denticles across right tooth row at distal end	circa 18*
Number of longitudinal ridges/10 mm on right side of lower jaw	est. 13*

rostra of *Aglyptorhynchus* (Fierstine, 2001; Fierstine and Monsch, 2002), but absent in adult *Xiphias*. Fierstine and Monsch (2002) were unable to determine if the denticles of *Blochius* were in grooves, or in single or multiple rows. Longitudinal ridges and sulci are absent on the rostra of all extant billfishes, *Palaeorhynchus* and *Xiphiorhynchus*, but are present on the rostra of *Aglyptorhynchus* and *Blochius*.

As seen in cross-section (Fig. 3), the fused portion of the rostrum contains two types of longitudinal canals, an unpaired central canal (cc) and two pairs of lateral nutrient canals (nc). Only *Xiphiorhynchus* has a canal system similar to that of *Aglyptorhynchus*. Istiophorids and *Xiphias* have only one pair of nutrient canals. A central chamber (homologue of the central canal) is present in *Xiphias*, whereas the central canal is absent in istiophorids. It is not known whether the rostra of *Blochius*, *Hemingwaya*, and *Palaeorhynchus* possess longitudinal canal systems (Fierstine and Monsch, 2002; Sytchevskaya and Prokofiev, 2002). Because the distal portion of the rostrum of *A. columbianus* is missing, it is impossible to determine if the canals unite distally into a single pair of canals as seen in *A. maxillaris* (Table 2). The right dorsal canal is slightly larger than the right ventral canal (Figs. 3A, B) in *A. columbianus*, but this size difference is probably due to individual variation and is not of systematic importance. Fierstine and Voigt (1996) showed that the central chamber of *Xiphias* and the nutrient canals of istiophorids displayed intraspecific variation in placement, presence, and size.

The rostrum of *A. columbianus* differs from the rostra of all other species of *Aglyptorhynchus* by a combination of characters that are listed in the species diagnosis (see also Fierstine, 2001:table 3). Table 2 lists three species of *Aglyptorhynchus* with rostra that are most similar to the Lincoln Creek specimen and that are found in the Oligocene. None of the three species have a central canal, both *A. maxillaris* and *A. robustus* have rostra with horseshoe-shaped cross-sections, and both *A. maxillaris* and *A. denticulatus* have more narrow rows of alveoli (denticles).

FIGURE 3. Rostrum and lower jaw of *Aglyptorhynchus columbianus*, sp. nov., holotype (LACM 143980) and neurocranium of referred specimen (UWBM 29536), late Oligocene, Lincoln Creek Formation, Pacific County, Washington. **A**, rostrum and lower jaw, anterior view. **B**, close-up of anterior tip of rostrum illustrating the canal system. **C**, computer tomography image through cranial cavity and posterior myodome of the neurocranium. Scale equals 10 mm (A), 5 mm (B), 15 mm (C). Abbreviations defined in text.

If the holotype of *A. columbianus* was more complete, I predict the posterior part of the rostrum would have a maxilla morphologically similar to the maxilla of *A. maxillaris* (Fierstine, 2001) and maxillae of five specimens of *Aglyptorhynchus* (ChM GPV685, PV5990, PV6951, PV6989, and PV6995) from the mid-Oligocene of South Carolina (Fierstine and Weems, pers. obs.).

That is, it would be composed of a pair of well-developed maxillae and each maxilla would terminate posteriorly in a flat flange situated at right angles to the main axis of the maxilla. The dorsal margin of each maxilla would contain one or two condyles presumably for articulation with the ethmoid. Bannikov (1993) described and figured a small ventral maxillary flange in *Palaeo-*

TABLE 2. Morphological comparison of the rostrum of *Aglyptorhynchus columbianus*, sp. nov., holotype (LACM 143980), with the holotypes of three other species of *Aglyptorhynchus*, each with a rostrum of similar morphology and/or chronological range (modified from Fierstine, 2001: table 3). Abbreviations defined in text.

