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NEW PARTIAL SKELETON AND RELATIVE BRAIN SIZE IN THE LATE EOCENE ARCHAEOCETE *ZYGORHIZA KOCHII* (MAMMALIA, CETACEA) FROM THE PACHUTA MARL OF ALABAMA, WITH A NOTE ON CONTEMPORANEOUS *PONTOGENEUS BRACHYSPONDYLUS*

BY

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Abstract — A new partial skeleton of the late Eocene archaeocete *Zygorhiza kochii* (Reichenbach, 1847) is described, based on specimen PM-459 in the Field Museum, Chicago. The specimen was collected from the Pachuta Marl member of the Yazoo Formation near Melvin, Alabama, as were many early specimens of *Zygorhiza kochii* and the contemporaneous larger species *Pontogeneus brachyspondylus* and *Basilosaurus cetoides*. The new *Zygorhiza* skeleton includes a cranium with a well-preserved braincase, which has yielded one of the best endocranial casts known for an archaeocete. The endocast shows evidence of the large dorsal and rostral retia mirabilia typical of basilosaurids. The dorsolateral surface of the cerebrum, where exposed, is smoothly curved, with no suggestion of the cortical folding characteristic of modern cetacean brains. PM-459 includes a dentary with roots or alveoli for double-rooted cheek teeth from P₁ through M₃. The dentary preserves the large mandibular foramen and mandibular canal typical of basilosaurids. Vertebrae include several cervicals, a series of thoracics, and parts of two lumbar. The only appendicular element is a scapula that is relatively long anteroposteriorly and short dorsoventrally, with a strong acromion but weak scapular spine.

The body weight of *Zygorhiza kochii* is estimated to have been about 998 kg based on vertebral size. The endocranial volume of the skull of PM-459 measures 1189 cm³, which, when retia mirabilia are subtracted, corresponds to a brain weight of about 960 g. This yields an encephalization residual on a log base-2 doubling scale of ER_{TC} = -0.84.

The large, medium-sized, and smaller Yazoo Formation late Eocene archaeocetes *Basilosaurus cetoides*, *Pontogeneus brachyspondylus*, and *Zygorhiza kochii* have been known since 1849. Medium-sized *Cynthiacetus maxwelli* from the Yazoo Formation is synonymized with *Pontogeneus brachyspondylus*.

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INTRODUCTION

Cranial characteristics distinguish the major clades and grades of Eocene archaeocetes in the evolutionary transition of whales from land to sea. However, within successive archaeocete faunas the contemporaneous genera and species are often distinguished by differences in size and differences in vertebral proportions. Continuous series of associated vertebrae are required to identify individual elements to position within the vertebral column, thus assuring that comparisons within and between species are based on homologous elements. Important archaeocete vertebral columns remain undescribed, and others have limited utility because the specimens are only partially prepared.

Here I describe a previously unreported skeleton of *Zygorhiza kochii*, Field Museum of Natural History specimen PM-459, collected in 1947. The specimen is important because it includes a partial cranium with a well-preserved braincase, and also because it has a seemingly continuous series of 15 cervical and thoracic vertebrae (but neither series is complete). FMNH PM-459, hereafter PM-459, is also important because it came from a classic archaeocete collecting area near ‘Cocoa,’ or later ‘Old Cocoa Post Office,’ one mile (1.6 kilometers) southeast of the village of Melvin, in Choctaw County, Alabama (Fig. 1).

Archaeocetes from Choctaw County, Alabama

Charles Schuchert of the U. S. National Museum (USNM) arrived in Cocoa, in Choctaw County, Alabama, on November 2, 1894, to search for remains of *Basilosaurus*. One of the first specimens he collected included five lumbar vertebrae and one caudal vertebra identified as *Zeuglodon brachyspondylus* (USNM 2211), which came from Section 24, Township 11 North, Range 5 West, Choctaw County (Cocoa is a mile north of this in Section 13; Fig. 2). The Sanford Mitchell farm in Section 24 was the source of left and right dentaries of *Zygorhiza kochii* (USNM 4673), a partial skull of *Basilosaurus cetoides* (USNM 4674), and a series of vertebrae of *B. cetoides* (USNM 4675), all collected by Schuchert in 1894. Schuchert returned to the same Section 24 in 1896. On this second visit he collected a tympanic bulla of *Basilosaurus cetoides* (USNM 6125), the manubrium of a sternum of *B. cetoides* (USNM 13681), and a subadult specimen of *Zygorhiza kochii* (USNM 4748). Schuchert recorded all of these fossils as coming from a 5–10 foot (2–3 meter) thick unit he called ‘Zeuglodon beds’ of Jacksonian Eocene age (Lucas, 1900, p. 328–329). The ‘Zeuglodon beds’ are part of what is today called the Pachuta Marl member of the Yazoo Formation (Murray, 1947).

