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

HARRY L. FIERSTINE

Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407 U.S.A., hfierstine@calpoly.edu

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 cephalic occipital condyle composed equally of the basiooccipital 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 cephalic condyle was unknown in a non-scombroid 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-prorotusible rostrum or bill. Billfishes include the families Blochidae (Blochius Volta, 1796), Hemingwayidae (Heningwaya Sytchevskaya and Prokofiev, 2002), Istiophoridae (Istiorhorhynchus Van Beneden, 1873; Palaeorhynchus Blainville, 1818; Pseudotetrapturus Raffnesque, 1810), Palaeorhynchidae (Hororhynchus Van Beneden, 1873; Palaeorhynchus Blainville, 1818; Pseudotetrapturus Raffnesque, 1810), Palaeorhynchidae (Hororhynchus Van Beneden, 1873; Palaeorhynchus Blainville, 1818; Pseudotetrapturus Raffnesque, 1810), Xiphidae (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; Cephalorhynchus Dartveille and Casier, 1949; Cylindracanthus Leidy, 1856; Enniskillenius Casier, 1966; Hemitrabidrhynchus 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 with other scombroid taxa (Casier, 1966; Weems, 1999; Fierstine and Monsch, 2002). For example, Aglyptorhynchus has been placed in the Xiphidae (Casier, 1966), Tetrapturidae (Schultz, 1987), and most recently in the ‘Blochidae’ (Fierstine, 2001; Fierstine and Monsch, 2002).

The discovery of four specimens of Aglyptorhynchus, a partial rostrum and lower jaw, and a posterior neurocranium from the Lincoln Creek Formation, late Oligocene, Washington, and ten articulated anterior caudal 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 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).

Blochidae—Blochius longirostris Volta, 1796, holotype, MNHN 10868-10869, middle Eocene, Mont-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. Tetraparius angustotrichus, LACM 25499, skeleton, female, 1619 mm LFL, 15.9 kg, Kailua-Kona, Hawaii.

Scobniidae—Acantthophycium solandri, CAS-SU 112754, head skeleton, off San Francisco, California. Sphyraena sp., LACM 35732-18, skeleton, fish market, Guaymas, Mexico.

Xiphidae—Xiphias gladius, LACM 44458-1, skeleton, 2033 TL, no other data; CAS 25818, partial skeleton, no other data. Xiphiorhynchus kimbalocki Fierstine and Applegatt, 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 in the parasphenoid, two sphenotic ridges that are separated by an unpaired central canal: all paired canals gradually taper anteriorly, 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 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 a 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 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 Xiphirohynchus, 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 Xiphius 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, Sychkivskaya and Postoliev, 2002). Because 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 Xiphius 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 rows with horseshoe-shaped cross-sections, and both A. maxillaris and A. deniculatus have more narrow rows of alveoli (denticles).
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.

<table>
<thead>
<tr>
<th>Species/Series</th>
<th>Shape of X.S.</th>
<th>Denticles (alveoli)</th>
<th>Canals</th>
<th>Unusual feature(s)</th>
<th>FORMATION OR LOCALITY/AGE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. columbianus</em> sp. nov.</td>
<td>Round; distally</td>
<td>2 rows, each ~18 alveoli wide; ? groove between rows proximally or narrow space distally</td>
<td>Central; two pairs of large diameter nutrient canals both proximally and distally</td>
<td>Wide rows of alveoli</td>
<td>Lincoln Creek Fm, WA/late Oligocene</td>
</tr>
<tr>
<td><em>A. maxillaris</em> (Fierstine, 2001)</td>
<td>Horseshoe-shape, flat ventrally; dorsal keel mid-anteriorty; D/W ≠ 1 except for region of keel where D/W ≥ 1</td>
<td>2 rows, each ~5–11 alveoli wide; shallow groove between rows</td>
<td>No central; two pairs of large diameter nutrient canals proximally, one pair distally</td>
<td>Keel on dorum of distal rostrum; maxillary with a tuberosity and flange</td>
<td>Yaquina Fm, OR/late Oligocene</td>
</tr>
<tr>
<td><em>A. denticulatus</em> (Lerche, 1909)</td>
<td>Horseshoe-shaped, flat ventrally; D/W ≠ 1</td>
<td>2 rows, each ~2–10 alveoli wide; shallow groove between rows</td>
<td>No central; one pair of small canals</td>
<td>Only one pair of canals</td>
<td>Belgian Basin/early Oligocene</td>
</tr>
<tr>
<td><em>A. robustus</em> (Leidy, 1860)</td>
<td>Horseshoe-shaped, flat ventrally; D/W &lt; 1 posteriorly; D/W &gt; 1 anteriorly</td>
<td>2 rows, each 10–18 alveoli wide; groove (proximally) or narrow space (distally) between rows</td>
<td>No central; 9 unequal-sized nutrient canals not arranged into pairs</td>
<td>Wide rows of alveoli</td>
<td>Ashley River Fm, SC/late Oligocene</td>
</tr>
</tbody>
</table>