	<i>A. columbianus</i> sp. nov. LACM 143980	<i>A. maxillaris</i> (Fierstine, 2001) UCMP 123170	<i>A. denticulatus</i> (Leriche, 1909) IRSNB 882b	<i>A. robustus</i> (Leidy, 1860) AMNH 3087
PREMAXILLAE (FUSED REGION)				
Shape of X.S.	Round; distally	Horseshoe-shape, flat ventrally; dorsal keel mid-anteriorly; D/W $\equiv$ 1 except for region of keel where D/W > 1	D/W $\equiv$ 1	Horseshoe-shaped, flat ventrally; D/W < 1 posteriorly; D/W > 1 anteriorly
Denticles (alveoli)	2 rows, each ~18 alveoli wide; ? groove between rows proximally or narrow space distally	2 rows, each ~6–11 alveoli wide; shallow groove between rows	2 rows, each ~2–10 alveoli wide; shallow groove between rows	2 rows, each 10–18 alveoli wide; groove (proximally) or narrow space (distally) between rows
Canals	Central; two pairs of large diameter nutrient canals both proximally and distally	No central; two pairs of large diameter nutrient canals proximally, one pair distally	No central; one pair of small canals	No central; 9 unequal-sized nutrient canals not arranged into pairs
Unusual feature(s)	Wide rows of alveoli	Keel on dorsum of distal rostrum; maxillary with a tuberosity and flange	Only one pair of canals	Wide rows of alveoli
FORMATION OR LOCALITY/AGE	Lincoln Creek Fm, WA/ late Oligocene	Yaquina Fm, OR/ late Oligocene	Belgian Basin/ early Oligocene	Ashley River Fm, SC/ late Oligocene

rhynchus parini Bannikov, 1993, and Monsch (pers. comm., Oct., 2003) noted a small ventral flange in *Pseudotetrapturus*; however, they are much smaller than the 71 mm flange of *A. maxillaris*. Although there are many fishes representing numerous orders with an expanded posterior end of the maxilla (see figures in Gregory, 1933; Nelson, 1994), to the best of my knowledge, *Palaeorhynchus*, *Pseudotetrapturus*, and *Aglyptorhynchus* are the only known fishes with a downturned expansion.

The lower jaw (Fig. 1A) is a poorly preserved middle segment composed of a 126 mm long right dentary and a 136 mm long left dentary. The right dentary is better preserved than the left with at least half of its superficial bone, most of its tooth row, and possibly all of its distal ventral margin complete. The number of denticles across the right tooth row (circa 18) and the number of longitudinal ridges and sulci for each 10 mm of surface area (est. 13) are identical in number to those of the rostrum (Table 1). The depth of the lower jaw is much greater than (nearly twice) the depth of the rostrum at the same level (Figs. 1A, 3). For example, the depth of the left dentary at its distal end is 43.5 mm, whereas the depth of the distal rostrum is approximately 22.6 mm (Table 1).

There are no published accounts of a lower jaw in *Aglyptorhynchus* with which to compare the Lincoln Creek specimen; however, a deep lower jaw is not unexpected in a fish with a large ventral projecting maxillary flange. In all known percomorphs, the maxilla has a ligamentous attachment with the lower jaw (Lauder, 1982; Motta, 1984) and does not project below it. The lower jaw of *Palaeorhynchus parini* is very deep posteriorly compared to the rostrum and anterior part of the lower jaw (Bannikov, 1993).

Neurocranium

Only the posterior neurocranium from approximately mid-orbit to the occipital condyle is preserved (Figs. 3C, 4, 5). The right side is fairly complete, whereas most of the left side is missing. Its greatest (actual) width, depth, and length is 116 mm, 130 mm, and 90 mm, respectively. I estimate its greatest width was approximately 130 mm and the greatest width across the occipital condyle was 33.4 mm. Superficially, the posterior neurocranium is morphologically similar to one from a similar-sized istiophorid. Because the detailed morphology of the Lincoln

Creek specimen is nearly identical to the morphology, when preserved, of six posterior neurocrania of *Aglyptorhynchus* (ChM PV4751, PV4752, PV6942, PV6944, PV6948, PV6958) from the mid-Oligocene of South Carolina (Fierstine and Weems, pers. obs.), only differences in the Lincoln Creek and South Carolina specimens are noted.

