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Cetorhinus cf. C. maximus (Gunnerus) (Lamniformes: Cetorhinidae), A Basking Shark from the Late Miocene Empire Formation, Coos Bay, Oregon

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Abstract.—The family Cetorhinidae Gill includes one extant genus, Cetorhinus Blainville, and a single living species, the basking shark, C. maximus (Gunnerus). Basking sharks are coastal pelagic to oceanic with circumglobal distribution in boreal to warm-temperate waters of the continental and insular shelves. Second only in size to the whale shark, Rhincodon typus, basking sharks attain a maximum total length of 12 to 15 m (although generally not exceeding 9.8 m), and are planktivorous, feeding by filtering copepods, barnacles, decapod larvae and fish eggs from the water. The first Tertiary records of undisputed cetorhinids are from the middle Eocene of Antarctica, possibly the middle Eocene of Russia, and the late Eocene of Oregon. Eocene cetorhinids are referred to Keasius taylori, and Oligocene through early Miocene basking sharks are traditionally assigned to Keasius parvus. The earliest occurrence of Cetorhinus in the northeastern Pacific is early Miocene, and fossils attributed to this genus are relatively common in middle Miocene through Pleistocene marine sediments of Oregon, California, and Baja California, Mexico. Late Miocene and younger Cetorhinus are conventionally placed in the extant species, C. maximus. Late Miocene fossils of a basking shark from the Coos Conglomerate Member of the Empire Formation, Oregon, were collected in 1972 by students from the University of California, Berkeley. Associated vertebrae and gill rakers compare favorably in size and overall morphology with those of adult Recent C. maximus. Based on correlations of vertebral and gill raker dimensions with the total length for Recent C. maximus, the Empire basking shark is estimated to have been between 4.5 and 5.75+ m in total length. Although gill rakers and vertebrae from the Empire Formation compare favorably with those of C. maximus, a definitive identification requires dentition. The occurrence of Cetorhinus cf. C. maximus in the late Miocene of Oregon is consistent with other late Miocene records of this species in California and Chile. C. maximus may range no earlier than late Miocene in the eastern North Pacific.

Introduction

The Family Cetorhinidae Gill, 1862, includes one extant genus, Cetorhinus Blainville, 1816, and a single living species, the basking shark, C. maximus (Gunnerus, 1765) (Springer and Gilbert, 1976; Compagno, 1984, 2001). Basking sharks are among the largest living neoselachians, exceeded only in size by the whale shark Rhincodon typus (Smith, 1828), attaining a maximum total length of 12.2 to 15.2 m, although generally not exceeding 9.8 m in total length (Compagno, 2001). Cetorhinus maximus is also characterized by having large gill slits that nearly encircle the head, numerous long, filamentous dermal denticle gill rakers lining the anterior and posterior sides of each
branchial arch, a strongly pointed snout and large subterminal mouth with numerous small, monocuspid teeth, strong lateral keels on the caudal peduncle and a large lunate caudal fin (Compagno, 2001).

The living basking shark is coastal pelagic to oceanic with a circumglobal distribution in boreal to warm-temperate waters of the continental and insular shelves; it occurs both offshore and in shallow coastal waters and enters enclosed bays (Compagno, 2001). In the northeastern Pacific, *Cetorhinus maximus* ranges from the Gulf of California, northern Mexico to the Gulf of Alaska and perhaps the Aleutian Island chain (Mecklenburg et al., 2002; Lamb and Edgell, 2010). Basking sharks are planktivorous, feeding by filtering copepods, barnacles, decapod larvae, and fish eggs from the water (Compagno, 2001). They feed, while swimming slowly with their mouths wide-open, allowing water and plankton to pass through the buccal cavity, into the pharynx and across the branchial arches, which are lined with numerous gill rakers (1260 gill rakers per gill: Bigelow & Schroeder, 1948, p. 150; Matthews and Parker, 1950, p. 564). Plankton are sieved out as the water passes between the gill rakers and is expelled through external gill openings. Matthews and Parker (1950) suggest that mucous excreted along the base of the gill rakers aids in the capture of food.