According to Remington Kellogg (1936, pp. 105–106), J. Magruder Sullivan collected a Millsaps College skull of *Zygorhiza kochii* (now USNM 16638) in 1926, on Robert Land farmland in Section 14, just northwest of Schuchert’s Section 24 localities. Kellogg and Norman Boss of the U. S. National Museum followed up on Schuchert’s and Sullivan’s field work

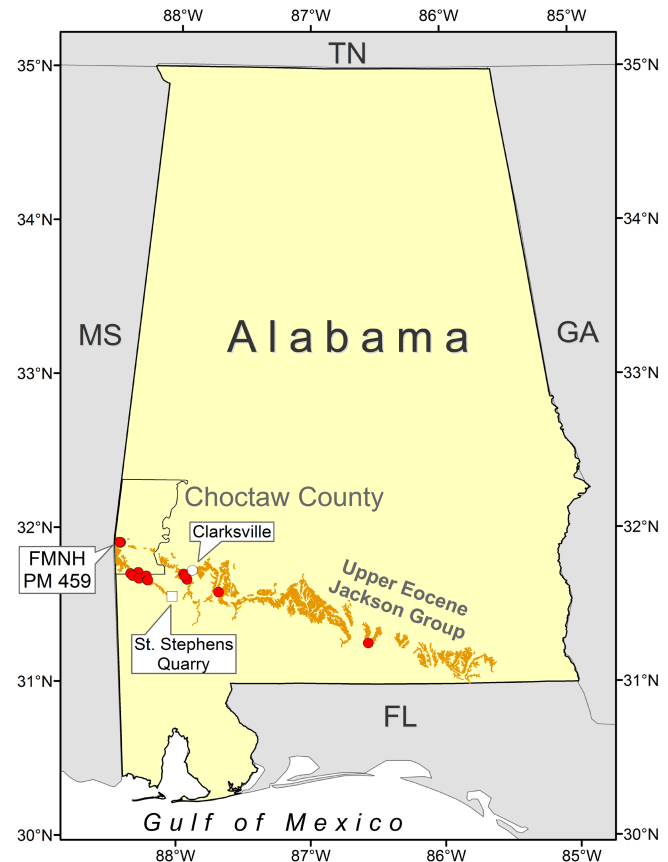


FIGURE 1 — Location map showing the distribution of Jackson Group geological formations, including the Pachuta Marl, in Choctaw County and across southern Alabama. Filled circles are archaeocete localities. The partial skeleton of *Zygorhiza kochii* described here, FMNH PM-459, was found in Pachuta Marl at the western edge of Choctaw County (see Fig. 2 for details). The type specimen of *Zygorhiza kochii* was found near Clarksville (open circle) in Clark County. St. Stephens Quarry (open square) in Washington County is the site, a little farther offshore, where detailed biostratigraphic research has been carried out on Jackson Group formations. Abbreviations: FL, Florida; GA, Georgia; MS, Mississippi; TN, Tennessee.

near Melvin and Cocoa by collecting a nearly complete skull and partial skeleton of *Zygorhiza kochii* (USNM 11962) and a second partial skull and skeleton of this species (USNM 12063). Both came from Section 24. Kellogg and Boss also collected a partial skull of *Z. kochii* (USNM 13773) from a locality one mile (1.6 kilometers) west of Melvin, across the state line in Mississippi. Additional specimens have been found near Cocoa and Melvin by later collectors (Table 1).

