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 colombianus 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 scombrid fish. Aglyptorhynchus is placed in the Scombroidei, family incertae sedis, because of the paucity of shared characters with other scombrid 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 Blochidae (Blochius Volta, 1796), Hemingwayidae (Hemingwaya Sytchevskaia and Prokofiev, 2002), Istiophoridae (Istiophorus Lacépède, 1801; Makaira Lacépède, 1802; Tetrapurus Rafinesque, 1810). Palaeorhynchidae (Homorhynchus Van Beneden, 1873; Palaeorhynchus Blainville, 1818; Pseudotetrapurus Danil’chenko, 1960), and Xiphiidae (Xiphus Linnaeus, 1758; Xiphiorynchus Van Beneden, 1871) (Casier, 1966; Fierstine and Monsch, 2002; Sytchevskaia 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; Sytchevskaia 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; Cynodontacanthus Leidy, 1856; Emiiskilenus Casier, 1966; Hemirhabdorhynchus 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), Tetrapurridae (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 extinct and extant 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 Sytchevskaia 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 scombrids, 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).

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


Carangidae—Caranx hippos, LACM 37975-1, skeleton, Gulf of Mexico, off Florida.
Chirocentridae—Chirocentrus nudus, LACM 38292-22, skeleton, fish market, Karachi, Pakistan.


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


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

Xiphiidae—Xiphius gladius, LACM 44458-1, skeleton, 2033 TL, no other data; CAS 25818, partial skeleton, no other data. Xiphiorhynchus kimbalocki 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, basiphenoid; Bo, basiocipital; cc, central canal; cpm, curved posterior margin of hyomandibular; crc, cranial cavity; D, depth of rostrum; De, dentary; dent, denticle(s); df, depth of rostrum at f (see below for definition of f); dlif, dilatator fossa; dpoz, dorsal postzygapophyseal; dpz, dorsal prezygapophyseal; Eo, exoccipital; Ep, epioic; 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; ne, nutrient canal; ns, neural spine; oc, occipital condyle; Pa, parietal; Pas, parasphenoid; ptf, 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.


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.


1917 Xiphis?: Eastman, p. 298.

1966 Aglyptorhynchus: Casier, p. 393.


2001 Hemirhabdorhynchus: Purdy et al., p. 184.

2001 Aglyptorhynchus: Fierstine, p. 28.

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...
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.
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 su-
cle on the top of the rostrum (Figs. 1A, 3). A central chamber (homologue of the central canal) is present in the rostrum of Aglyptorhynchus but is absent in adult Xiphias. 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 Aglypto-
rhynchus. Istiophorids and Xiphias have only one pair of nutri-
tional 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 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. The right dorsal canal is slightly larger than the right ventral canal. As seen in cross-section (Fig. 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. deniculatus have more narrow rows of alveoli (denticles).

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**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.

<table>
<thead>
<tr>
<th>Structures</th>
<th>Measurements/counts</th>
<th>Rostrum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest (actual) length</td>
<td>134.0</td>
<td></td>
</tr>
<tr>
<td>Greatest depth at proximal (posterior) end</td>
<td>38.2</td>
<td></td>
</tr>
<tr>
<td>Greatest width at proximal end</td>
<td>45.5</td>
<td></td>
</tr>
<tr>
<td>Depth at distal (anterior) end</td>
<td>est. 22.6</td>
<td></td>
</tr>
<tr>
<td>Width at distal end</td>
<td>22.6</td>
<td></td>
</tr>
<tr>
<td>Length of fused portion from broken tip</td>
<td>21.5</td>
<td></td>
</tr>
<tr>
<td>wf (measured from CT image)</td>
<td>23.4</td>
<td></td>
</tr>
<tr>
<td>df (measured from CT image)</td>
<td>23.9</td>
<td></td>
</tr>
<tr>
<td>Width of right tooth row at distal end</td>
<td>10.0</td>
<td></td>
</tr>
<tr>
<td>Number of denticles across right tooth row at distal end</td>
<td>circa 18*</td>
<td></td>
</tr>
<tr>
<td>Width of denticle free space between right and left tooth rows at distal end</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>Number of longitudinal ridges/10 mm on right side of rostrum</td>
<td>est. 13*</td>
<td></td>
</tr>
<tr>
<td>Lower jaw</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest (actual) length of right ramus</td>
<td>126.0</td>
<td></td>
</tr>
<tr>
<td>Greatest depth of right ramus</td>
<td>47.8</td>
<td></td>
</tr>
<tr>
<td>Greatest width across both rami at distal end</td>
<td>28.6</td>
<td></td>
</tr>
<tr>
<td>Depth of right ramus at distal end</td>
<td>43.5</td>
<td></td>
</tr>
<tr>
<td>Length of tooth row of right ramus</td>
<td>125.0</td>
<td></td>
</tr>
<tr>
<td>Width of right tooth row at distal end</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>Number of denticles across right tooth row at distal end</td>
<td>circa 18*</td>
<td></td>
</tr>
<tr>
<td>Number of longitudinal ridges/10 mm on right side of lower jaw</td>
<td>est. 13*</td>
<td></td>
</tr>
</tbody>
</table>
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-
rhynchus parini Bannikov, 1993, and Monsch (pers. comm., Oct., 2003) noted a small ventral flange in Pseudotetraporus; 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, Pa­laeortynchus, Pseudotetraporus, and Aglyptorhynchus are the only known fishes with a down turned 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 an expanded posterior end of the maxilla (see figures in Fierstine, 2001: table 3). Abbreviations defined in text.