The Family Cetorhinidae includes two extinct genera, *Pseudocetorhinus* Duffin, 1998, and *Keasius* Welton, 2013. Teeth and gill rakers of *P. pickfordi* Duffin, 1998, were originally described from the Rhaetian of England and also occur in the Late Triassic of France (Cuny et al., 1994; Cuny, 1995; Cuny et al., 2000), Belgium (Cuny et al., 1994) and Luxembourg (Godefroit et al., 1998). According to Duffin (1998), *P. pickfordi* may represent the earliest known cetorhinid and the first filter-feeding shark. Allocation of *Pseudocetorhinus* to the Cetorhinidae is not particularly convincing, and probably has no phylogenetic relationship with Tertiary and Recent Cetorhinidae. A gap in the fossil record of the Cetorhinidae exists from the Early Jurassic through early Eocene, with the first Tertiary records of undisputed cetorhinids in the middle Eocene of Antarctica (Cione and Ruguero, 1998), the Eocene of Oregon (Welton in Cappetta, 1987, p. 107; Welton, 2013), and possibly the middle Eocene of Russia (Malyskhina, 2006).

There are approximately six nominal extinct cetorhinid species, ranging in age from the middle Eocene to late Pleistocene (Cappetta, 2006; Welton, 2013). Of these six species, three (*Cetorhinus duponti* Hasse, 1882) and *C. selachoides* (Hasse, 1882), both from the early Pliocene of Anvers, Belgium, and *C. glauconiticus* (Noetling, 1885), from the upper Rupelien (Oligocene) of Russia) are based on vertebrae. Two species (*Keasius parvus* (Leriche, 1908), from the upper Rupelian (Oligocene) Boom Clay of Belgium, and *C. auratus* (Van Beneden, 1871, from the early Pliocene of Anvers, Belgium) are based on gill rakers, and *K. taylori* Welton, 2013, was recently described from an associated skeleton with teeth, vertebrae and gill rakers. The validity of *C. glauconiticus* and *C. selachoides* is questionable (Cappetta, 2006), and *C. duponti* and *C. auratus* are junior synonyms of *C. maximus* (Woodward, 1889; Leriche, 1908, 1921; Cappetta, 2006). *Keasius parvus* is a valid Oligocene through perhaps early Miocene species, and *K. talyori* is known from the middle and late Eocene.

Conventionally, almost all late Miocene and younger cetorhinids are referred to *Cetorhinus maximus*, and early Miocene and Oligocene basking sharks are assigned to *Keasius parvus*. A proximal gill raker referred to *Cetorhinus* sp. from the middle Eocene La Meseta Formation of Seymour Island, Antarctica (Cione and Reguero, 1998), was referred to *C. parvus* by Hovestadt and Hovestadt-Euler (2011), and has subsequently been assigned to *K. taylori* (Welton, 2013).

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Oligocene occurrences of *Keasius parvus* include Germany (Weiler, 1922, 1928, 1931; Leriche, 1948; Muller, 1976, 1983; Von Der Hocht, 1978a, 1978b; Pfeil, 1981; Freess, 1991, 1992; Reinecke et al., 2001, 2005; Haye et al., 2008; Gille et al., 2010; Hovestadt et al., 2010; Hovestadt and Hovestadt-Euler, 2011; De Pietri et al., 2010), Belgium (Leriche, 1908, 1910; Herman, 1979; Van Den Bosch, 1984; Baut and Genault, 1999), Switzerland (Frohlicher and Weiler, 1952), France (Dutheil, 1991; Baut, 1993; Genault, 1993; Pharissat, 1998; Merle et al., 2002), and questionably identified from a placoid scale from South Carolina, U.S.A. (Cicimurri and Knight, 2009). *Cetorhinus* sp. has been reported from the late Oligocene of Japan (Uyeno et al., 1984; Yabumoto and Uyeno, 1994), and Baja California, Mexico (Gonzalez-Barba and Thies, 2000). Indeterminate fragmentary cetorhinid gill rakers occur in the Oligocene Kirker Formation of California (Welton, unpublished data).