The label with PM-459 described here indicates that it was collected by the late William D. Turnbull (1922–2011), a Field Museum employee at the time (Turnbull was later curator of fossil mammals at the Field Museum). The specimen came from the Pachuta Marl member of the Yazoo Clay Formation,

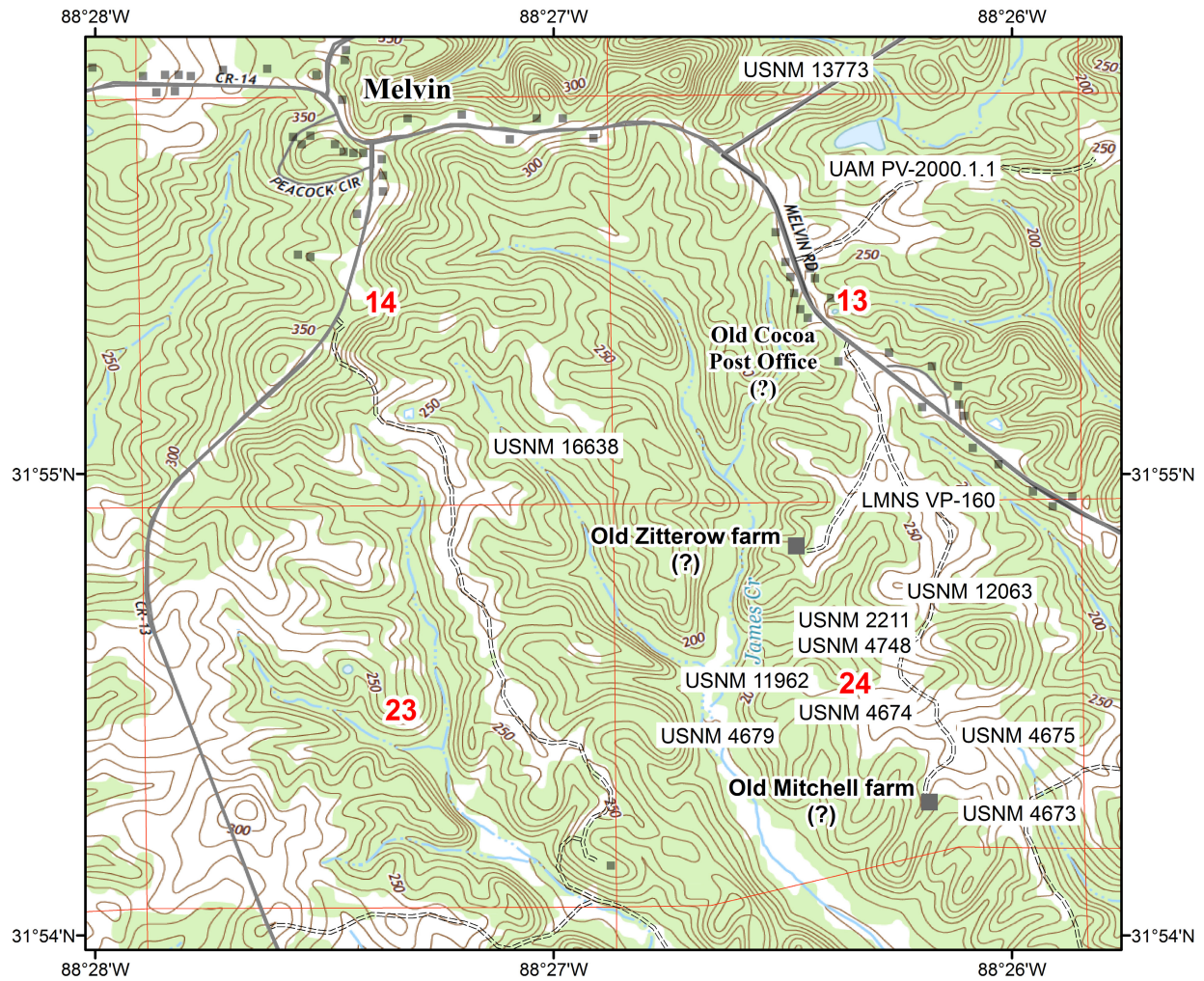


FIGURE 2 — Map of sites yielding Pachuta Marl late Eocene archaeocetes near Melvin, Alabama. Possible locations of the old Sanford Mitchell and G. W. Zitterow (later Robert Land) farms are shown in land survey Section 24, Township 11 North, Range 5 West, Choctaw County, south and east of Melvin and Old Cocoa Post Office. USNM specimen numbers are placed at the approximate location of *Zygorhiza kochii* (4673, 4748), *Pontogeneus brachyspondylus* (2211), and *Basilosaurus cetoides* (4674, 4675) specimens collected by Charles Schuchert in 1894 and 1896. Higher USNM numbers were collected by Remington Kellogg in 1929. These were recovered from ‘*Zeuglodon* beds’ (Pachuta Marl) in the upper part of the Jackson Group of geological formations. FMNH PM-459 described here was collected near the Mitchell/Land farm, probably in the southeast quarter of Section 24, but more precise information is not available. Cooke (1959, p. 71) records Old Cocoa Post Office as being in the SW¼ of Section 13. Land survey section numbers are in red.