In dorsal view (Figs. 4A, 5A), both the exoccipitals and the supraoccipital contribute to a supraoccipital crest (sc) that extends along the mid-line from the foramen magnum to the broken anterior edge of the skull roof. Because of the poor preservation in this area, I am unable to determine the crest's original height. The supraoccipital is relatively flat laterally, but becomes elevated into a peak near the midline. A supraoccipital crest is present in most scombrids, weakly developed in *Hemingwaya*, and absent in *Blochius*, palaeorhynchids, istiophorids, and *Xiphias* (Monsch, 2000; Fierstine and Monsch, 2002; Sytchevskaya and Prokofiev, 2002). There is no evidence that the supraoccipital becomes thin or contains a foramen to form a pineal window. A shallow supratemporal fossa or groove (suf) is present between the supraoccipital crest and temporal ridge (ter). The temporal ridge extends from the parietal to terminate at the posterolateral process of the epiotic (Fig. 5A). A more lateral and ventral crest, the pterotic ridge (ptr), extends from the frontal to terminate posteriorly at the bifurcated postero-lateral processes of the pterotic. A well-developed temporal fossa (tef) is located between the temporal and pterotic ridges. Temporal and pterotic ridges are present in all extant scombrids and billfishes, but are unstudied in most extinct billfishes primarily because of poor preservation. The bifurcated pterotic ridge differentiates *Aglyptorhynchus* from the condition in extant scombrids and extant billfishes.

In lateral view (Figs. 4B, 5B), the temporal and pterotic ridges and the dilatator (dif) and temporal fossae (tef) are prominent structures. In addition, two ridges (asr, psr) curve posteroventrally from the frontal and sphenotic (and possibly the pterosphenoid). A deep fossa is formed between the two ridges. The posterior ridge (psr) is more pronounced than the anterior ridge (asr) and forms the postero-dorsal margin of the orbit. I was unable to determine if the pterosphenoid contributed to part or all of the anterior ridge. The sphenotic contains a deep circular fossa (spf) for the anterior head of the hyomandibular and the pterotic has a deep, oval-shaped fossa (ptf) for the posterior head

FIGURE 4. Neurocranium and right hyomandibular of *Aglyptorhynchus columbianus*, sp. nov., referred specimen (UWBM 29536), late Oligocene, Lincoln Creek Formation, Pacific County, Washington. **A**, neurocranium, dorsal view. **B**, neurocranium, right lateral view. **C**, neurocranium, ventral view. **D**, neurocranium, posterior view. **E**, right hyomandibular, lateral view. Known sutures of the neurocranium have been emphasized in white. Scale equals 20 mm (A–D), 10 mm (E). Abbreviations defined in text.

of the hyomandibular. A deep dilatator fossa (dif) is present between the posterior sphenotic ridge anteriorly, the two articular fossae for the hyomandibular ventrally, and the pterotic ridge dorsally. The posterior sphenotic ridge, fossae for the two heads of the hyomandibular, and the dilatator fossa are typically found in all extant scombrids and billfish. However, the anterior sphenotic ridge and the fossa between the two sphenotic ridges are absent in extant scombrids, and it is unknown whether extinct billfishes other than *Aglyptorhynchus* possess them.

In ventral view (Figs. 4C, 5C), there are several prominent features: a midline ridge formed by the unpaired basioccipital and parasphenoid, an oval-shaped fossa (fo) in the parasphenoid,

a pair of deep subtemporal fossae (subtf), one on either side of the midline ridge, fossae for the two heads of the hyomandibular, and two more or less round fossae (fo), one anterior and the other ventral to the sphenotic fossa. The oval-shaped fossa that is totally enclosed in the parasphenoid, the subtemporal fossa, and the two round fossae anterior to each sphenotic fossa are not found in extant and unknown in extinct scombrids other than *Aglyptorhynchus*. The only neurocranium of *Aglyptorhynchus* from the mid-Oligocene of South Carolina with a well-preserved parasphenoid (ChM PV6942) has a pair of foramina (Fierstine and Weems, pers. obs.), thus a single, oval-shaped fossa may be an autapomorphy of *A. columbianus*.