Miocene occurrences of *Keasius parvus* include Germany (Kruckow, 1961; Barthelt et al., 1991; Bracher and Unger, 2007; Reinecke et al., 2008, 2011), Switzerland (Bolliger et al., 1995), Austria (Brzobohaty and Schultz, 1978; Schultz, 1978; Schmid et al., 2001), and France (Vialle et al., 2011).

Unidentified Oligocene species of *Cetorhinus* are reported from Romania (Jonet, 1947), Poland (Van Den Bosch, 1981; Bienkowska-Wasiluk and Radwanski, 2009), and Japan (Kikuchi and Takaoka, 1979; Tomita and Oji, 2010). Early to middle Miocene basking sharks are quite diverse, largely unstudied, and usually referred to *Cetorhinus* sp. (Applegate in Mitchell and Tedford, 1973; Domning, 1978; Karasawa, 1989; Yabumoto and Uyeno, 1994; Bolliger et al., 1995; Gottfried, 1995; Purdy et al., 2001; Gonzalez-Barba and Thies, 2000) or are variously assigned to *C. maximus* (Brzobohaty and Schultz, 1978; Karasawa, 1989; Uyeno et al., 1983; Yabumoto and Uyeno, 1994; Long, 1994). Jordan and Hannibal (1923, p. 31, pl. III-B and I, but not C-F, L-M, Q, W, and CC) figure two *Cetorhinus* teeth from California (most likely from the middle Miocene – Barstovian, Round Mountain Silt) under the genus *Gyrace* Jordan, 1923, a junior synonym of *Galeocerdo* Muller and Henle, 1837. Gonzalez-Barba and Thies (2000) report *Cetorhinus* sp. from the Torontian of Baja California, Mexico and *Cetorhinus* sp. occurs in the late Miocene-early Pliocene of Holland (Wijnker et al., 2008), and the late Miocene (Stewart, 1997; Barnes, 2008) and Pliocene (Applegate, 1978) of Baja California, Mexico. Almost all late Miocene through Pleistocene basking sharks are included in *C. maximus*, with occurrences in Belgium (Herman et al., 1974; Herman, 1979; Nolf, 1986; Van Der Brugghen, 2005), Italy (Lawley, 1876; Landini, 1977; Marsili, 2008; Cigala-Fulgosi et al., 2009), France (Cappetta and Nolf, 1991), Japan (Uyeno and Matsushima, 1974), the Czech Republic (Schultz et al., 2010), Chile (Long, 1993), California (Kanakoff, 1956; Fitch, 1970; Langenwalter, 1975; Long, 1994; Boessenecker, 2011), Oregon (Long, 1994; Welton, unpublished data), and Baja California, Mexico (Long, 1994).

In the summer of 1972, students of the University of California at Berkeley, Summer Institute, discovered associated skeletal elements of a basking shark in the Coos Conglomerate Member of the Empire Formation at Fossil Point, Coos Bay, Oregon (Fig. 1). The specimen was collected in a calcareous sandstone concretion and consists of three vertebrae and 11 fragmentary gill rakers. This paper describes the Empire Formation *Cetorhinus* fossils and compares them with vertebrae and gill rakers of the recent basking shark *C. maximus*. This paper is the second in a series of studies to document the taxonomy and stratigraphic distribution of Tertiary eastern North Pacific cetorhinids.
Material and Methods

Modern and fossil specimens described or referenced in this study are housed in scientific institutions in the United States and the Netherlands as indicated by the following acronyms:

KBIN - Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium
LACM - Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
UCMP - University of California, Museum of Paleontology, Berkeley, California, U.S.A.

The terminology for individual gill rakers (Fig. 2) has been modified from Hovestadt and Hovestadt-Euler (2011), and follows Welton (2013). Anatomical terms for vertebral centra and their internal calcifications are derived from Ridewood (1921), Wintner and Cliff (1999), Wintner (2000).