Jackson Group, in Choctaw County, Alabama (Fig. 1). The PM-459 label also states that the specimen was collected on “Land’s Farm near Old Cocoa.” This is presumably the Sanford Mitchell farm mentioned by Kellogg (1936, pp. 18 and 102). According to Kellogg, the Sanford Mitchell farm was later owned by Robert Land. This farm was located two miles southeast of Melvin, Alabama, and included localities near the center of Section 24 and in the southeast quarter of Section 24, Township 11 North, Range 5 West, Choctaw County (Fig. 2).

In 1998 I obtained further information about PM-459 in a telephone conversation with Turnbull. According to him,

PM-459 was found by Mr. Glen L. Evans of the University of Texas at Austin. Evans located the specimen in 1946 or 1947 while engaged in some way with a Rainer Zangerl field party working in the Cretaceous Selma Formation of Alabama. I speculate that Evans stopped to look for fossils at the Land farm near Cocoa while driving from Austin to Selma to visit Zangerl’s team. Zangerl does not list Evans in the acknowledgment section of any Selma Formation publications, so it is doubtful that Evans was collaborating or collecting with Zangerl in any formal way.

On learning of the *Zygorhiza* find, Field Museum curator Bryan Patterson arranged for Turnbull to join Mr. Charles

M. Barber of Hot Springs, Arkansas, to collect the specimen. According to Turnbull, the specimen was partially articulated when it was found. It was collected in a large plaster jacket constructed to fit on top of an old door, and Turnbull was impressed that Barber loaded both onto his pickup truck by jacking up the door to rest on buckets, and then backing the pickup under the door and jacket to load both inertially. The important point is that articulation in the field enabled the sequence of vertebrae to be determined when the jacket was opened in the laboratory. Unfortunately, according to Turnbull, no photographs or maps were made to document the positions of bones of PM-459 relative to each other.

According to William Turnbull, the Field Museum *Zygorhiza* skeleton was loaned to Shelton P. Applegate of the Los Angeles County Museum of Natural History for many years, where it remained unstudied. I borrowed PM-459 from the Field Museum in 1997 with Turnbull's encouragement. Final preparation of the specimen for study, including removal of sediment from the braincase, was completed at the University of Michigan.

Geological Age of the PM-459 *Zygorhiza* Skeleton

PM-459 was found in the Pachuta Marl member of the Yazoo Clay Formation in southwestern Choctaw County, Alabama. The Pachuta Marl and overlying Shubuta Clay member of the Yazoo Clay here are part of a coastal marine transgressive to condensed-section sequence tract (sequence Tejas A 4.3 of Haq et al., 1987) in the planktonic foraminiferal *Globorotalia cerroazulensis* interval zone (Mancini and Tew, 1991; Tew and Mancini, 1995; P17 of Berggren et al., 1995). The *Globorotalia cerroazulensis* interval zone is now considered the *Hantkenina alabamensis* highest-occurrence zone (E16 of Berggren and Pearson, 2005). The last appearance of *Hantkenina* is generally taken to mark the Eocene–Oligocene boundary. P17/E16 is latest Priabonian in age, late Eocene, in the middle to late part of magnetochron C13r, with an estimated numerical calibration in the range of 34.3–33.7 Ma (Berggren and Pearson, 2006).

Miller et al. (2008) studied the Pachuta Marl at St. Stephens Quarry southeast of Choctaw County and interpreted it to have a sequence boundary and hiatus within it, with a 1.1 million year interval of time, from 35.0 to 33.9 Ma, missing. If this hiatus is present near Melvin in Choctaw County, then it is unclear whether the Pachuta Marl archaeocete fauna that includes PM-459 is older than the hiatus, deposited in the interval from 35.4 to 35.0 Ma (in E15), or younger than the hiatus, deposited in the interval from 33.9 to 33.6 Ma (in E16–O1), or possibly both older in part and younger in part, spanning much of the interval from 35.4 to 33.6 Ma.