FIGURE 5. Labeled interpretation of the neurocranium of *Aglyptorhynchus columbianus*, sp. nov., referred specimen (UWBM 29536), late Oligocene, Lincoln Creek Formation, Pacific County, Washington. Left side of specimen has been reconstructed from the right side. A, left lateral view. B, dorsal view. C, ventral view. D, posterior view. Abbreviations defined in text.

In posterior view (Figs. 4D, 5D), the outline of the neurocranium is an upside-down isosceles triangle with the skull roof as the base and the basioccipital as the apex of the two equal sides. Five bones (paired epiotics, pterotics, intercalars, and exoccipitals, and the unpaired basioccipital) are visible in this view. The epiotic has a well-developed postero-lateral process presumably for articulation with the dorsal ramus of the posttemporal. A well-developed temporal fossa (tef) is present between the epiotic and pterotic. The lateral ridge of the pterotic is bifurcated

at its posterior end. The celous occipital condyle (oc) is tripartite, its ventral one-third composed of the basioccipital and its dorso-lateral two-thirds composed equally of the left and right exoccipitals. The paired exoccipitals join at the mid-line to form both the roof and floor of the foramen magnum (fm). Each exoccipital articulates dorso-laterally with the epiotic and laterally with the intercalar and pterotic. Posteriorly, each exoccipital forms a shallow posttemporal fossa (pof) lateral to the occipital condyle. Each intercalar has a pronounced short pro-

cess presumably for articulation with the ventral ramus of the posttemporal.

A celous occipital condyle that is formed by the basioccipital and the paired exoccipitals is found in the Osteoglossomorpha (Stewart, 1999), possibly the Protacanthopterygii (Chapman, 1941, 1942, 1944; Rosen, 1985), aulopiforms (Goody, 1969), Polymixiomorpha (Patterson, 1964), and beryciforms (Starks, 1904; Patterson, 1964). Rosen and Patterson (1969:448) stated that the tripartite occipital condyle with a central pit is the primitive condition in the paracanthopterygians. Fink (1984:204–205), who quoted in part from Fink and Weitzman (1982), considered salmonids to be neoteleosts based on the exoccipital forming part of the occipital condyle. Until now a tripartite celous occipital condyle has never been described in a non-beryciform percomorph fish.

In anterior view (unfigured), the large opening for the posterior myodome and the Y-shaped basisphenoid are visible features. The posterior myodome (Fig. 3C) is similar morphologically to the myodome of istiophorids and xiphiids. The upper part of the Y of the basisphenoid forms the floor of the cranial cavity and the single limb of the Y forms a strut that articulates with the parasphenoid. This morphology is similar to that observed in extant scombrids (Allis, 1903; Conrad, 1938; Gibbs and Collette, 1967; Collette and Chao, 1975; Collette and Russo, 1984) and istiophorids (Gregory and Conrad, 1937; Davie, 1990). In *Xiphias*, the basisphenoid is small, does not complete the floor of the cranial cavity, and lacks the vertical strut to the parasphenoid (Nakamura, 1983). The morphology of the basisphenoid and posterior myodome is unknown in *Blochius*, *Palaeorhynchus*, and *Xiphiorhynchus*.