The fossils of Cetorhinus cf. C. maximus (UCMP 77642, locality UCMP V-6726), are catalogued and housed in the Museum of Paleontology, University of California, Berkeley, and precise locality data for this specimen may be obtained from the same institution. Detailed descriptions and illustrations of gill rakers of extant C. maximus are found in Van Den Bosch (1984), Hovestadt-Hovestadt-Euler (2011), and Welton (2013). Comparisons with the Empire basking shark are also based on examination of the following specimens: C. maximus, LACM 35876-1, wet-preserved gill arch with gill
rakers, adult male, 6.0–6.7 m total length (TL), collected off Morro Bay, San Luis Obispo, California, 30 June 1976. Descriptions and illustrations of gill rakers belonging to the Oligocene *Keasius parvus* are found in Leriche (1910) and Hovestadt-Hovestadt-Euler (2011). Comparisons were also made with *K. parvus* gill rakers based on LACM 154925, 20 gill rakers from LACM Locality 3813, Oligocene (Rupelien), U. Meeressand, Weinheim bei Alzey Steinbruch an der Neumühle.

The associated skeletal elements are preserved in a calcareous concretion, and were initially prepared by etching in a weak (5%) acetic acid solution to expose gill rakers and calcified vertebral cartilages. Additional preparation was done with an air abrasive unit. All artwork and photographs are by the author. The illustrations in Figures 2 and 6 were drawn using a Wild M5 stereomicroscope and camera-lucida attachment.
CETORHINUS CF. C. MAXIMUS FROM THE LATE MIOCENE EMPIRE FORMATION, OREGON

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Superorder Galeomorphii Compagno, 1973
Order Lamniformes Berg, 1958
Family Cetorhinidae Gill, 1862
Genus Cetorhinus Blainville, 1816

Cetorhinus cf. C. maximus (Gunnerus, 1765)
Figs. 3a-e, 4–6a-d

Referred Specimen—UCMP 77642, three vertebrae, and 11 fragmentary gill rakers (Figs. 3–6).

Fig. 3. Acid etched calcareous concretion from the Coos Conglomerate Member of the Empire Formation (UCMP Locality V-6726, Fossil Point, Coos County, Oregon) with exposed vertebrae and gill rakers of Cetorhinus cf. C. maximus (UCMP 77642). a, transverse section of abdominal or trunk vertebra showing concentric calcifications of intermedialia; b, axial view of intermediate sized vertebra showing the corpus calcareum and radial calcifications on broken surface (upper left margin of centrum); c, axial view of caudal? vertebra with exposed radial calcifications; d, fragmentary gill raker filaments; e, incomplete gill raker with a well preserved base. Scale = 2 cm.
**Locality**—UCMP V-6726, Fossil Point, Coos County, Oregon, approximately 900 meters southwest of Pigeon Point and about 2400 meters north of Charleston, Coos County, Oregon (Fig. 1).

**Formation**—UCMP 77642 was collected from the Coos Conglomerate Member of the Empire Formation (Diller, 1896; Dall, 1898, 1909; Howe, 1922; Weaver, 1945; Armentrout, 1973, 1980). The Coos Conglomerate is composed of cobbles and boulders of fossiliferous lower Empire Formation sandstone, rounded beach pebbles and cobbles of chert, basalt, quartzite, and reworked Empire Formation fossils mixed with contemporaneous shallow water fauna (Armentrout, 1973, p. 4). Dall (1909) was able

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**Fig. 4.** Acidized transverse section through largest vertebra of *Cetorhinus cf. C. maximus* (UCMP 77642), showing calcifications of the intermedia. **Abbreviations:** bd - basidorsal insertion; bv - basiventral insertion; cc - corpus calcareum; ci - calcified wedge face of intermediale; ct - calcified tube; n - passage of notochord; p - uncalcified cartilaginous part of the intermediale; p' - calcified concentric lamellae of the intermediale. Scale = 1 cm.
to make a distinction between fossils derived from the underlying Empire Formation sandstone and those deposited contemporaneously with the Coos Conglomerate by carefully noting color and matrix composition. The *Cetorhinus* skeletal elements are contained in a fine to medium grained, gray, calcareous sandstone nodule, surrounded by a matrix of basalt and quartzite pebbles up to 5.0 mm in diameter. Based on similarities in lithology, this nodule was probably reworked from lower Empire Formation sandstone.