### 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, palaerhynchids, 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 postero-lateral 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 dilator (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 posterior head of the hyomandibular and the pterotic has a deep, oval-shaped fossa (pft) for the posterior head
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 scombroids, 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 (subf), 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 scombroids 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*. 

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**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.
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 Ostoglossomorpha (Stewart, 1999), possibly the Protacanthopterygii (Chapman, 1941, 1942, 1944; Rosen, 1985), aulopiforms (Goody, 1969), Poly-

mixiormorpha (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 exoccpital forming part of the occipital condyle. Until now a tripartite celous occipital con-
dyle has never been described in a non-beryciform percomorph fish.

In anterior view (unfigured), the large opening for the poste-
rior myodome and the Y-shaped basisphenoid are visible fea-
tures. The posterior myodome (Fig. 3C) is similar morphologi-
cally 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 ob-
served in extant scombroids (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 ventral strut to the parasphe-
noid (Nakamura, 1983). The morphology of the basisphenoid and
posterior myodome is unknown in Blochius, Palaeorhyn-
chus, and Xiphiorhynchus.

Hyomandibular

A proximal fragment of the right hyomandibular (Fig. 5E) was
removed from the sphenotic and pterotic fossae during prepara-
tion 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
(sp) and pterotic (pte) condyles mirror the shape of their re-
spective 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 con-
dyle 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 sphen-
otic 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 later-
ally (outward) and its dorsal corner is round; however, the corner
has a broken edge that could have contained a posteriorly pro-
jecting spine or sharp angle in the undamaged state. The prox-
imal 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 pre-
served.

In most scombroids, including Aglyptorhynchus colombianus,
the pterotic condyle is larger (long axis) than the sphenotic con-
dyle (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 ele-
ment (Fierstine, pers. obs.). No scombroid, other than A. colum-

bians, has a lateral curve in the posterior margin of the hyo-
mandibular. All scombroids, 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 scombroids, except Blochius
and possibly A. colombianus, have the posterodorsal corner of
the hyomandibular attenuated into a spine or sharp angle. The
morphology of the hyomandibular of Hemingwaya, Palaeorhyn-
chus, and Pseudotetrapturus is unknown.

AGLYPTORHYNCHUS SP.

(Fig. 6)

Material—From locality UWBM A8967: ten articulated vert-
ebrae (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 (Figs. 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.

Vertebræ

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 verteb-
rae (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 mea-
surements) 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 (dpvrz) and ventral (vpvrz) prezy-
gapophyses are well-developed, especially on vertebrae 4–9. Dor-
sal postzygapophyses (dpoz) are present on vertebrae 1–9. Be-
cause the hemal spine of the tenth vertebra tends to point pos-
teroventrally (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
scombroids 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. colombianus. 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) (Pharris, 1991; Banikov, 1993). Scom-
broids have a variable number of caudal vertebrae (17–32) (Col-
lette et al., 1984). Hemingwaya has approximately 32 caudal ver-
tebrae (Sytchevskaya 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
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* (Xiphidiidae), has longitudinal ridges and sulci similar to *Blochius* (Blochidae), and has a maxillary flange and probably a deep lower jaw similar to *Palaeorhynchus* and *Pseudotetrapturus* (Palaeorhynchidae). *Aglyptorhynchus* has several autapomorphies: a tripartite cefous 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 (Blochidae, 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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relationships of the Family Blochidiidae (Perciformes: Scombroidae), middle Eocene, Monte Bolca, Italy. Miscellanea Paleontologica, Studi e Ricerche sui Giacimenti di Bolca, Museo Civico di Storia Naturale di Verona 9:121-163.


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