Hyomandibular

A proximal fragment of the right hyomandibular (Fig. 5E) was removed from the sphenotic and pterotic fossae during preparation of the neurocranium. Because this is the first record of a hyomandibular for *Aglyptorhynchus*, a detailed description is warranted in spite of its fragmentary condition. The specimen has a maximum width of 59 mm and a depth of 28 mm from the sphenotic condyle to the broken ventral border. The sphenotic (spc) and pterotic (ptc) condyles mirror the shape of their respective fossae in the neurocranium, except that the posterior margin of the sphenotic condyle is missing so that it is oval rather than round. The longest (undamaged) axis of the sphenotic condyle is 19 mm and the surface of the pterotic condyle has a long axis of 32 mm and short axis (measured in the center of the condyle) of 11.5 mm. The sphenotic condyle projects anteriorly on a short neck at a 42° angle to the long axis of the pterotic condyle. There are two shallow notches, one between the two condyles that interdigitates with the posterior rim of the sphenotic fossa, and the other at the posterior margin of the pterotic condyle that interdigitates with the posterior rim of the pterotic fossa. The posterior margin of the hyomandibular curves laterally (outward) and its dorsal corner is round; however, the corner has a broken edge that could have contained a posteriorly projecting spine or sharp angle in the undamaged state. The proximal hyomandibular lacks a lateral keel (crest) for articulation with the preopercle. It would be premature to conclude that the complete hyomandibular lacked a keel, because it could have been an extension of the distal hyomandibular that was not preserved.

In most scombrids, including *Aglyptorhynchus columbianus*, the pterotic condyle is larger (long axis) than the sphenotic condyle (de Sylva, 1955; Collette and Chao, 1975; Collette and Russo, 1984; Fierstine, pers. obs.). Exceptions include *Scomber*, where the condyles have a similar size (Allis, 1903), and *Blochius* (BMNH P4142), where the sphenotic condyle is the larger element (Fierstine, pers. obs.). No scombroid, other than *A. colum-*

bianus, has a lateral curve in the posterior margin of the hyomandibular. All scombrids, other than *Blochius* and possibly *A. columbianus*, have a lateral keel (usually L-shaped) (Allis, 1903; de Sylva, 1955; Collette and Chao, 1975; Collette and Russo, 1984; Fierstine, pers. obs.) and most scombrids, except *Blochius* and possibly *A. columbianus*, have the posterodorsal corner of the hyomandibular attenuated into a spine or sharp angle. The morphology of the hyomandibular of *Hemingwaya*, *Palaeorhynchus*, and *Pseudotetrapturus* is unknown.

AGLYPTORHYNCHUS SP.

(Fig. 6)

Material—From locality UWBM A8967: ten articulated vertebrae (UWBM 40763).

Locality—UWBM A8967 is located at 46° 17.2'N, 123° 47.9'W and the label and catalogue list the specimen in the Astoria Formation, earliest Miocene (Fig. 2B). According to J. Goedert (pers. comm., Feb., 2003), both the longitude/latitude data and the written directions on file at UWBM (0.5 mi E of roadside park near old site of Knappton) place it clearly in the Lincoln Creek Formation as mapped by Wells (1989), late Oligocene, Pacific County, Washington.

Vertebrae

The vertebrae are identified only to genus for three reasons. The exact locality and age of the specimens are controversial, scombroid vertebrae usually lack species specific characters (Fierstine, 2001; Schneider and Fierstine, 2004), and vertebrae of *Aglyptorhynchus* are poorly known (see discussion below).

Specimen UWBM 40763 consists of ten articulated caudal vertebrae (Figs. 6A–C). The first and last vertebrae in the series are only partially preserved, whereas the middle eight vertebrae are more or less complete, except for the distal extensions of their neural and hemal spines. It is difficult to tell if vertebra 2 is the first caudal or last precaudal vertebra because the hemal arch is incomplete (Fig. 6B). In general, all the centra are cube-shaped (i.e., length, width, and height of each centrum have similar measurements) and all vertebrae, except the incomplete tenth, have expanded neural spines. The neural spines (ns) of the anterior vertebrae were probably much broader in a complete specimen. Vertebrae 3–9 (and possibly the tenth) have expanded hemal spines (hs). Each of the eight anteriormost centra has a shallow fossa both dorsal and ventral to a low, mid-lateral keel. The ninth and tenth centra lack a keel and the centra are etched with several small fossae. The dorsal (dprz) and ventral (vprz) prezygapophyses are well-developed, especially on vertebrae 4–9. Dorsal postzygapophyses (dpz) are present on vertebrae 1–9. Because the hemal spine of the tenth vertebra tends to point posterovertrally (Fig. 6C), then there are probably only three to five more caudal vertebrae, including the hypural, in the complete vertebral column. This supposition is based on the fact that in scombrids and extant billfishes, the last 4–5 vertebrae possess hemal and neural spines that have a more oblique angle than the more anterior spines. Thus, if the second vertebra of specimen UWBM 40763 is the first caudal, then I predict that there would be a total of 12 to 15 caudal vertebrae in *A. columbianus*. This range of values is similar to the number of caudal vertebrae in istiophorids (12 or 13), *Xiphias* (10 or 11), and *Blochius* (11–13) (Nakamura, 1983; Fierstine and Monsch, 2002), but much less than the number in *Palaeorhynchus parini* (37) or *P. glarisianus* Blainville 1818 (35–36) (Pharisat, 1991; Bannikov, 1993). Scombrids have a variable number of caudal vertebrae (17–32) (Collette et al., 1984), *Hemingwaya* has approximately 32 caudal vertebrae (Sytychevskaya and Prokofiev, 2002), and the number of vertebrae in *Xiphiorhynchus* is unknown.