**Description**—The skeletal elements of *Cetorhinus* were first recognized in the field as a series of associated, but disarticulated, calcified centra and gill rakers, weathering *in situ* from the Coos Conglomerate Member of the Empire Formation. The skeleton is preserved in a single calcareous sandstone concretion (Fig. 3), and the association is assumed to represent one individual for the following reasons: 1) all skeletal elements belong to the same taxon; 2) all gill rakers are within a size range found on a single gill arch (Hovestadt and Hovestadt-Euler, 2011, p. 79, fig. 9m-u; Fig. 6), and the three associated centra are within the size range for one individual (Natanson et al., 2008). Evidence of some postmortem transport is indicated by the juxtaposition of vertebrae from different positions along the vertebral column, in combination with scattered gill rakers in the matrix.

**Vertebrae**—The largest vertebra (Figs. 3a, 4) is seen in transverse section broken midway between the anterior and posterior ends of the centrum. A wedge-shaped section of the corpus calcareum is preserved (Fig. 4) and covers one of the wedge cartilages. The *CETORHINUS CF. C. MAXIMUS FROM THE LATE MIOCENE EMPIRE FORMATION, OREGON* 81
The corpus calcareum of the intermediate-sized vertebra is exposed in axial view. Poorly preserved growth band pairs of alternating ridges and troughs are visible in Figure 3b. Radial calcifications are exposed along the broken perimeter of the centrum. The centrum is 58 mm in transverse width. The smallest centrum is partially broken along

Fig. 6. Incomplete gill rakers of *Cetorhinus* cf. *C. maximus* (UCMP 77642), from the Coos Conglomerate Member of the late Miocene Empire Formation, Coos County, Oregon (UCMP locality V-6726). The gill raker sequence a through d approximates distal-most to central-most positions on the gill arch. Scale = 2 mm.
one side revealing numerous lamellar perforations (Figs. 3, 5) and radial calcifications. The radii extend from the perimeter of the centrum, inward toward the notochord for a distance of one-half the radius. The centrum is approximately 42 mm in transverse width and 27 mm in anteroposterior length.

**Gill Rakers**—Eleven fragmentary gill rakers are preserved, four of which have bases (Fig. 6), and the remainder consist of filament sections. The longest incomplete gill raker (Fig. 6c) is 26+ mm. The filaments are gently curved medially, taper apically, are laterally thin, and may have either a weak median longitudinal trough developed just above the point at which the filament connects with the base (Fig. 2), or this surface is flat to weakly convex. The oral and aboral filament surfaces are rounded, and the filaments are widest and most strongly curved at their junction with the base. The base of one gill raker (Fig. 6a) has a well developed distal projection, and basal edges range from flat to moderately rounded (Fig. 6 a, b, d). The medial process is long in all gill rakers, tapers apically with a broad base, and ranges from narrow (Fig. 6b) to somewhat triangular in shape (Fig. 6a). The mesial edge of the medial process is straight (Fig. 6b) to rounded (Fig. 6a, d) and the intersection of the basal edge of the base and the mesial edge of the medial process ranges from angular (Fig. 6b) to subangular (Fig. 6a, d). A narrow, rugose basal attachment surface is continuous from the distal basal projection to the apical tip of the medial process. The bight is subangular in all gill rakers, and the basal height, as measured at the point of greatest bight curvature (Figs. 2, 6) is relatively wide. Except for the basal attachment surface, all gill raker surfaces are covered by smooth to very finely textured enameloid. Broken filament cross sections show a hollow pulp cavity that persists medially throughout the length of the gill raker.