INSTITUTIONAL ABBREVIATIONS

AUMP — Auburn University Museum of Paleontology, Auburn, Alabama (U.S.A.)

FMNH — Field Museum of Natural History, Chicago, Illinois (U.S.A.)
 LACM — Los Angeles County Museum, Los Angeles, California (U.S.A.)
 LMNS — Louisiana Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana (U.S.A.)
 MMNS — Mississippi Museum of Natural Science, Jackson, Mississippi (U.S.A.)
 MNB — Museum für Naturkunde, Berlin (Germany)
 MSC — McWane Science Center, Birmingham, Alabama (U.S.A.)
 RMM — Red Mountain Museum collection at McWane Science Center, Birmingham, Alabama (U.S.A.)
 TMH — Teyler Museum, Haarlem (Netherlands)
 UAM — University of Alabama Museum of Natural History, Tuscaloosa, Alabama (U.S.A.)
 UM — University of Michigan Museum of Paleontology, Ann Arbor, Michigan (U.S.A.)
 USNM — U. S. National Museum, Washington, D.C. (U.S.A.)

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order CETACEA Brisson, 1762
 Suborder ARCHAEOCETI Flower, 1883
 Family BASILOSAURIDAE Cope, 1868

Zygorhiza True, 1908
Zygorhiza kochii (Reichenbach, 1847)
 Figs. 3–8, 10–11

Basilosaurus kochii Reichenbach in Carus, 1847, p. 13, pl. 2.
Zeuglodon hydrarchus Carus, 1849, p. 385, pl. 39.
Zeuglodon brachyspondylus (part), Müller, 1849, p. 9, pl. 3; p. 28, pl. 19–20; p. 31, pl. 26.
Zeuglodon brachyspondylus minor Müller, 1851, p. 240.
Zygorhiza brachyspondylus minor, True, 1908, p. 78.
Zygorhiza minor, Kellogg, 1928, p. 40.
Zygorhiza kochii, Kellogg, 1936, p. 101, figs. 29–75, pl. 10–17.
 Uhen, 2013a, p. 11, fig. 8.

Holotype.— MNB specimen Ma 43248 (previously 15324), a posterior cranium with occipital condyles (Müller, 1849, plate 3). Uhen (2013b) petitioned the International Commission on Zoological Nomenclature to make USNM 11962 the neotype of *Zygorhiza kochii*, arguing that the existing type, MNB Ma 43248, is non-diagnostic. I do not think replacement is justified (see below) and published a comment asking the ICZN to decline this request (Gingerich, 2015a).

Type locality.— Near Clarksville, in Clark County, Alabama (Müller, 1849, p. 20; Kellogg, 1936, p. 101). Decimal degree coordinates are approximately -87.893°E and 31.729°N . Note that 'near' can be up to 4.5 miles from Clarksville itself (Müller, 1849, p. 3).

Referred specimens.— The most important specimens included in *Zygorhiza kochii* are listed in Table 1.

Diagnosis.— *Zygorhiza kochii*, the only species of the genus recognized at present, is distinctive in being the smallest archaocete known from the Yazoo Formation of late Priabonian, late Eocene, age. Skeletally mature specimens have occipital condyles measuring 110–120 mm across their outer margins (Kellogg, 1936, p. 246–247), in contrast to contemporaneous *Pontogeneus brachyspondylus* (including *Cynthiacetus maxwelli*) measuring 142 mm (Uhen, 2005, p. 163) and *Basilosaurus cetoides* measuring 145 mm (Kellogg, 1936, p. 246–247). *Z. kochii* has posterior thoracic vertebrae (e.g., T11) measuring 69 mm in centrum length and 79 mm in transverse diameter (Kellogg, 1936, p. 143), in contrast to contemporaneous *P. brachyspondylus* (*C. maxwelli*) measuring 85+ mm in centrum length and 112 mm in transverse diameter (Uhen, 2005, p. 163), and *B. cetoides* measuring 302 mm in centrum length and 177 mm in transverse diameter (Kellogg, 1936, p. 246–247). *Zygorhiza* resembles contemporaneous *Pontogeneus* (including *Cynthiacetus*) in having unusually large vertebral arterial canals perforating the transverse processes of cervical vertebrae C3 and C4 (Kellogg, 1936, p. 133; Uhen, 2005, p. 158), which is a conspicuous difference from the smaller canals of slightly older *Dorudon* (Uhen, 2004, p. 69) and contemporaneous *Basilosaurus* (Kellogg, 1936, p. 39).