In the only well-documented account of vertebrae belonging to *Aglyptorhynchus*, Leriche (1910) described and illustrated

FIGURE 6. Ten articulated caudal vertebrae (UWBM 40763) of *Aglyptorhynchus* sp., presumably collected in the Lincoln Creek Formation, late Oligocene, Pacific County, Washington. **A**, vertebral column, left lateral view. **B**, close-up of vertebrae 2 and 3. **C**, close-up of vertebrae 8 and 9. Scale equals 20 mm (**B**), 10 mm (**C**, **D**). Abbreviations defined in text.

three precaudal (plate 25, figs. 4–6) and eight caudal vertebrae (text figs. 137–144) that were associated with the rostra of *A. denticulatus*. The morphology of vertebra 2 from Knappton is nearly identical to one illustrated by Leriche (1910:fig. 137) and vertebra 9 from Knappton is similar to two others illustrated by Leriche (1910:figs. 138 and 139). Thus, there is no doubt that the vertebrae collected near Knappton belong to *Aglyptorhynchus*.

GENERAL DISCUSSION AND CONCLUSIONS

Because *Aglyptorhynchus* has its premaxillaries elongated into a non-protrusible rostrum, there is little debate that the genus is a billfish within the Suborder Scombroidei. However, within the suborder, *Aglyptorhynchus* has been included in the Xiphiidae (Casier, 1966), Tetrapturidae (Schultz, 1987), and ?Blochiidae (Fierstine, 2001; Fierstine and Monsch, 2002). A close relationship with any one of these families is equivocal. Fierstine and Voigt (1996) concluded that the Tetrapturidae was defined on variable characters and noted that the type genus (*Pseudotetrapturus*) is a synonym of *Tetrapturus* (Nakamura, 1983; Eschmeyer and Bailey, 1990), one of three extant genera included in the Istiophoridae (Nakamura, 1983). Very few synapomorphies are known to link *Aglyptorhynchus* with other scombroids. The rostrum of *Aglyptorhynchus* has a nutrient canal system that is morphologically similar to the rostrum of *Xiphiorhynchus* (Xiphiidae), has longitudinal ridges and sulci similar to *Blochiidae*, and has a maxillary flange and probably a deep lower jaw similar to *Palaeorhynchus* and *Pseudotetrapturus* (Palaeorhynchidae). *Aglyptorhynchus* has several autapomorphies: a tripartite celous occipital condyle, a subtemporal fossa, an oval-

shaped fossa in the parasphenoid, two fossae adjacent to the sphenotic fossa, two sphenotic ridges with a fossa in between, and a bifurcated pterotic ridge. Rather than include *Aglyptorhynchus* in one of the above families (Blochiidae, Palaeorhynchidae, or Xiphiidae) based on very few synapomorphies, or erect a new family based on its abundant autapomorphies and lack of unequivocal synapomorphies, it seems prudent to place *Aglyptorhynchus* in Scombroidei, family incertae sedis, until better preserved specimens of *Aglyptorhynchus* yield additional morphological information to support a detailed phylogenetic analysis.

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