**Discussion**

**Vertebrae**—Calcifications in the centra in Recent *Cetorhinus maximus* have been described by Hasse (1882), Ridewood (1921), and illustrated by Natanson et al. (2008, p. 272, fig. 1). The calcifications found in the Empire basking shark (Figs. 3–5) compare favorably with those of *C. maximus* in sharing the following attributes: centrum nearly oval in axial view; diagonal lamellae absent in large trunk vertebrae and present in much small caudal centra; intermedialia weakly calcified with well-developed concentric lamellae; basidorsal and basiventral insertions for the neural and haemal arch cartilages well developed with moderately calcified wedge faces; small tubes radiate from the centrum focus (Wintner and Cliff, 1999), passing through concentric lamellae and extend to the margin of the centrum; primary double cone angle, measured from the focus to the anterior or posterior margin of the corpus calcareum, is high; length of centrum much greater than other lamniforms.

According to Ridewood (1921, p. 361–362), ventral intermediale in trunk vertebrae are wider than the dorsal intermediale. In the cloacal region, they are about equal, and the ventral intermediale continue to narrow in the caudal region. Natanson et al. (2008, p. 272, fig. 1) figured a series of *Cetorhinus maximus* vertebrae representing cranial, abdominal and trunk vertebrae, illustrating a trend from ventrolaterally directed basopophyses in cranial vertebrae, increasing lateral direction in abdominal vertebrae, and a reverse of the trend in trunk vertebrae. The trends noted above are potentially useful in determining the relative position of isolated vertebrae in the vertebral column. Unfortunately, as pointed out by Ridewood (1921), it is not possible with certainty to determine the dorsal orientation of an isolated centrum. As an alternative, one can infer relative position based on vertebral size, if the sample represents an association from one
individual. Applying the above criteria, the presence of concentric lamellae and lack of radii in the largest Empire centrum (Figs. 3a, 4) suggests this vertebra is from the trunk region. Although one basopophyses is hidden by a fragment of the corpus calcareum, it appears that one pair is more ventrolaterally directed than the other. On this basis, the centrum illustrated in Figure 4 is oriented with the most laterally directed basopophyses in the ventral position. The smallest Empire centrum (Fig. 3c) possesses radial calcifications on the external surface of the outermost concentric lamellae. A caudal position for this centrum is indicated by its small size, in combination with the presence of radial calcifications.

There are currently no studies documenting individual, ontogenetic, or geographic variations in the vertebrae of Recent *Cetorhinus maximus*. In the absence of these data, it is not possible to define specific attributes of their morphology that can be used to identify interspecific differences between fossil and Recent vertebrae. In addition, there are no valid extinct species of *Cetorhinus* with vertebrae, to serve as a basis for comparison with extant *C. maximus*.

**Gill Rakers**—Gill rakers are modified mucous membrane denticles (Peyer 1968). The base is fixed to the branchial arch by connective tissues and perforated by nutrient canals along the entire basal edge. Vascular canals filled with dentinal tubes and surrounded by interosteal tissue form the base. A median vascular canal arising from the base runs up the center of the filament. Dentinal tubes, originating along the outer margin of the pulp cavity, penetrate a thick layer of pallial dentine, which, with the exception of the basal attachment surface, covers the entire gill raker. A thin pigment layer overlain by enameloid covers the outermost surface of the gill raker.

Gill rakers in *Cetorhinus maximus* are present on both sides of each of the five branchial arches. From the inner edge of each arch extends a 10-cm diameter strip of mucous membrane (LACM 35876-1), and to either side of this lies a single continuous row of gill rakers with their free ends (filaments) directed towards the mouth. The semilunar base of each gill raker is attached to the mucous membrane of the gill arch. The longest gill rakers occur near the center of the arc and are about 9 cm long in the LACM specimen. They are spaced at about 12–13 per centimeter and decrease in length toward either end of the gill arch. Bigelow & Schroeder 1948:150) estimated the number of gill rakers in one series on one branchial arch to be 1260. Matthews and Parker (1950:564) estimated the total number to be from 1200 to 1300 on the anterior larger gill arches and from 1000 to 1100 on the shorter arches.