Age and distribution.— The type and referred specimens all come from the Yazoo Clay and equivalent Jackson Group formations of late Priabonian, late Eocene, age. *Zygorhiza kochii* is known from Jackson Group strata ranging from the U. S. state of Louisiana in the west through Mississippi and Alabama to the state of Georgia in the east (Table 1).

Discussion.— Reichenbach (in Carus, 1847) described the species *Basilosaurus kochii* based on a braincase in the Museum für Naturkunde in Berlin (Germany). Carus (1849) named the species *Zeuglodon hydrarchus* based on a skull in the Teyler Museum in Haarlem (Netherlands). Müller (1851) named the species *Zeuglodon brachyspondylus minor* for a “small *Zeuglodon* with short vertebrae,” referring to the sequence of vertebrae figured on plate 19 of his 1849 monograph. True (1908, p. 78) clearly stated that the latter, *Zeuglodon brachyspondylus minor*, is the type species of *Zygorhiza*. *Z. minor* is a junior synonym of the first available species-group name, *Z. kochii*, but *Z. minor* (type lost) is the basis for the genus *Zygorhiza*.

Uhen (2013b) asked the International Commission on Zoological Nomenclature to set aside the existing holotype of *Basilosaurus kochii* Reichenbach, 1847 (*Zygorhiza kochii*) and to designate a more complete specimen as the neotype. Uhen argued that this was to resolve questions of synonymy of *Zygorhiza kochii* and geologically older species in other genera (*Dorudon* and *Chrysocetus*). However, what *Zygorhiza* is as a genus depends not on the type specimen of the first-named species *Basilosaurus kochii*, but on the type specimen of the type species of the genus: *Zeuglodon brachyspondylus minor*. My sense of the issue (Gingerich, 2015a) is that *Zygorhiza kochii*, like all species, should be thought of as a population

of individual animals represented by a collection of similar specimens. Replacement of the existing holotype of *Z. kochii* by a neotype will not solve any pressing problem, nor will it change the sample of known specimens of *Zygorhiza kochii* in any way.

NEW SKELETON OF *ZYGORHIZA KOCHII*

FMNH PM-459 is a specimen of *Zygorhiza kochii* that includes a partial cranium, a dentary, a series of vertebrae, and a scapula. Each is described in turn. The teeth of PM-459 are fully erupted and it appears that vertebral epiphyses were solidly fused (although some are thin and eroded, exposing cancellous bone). This indicates that the specimen was adult and full-grown. There is as yet no evidence of dimorphism enabling determination of the sex of individual specimens of *Z. kochii*.

Cranium and Dentary

Cranium.— The cranium of PM-459 is in three pieces: (1) a portion of the frontal attached to the presphenoid; (2) much of the braincase; and (3) much of the left sphenoid, which was removed from the braincase to enable preparation of a cast of the endocranium. There is nothing about the sphenoid of the cranium that warrants separate description. Cranial elements are illustrated in Figure 3.

The presphenoid piece of the cranium of PM-459 is a robust midline bone approximately 170 mm long. It has a high and narrow cross section measuring approximately 65 × 20 mm anteriorly where it had a cartilaginous connection with the vomer. The vomer itself is not preserved. For the anterior one-third of its length the presphenoid bears the impression of the left internal narial passage dorsally on the left side, and a natural stone endocast of the right internal narial passage dorsally on the right side. For the remainder of its length the presphenoid is similarly rounded but more triangular in cross section. The dorsal surface of the posterior two-thirds of the presphenoid bears a midline impression of the olfactory stalk (cranial nerve I), which continues forward on the right side to the cribriform plate, which is preserved in cross section.

The midline impression of the olfactory stalk is flanked left and right by impressions of the optic nerve (cranial nerve II). These diverge anteriorly toward the positions of the left and right orbits, which are not preserved. Impressions of the left and right optic nerves are flanked laterally by common impressions for the left and right nerve bundles containing the oculomotor, trochlear, and ophthalmic branch of the trigeminal nerves (cranial nerves III, IV, and part of V) diverging toward the orbital fissure (also not preserved). On the right side, dorsal and anterior to the cribriform plate, there is a sediment-filled endocast of the frontal sinus. The presphenoid ends posteriorly in a cartilaginous connection with the sphenoid. Here the presphenoid measures approximately 40 mm high × 50 mm wide.