*Aglyptorhynchus parini* Bannikov, 1993, and Monsch (pers. comm., Oct., 2003) noted a small ventral flange in *Pseudotetrapodus*; 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*, *Pseudotetrapodus*, and *Aglyptorhynchus* are the only known fishes with a downturned expansion.

The lower jaw (Fig. 1A) is a poorly preserved middle segment comprised 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 *Hemignawaya*, 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 postero-lateral process of the epicranius (Figs. 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 anterior head of the hyomandibular and the pterotic has a deep, oval-shaped fossa (ptf) 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*. 
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-thirds 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 celeous occipital condyle that is formed by the basioccipital and the paired exoccipitals is found in the Ostoglossomorph (Stewart, 1999), possibly the Procatantopterygii (Chapman, 1941, 1942, 1944; Rosen, 1985), aulopiforms (Goody, 1969), Poly-
mixiomorpha (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 salmonsids to be neoteleosts based on the exoccipital forming part of the occipital condyle. Until now a tripartite celeous occipital condyle has never been described in a non-beryciform percomorph fish.

In anterior view (unfigured), the large opening for the poste-
terior 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 xiphids. 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 scambroid (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 para-
phenoid (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 (spc) and pterotic (ptc) 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 laterally (outward) and its dorsal corner is round; however, the corner has a broken edge that could have contained a posteriorly pro-
going spine or sharp angle in the undamaged state. The proxi-
mal 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 scambroids, including Aglyptorhynchus columbianus, 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 scambroid, other than A. colum-
bianus, has a lateral curve in the posterior margin of the hyomandibular. All scambroids, 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 scambroids, 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, Palaeorhyn-
chus, and Pseudotetrapus is unknown.

*Aglyptorhynchus* sp.

(Fig. 6)

**Material**—From locality UWBM A8967: ten articulated verteb-
brae (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, scambroid 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-
brae (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 measure-
ments) 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. Vertebras 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) prezy-
gapophyses are well-developed, especially on vertebrae 4–9. Dor-
sal postzygapophyses (dppez) are present on vertebrae 1–9. Be-
cause the hemal spine of the tenth vertebra tends to point pos-
terovertrally (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 scambroids 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. glarisiatus* (Blainville 1818:35–36) (Pharris, 1991; Bananikov, 1993). Scambroides have a variable number of caudal vertebrae (17–32) (Col-
lette et al., 1984). *Hemingwaya* has approximately 32 caudal ver-
tebrae (Stytshevskaya 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), Tetrapurturidae (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 Tetrapurturidae was defined on variable characters and noted that the type genus (Pseudoctetrapurus) is a synonym of Tetrapurus (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 Xiphiocetus (Xiphiidae), has longitudinal ridges and sulci similar to Blochius (Blochiidae), and has a maxillary flange and probably a deep lower jaw similar to Palaeorhynchus and Pseudoctetrapurus (Palaeorhynchidae). Aglyptorhynchus has several autapomorphies: a tripartite celtous 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.

ACKNOWLEDGMENTS

I am indebted to J. Goedert (UWBM) for bringing the type specimen (LACM 143980) to my attention and for graciously providing me with locality data and pertinent references. D. Catania (CAS), R. Feeney, J. Seigel, and J. D. Stewart (LACM), J. Rensberger (UWBM), and A. Sanders (ChM), gave me access to specimens in their custody. I profited greatly from discussions with G. Arratia (Museum für Naturkunde der Humboldt Universität, Berlin, Germany) and J. D. Stewart (LACM) on the tripartite occipital condyle and from references they provided. J. Goedert (UWBM), K. Monsch (University of Wroclaw, Poland), and two anonymous reviewers deserve special credit for previewing an earlier version of the manuscript and offering suggestions for improvement. F. Vernacchia (San Luis Diagnostic Center) furnished computer tomography (CAT) scans at minimal cost, and J. McLaughlin (California Polytechnic State University, San Luis Obispo, California) assisted with data retrieval. A. Fierstine offered support and encouragement throughout the study.

Received 5 November 2003; accepted 29 September 2004.