Van Den Bosch (1984), Hovestadt and Hovestadt-Euler (2011), and Welton (2013) figure gill rakers from Recent *Cetorhinus maximus*, representing central through distal positions along the gill arch, from individuals of both sexes, and a range of body lengths. Comparison of *C. maximus* gill rakers having the same relative position on the gill arch, but from individuals ranging in size from 360 cm (TL) to greater than 600 cm (TL), shows a morphologic (ontogenetic) trend with increasing body length (Hovestadt and Hovestadt-Euler, 2011). Ontogenetic changes in the morphology of *C. maximus* gill rakers from a central position on the gill arch, include: an increase in gill raker length, a shift in the basal angle from rounded to subangular, an increase in length of the medial process, and development of a concave mesial edge to the medial process. Variable attributes include degree of filament curvature at its base, basal width, and bight angles that range from curved to angular. It is possible that sexual dimorphism, or individual variation, might explain some differences in gill raker morphology; however, the sample size is too small to test this hypothesis.
Large adult *Cetorhinus maximus* gill rakers exceed 20 cm in total length (TL), whereas the most complete Empire gill raker is 2.6 cm (Fig. 6c). Comparing the Empire gill raker bases (Fig. 6a-d) with the approximately equal sized *C. maximus* gill raker bases shown in the series illustrated by Hovestadt and Hovestadt-Euler (2011, p. 79, m-u, from a 672 cm (TL) female) I estimate that the Empire gill rakers shown in Figure 6, if complete, would have total lengths ranging from a minimum of five cm (Fig. 6a) to a maximum of about eight cm (Fig. 6d). These estimates are derived using a ratio of base height to gill raker length, established on the Hovestadt and Hovestadt-Euler (2011) figured gill rakers (fig. 9m-u), and applied to the Empire specimens. The Empire gill rakers (Fig. 6a-d) compare favorably with those adult *C. maximus* (Hovestadt-Hovestadt-Euler, 2011, p. 79, fig. 9m-u) in having moderately to strongly curved filament bases, and relatively flat to weakly convex distal protuberances. The basal margins are moderately long, and the medial processes are very long and narrow with weakly concave to weakly convex medial edges. Basal heights are moderately high, and basal angles are rounded to subangular. Bights are moderately wide and all appear to be subangular. Trends from a distal to central position on the gill arch include increasing curvature of the filament base, increasing basal length, increasing length of the medial process, development of a concave mesial edge of the medial process in the most central gill rakers, and an increase in gill raker length, with the longest gill rakers either in the central-most position on the gill arch (Hovestadt and Hovestadt-Euler, 2011) or just distal to the central position (Welton, 2013, fig. 12, LACM 35876-1). The Empire gill rakers differ from those of LACM 35876-1 (Welton, 2013, fig. 12) in having subangular rather than rounded bights, less curvature at the filament base, and in some gill rakers, and a less rounded mesial edge of the medial process. The gill raker sequence illustrated in Figure 6a-d approximates distal-most to central-most positions on the gill arch.

The Empire *Cetorhinus* gill rakers and vertebrae differ significantly from those of the *Keasius taylori* (Welton, 2013) and *K. parvus* (Hovestadt and Hovestadt-Euler, 2011; LACM 154925), by having much larger gill rakers, from *K. parvus* in having less curvature at the filament just above it attachment with the base, and from both *K. parvus* and *K. taylori* in having a less robust base with a much longer and narrower medial process, a more horizontal basal edge of the base, a subangular to rounded basal angle, subangular to rounded bight, and relatively short basal height. The Empire vertebrae are large and have well developed concentric lamellae. The vertebrae of *K. taylori* and *K. parvus* are much smaller and lack concentric lamellae (Welton, 2013).

**Estimated Total Length of the Empire Formation Basking Shark**—The total length of the Empire basking shark can be estimated using vertebral size (Natanson et al., 2008) and gill raker length (Hovestadt and Hovestadt-Euler, 2011). In the absence of a complete Empire skeleton, maximum vertebral dorsoventral heights and gill raker lengths in this individual are unknown. Assuming there were larger vertebrae and gill rakers in the shark, total length estimates based on the preserved vertebrae and gill rakers are conservative. The largest Empire centrum measures about 80 mm in dorsoventral height. According to a graph correlating vertebral dimensions to total length for Recent *Cetorhinus maximus* (Natanson et al., 2008, p. 272, fig. 2), the Empire basking shark has an estimated total length of about 450 cm. Using a correlation of gill raker length to total length of *C. maximus* (Hovestadt and Hovestadt-Euler, 2011, p. 80, fig. 11), an 80 mm Empire gill raker (TL estimated above) correlates with a 575 cm (TL) shark.

**Comments on the Use of Vertebrae, Gillrakers and Teeth in Fossil Cetorhinid Taxonomy**—All nominal fossil species of *Cetorhinus* are based on gill rakers or vertebrae.
The issues related to the use of vertebrae in defining new species have been noted above, and most of the same problems apply to the use of gill rakers in taxonomy. Recent studies of extant *C. maximus* (Van Den Bosch, 1984; Hovestadt-Hovestadt-Euler, 2011; Welton, 2013) provide significant new data on gill raker morphology, and especially changes in their shape with age and position on the gill arch. However, additional work is needed to document individual, ontogenetic, perhaps sexual, and geographic variation in gill raker morphology. The use of gill rakers in fossil cetorhinid taxonomy is further complicated by the fact that some undescribed Neogene *Cetorhinus* have gill rakers very much like Recent *C. maximus*, but teeth that are distinct and warrant assignment to a new species (Welton, unpublished data).

Identification of the Empire *Cetorhinus* would have been greatly facilitated with oral teeth, but none were found with the fossil, and to my knowledge, no teeth of *Cetorhinus* have been collected from the Coos Conglomerate. Although gill rakers and vertebrae from the Empire Formation compare favorably with those of the Recent basking shark *C. maximus*, a definitive identification requires dentition.

**Fossil Record of the Genus *Cetorhinus* in Oregon and California**—The fossil record of the genus *Cetorhinus* in Oregon and California ranges from early Miocene through Pleistocene (Long, 1994; Welton, unpublished data). Based primarily on teeth, and to a lesser extent gill rakers and vertebrae, early and middle Miocene *Cetorhinus* from the eastern North Pacific are morphologically distinct from *C. maximus*, and represent undescribed species (Welton, unpublished data). The occurrence of *Cetorhinus* cf. *C. maximus* in the late Miocene of Oregon (Long, 1994; this study) is consistent with other late Miocene records of the species in California (Long, 1994) and Chile (Long, 1993).

**Conclusions**

1. A calcareous sandstone concretion containing three vertebrae and 11 fragmentary gill rakers belonging to the genus *Cetorhinus* Blainville, 1816, was collected from the Coos Conglomerate Member of the late Miocene Empire Formation, Coos County, Oregon.
2. Taphonomic data suggest the vertebrae and gill rakers represent an associated but disarticulated skeleton from one individual. The skeleton shows evidence of transport prior to deposition.
3. The Empire *Cetorhinus* gill rakers and vertebrae differ significantly from those of the *Keasius taylori* and *K. parvus*, and compare favorably with those of the Recent basking shark *C. maximus*.
4. The total length of the Empire basking shark is estimated to be between 4.5 and 5.75+ m based on correlations of vertebral and gill raker dimensions with the total length for Recent *C. maximus*.
5. Although the gill rakers and vertebrae from the Empire Formation compare favorably with those of the Recent basking shark *Cetorhinus maximus*, a definitive identification requires dentition.
6. Based primarily on teeth, and to a lesser extent gill rakers and vertebrae, early and middle Miocene *Cetorhinus* from the eastern North Pacific are distinct from *C. maximus* (Welton, unpublished data). The occurrence of *Cetorhinus* cf. *C. maximus* in the late Miocene Empire Formation of Oregon (Long, 1994; this study), is consistent with other late Miocene records of the species in California.
(Long, 1994) and Chile (Long, 1993), and suggests that *C. maximus* may range no earlier than late Miocene in the eastern North Pacific.

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CETORHINUS CF. C. MAXIMUS FROM THE LATE MIOCENE EMPIRE FORMATION, OREGON


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