TABLE 1 — Principal specimens referred to *Zygorhiza kochii*. All are from upper Jackson Group formations of late Priabonian age. Clarksville localities of Albert Koch were about 4.5 miles SW of Clarksville itself (Müller, 1849). Geographic coordinates are in decimal degrees (WGS84), rounded to the nearest 0.001 degree. One one-hundredth of a decimal degree here is approximately equivalent to one kilometer on the ground. Localities generally have a recorded precision of the nearest quarter-section or ca. ±400 meters.

Specimen	Description	Settlement	State	East°	North°	Reference	Remarks
1 MNB Ma-43248	Type partial cranium	Clarksville	Alabama	-87.956	31.699	Müller (1849: 20)	Type of <i>Basilosaurus kochii</i>
2 TMH 8501	Type skull	Isnay	Alabama	-88.438	31.779	Kellogg (1936: 102)	Type of <i>Zeuglodon hydrarchus</i>
3 MNB Ma (?)	Type lumbar vert.	Clarksville	Alabama	-87.956	31.699	Müller (1849: 20)	Type of <i>Zeug. brachys. minor</i>
4 MNB Ma-43247	Occiput	Clarksville (?)	Alabama	—	—	Kellogg (1936: 102)	
5 MNB Ma-28384	Atlas	Clarksville	Alabama	-87.956	31.699	Müller (1849: 20)	
6 USNM 4673	L and R dentaries	Melvin	Alabama	-88.433	31.904	Kellogg (1936: 102)	
7 USNM 1599	Lumbar vertebrae	Montgomery	Mississippi	-92.901	31.655	Kellogg (1936: 102)	
6 USNM 4673	L and R dentaries	Melvin	Alabama	-88.433	31.904	Kellogg (1936: 102)	
8 USNM 4679	Partial skull, skeleton	Melvin	Alabama	-88.444	31.907	Kellogg (1936: 103)	
9 USNM 4748	Partial skull, subadult	Melvin	Alabama	-88.439	31.910	Kellogg (1936: 103)	
10 USNM 11962	Good skull, vertebrae	Melvin	Alabama	-88.443	31.909	Kellogg (1936: 104)	
11 USNM 12063	Partial skull, skeleton	Melvin	Alabama	-88.435	31.912	Kellogg (1936: 104)	
12 USNM 12335	Dentary, vertebrae	Melvin	Mississippi	-88.473	31.922	Kellogg (1936: 104)	
13 USNM 13773	Partial skull	Melvin	Alabama	-88.441	31.931	Kellogg (1936: 104)	
14 USNM 13774	L and R dentaries	Flint River	Georgia	-83.924	31.895	Kellogg (1936: 105)	
15 USNM 16638	Skull	Melvin	Alabama	-88.450	31.918	Kellogg (1936: 105)	Millsaps College specimen
16 USNM 16639	Skull, subadult	Jackson	Mississippi	-90.159	32.323	Kellogg (1936: 105)	Millsaps College specimen
17 LACM 25178	Skull, vertebrae	Sherman Hill	Mississippi	-89.387	32.273	Fierstine & Applegate (1974: 15)	
18 LMNS VP-160	Partial skeleton	Melvin	Alabama	-88.437	31.916	Lancaster (1990: 118)	
19 RMM 2739/AUMP 2368	Skull/partial skeleton	Clarksville	Alabama	-87.974	31.729	Lancaster (1990: 118)	Five miles W of Clarksville AL
20 MMNS VP-5021	Partial skeleton	Benton	Mississippi	-90.334	32.884	Starnes & Berry (2010: 6)	
21 MSC 9508	Partial Skull	Brooklyn	Alabama	-86.765	31.260	Ebersole (pers. comm., 2014)	
22 UAM PV-2000.1.1	Partial skull, skeleton	Melvin	Alabama	-88.438	31.926	Uhen (pers. comm., 2015)	
23 FMNH PM-459	Partial skull, skeleton	Melvin	Alabama	-88.435	31.906	This study	

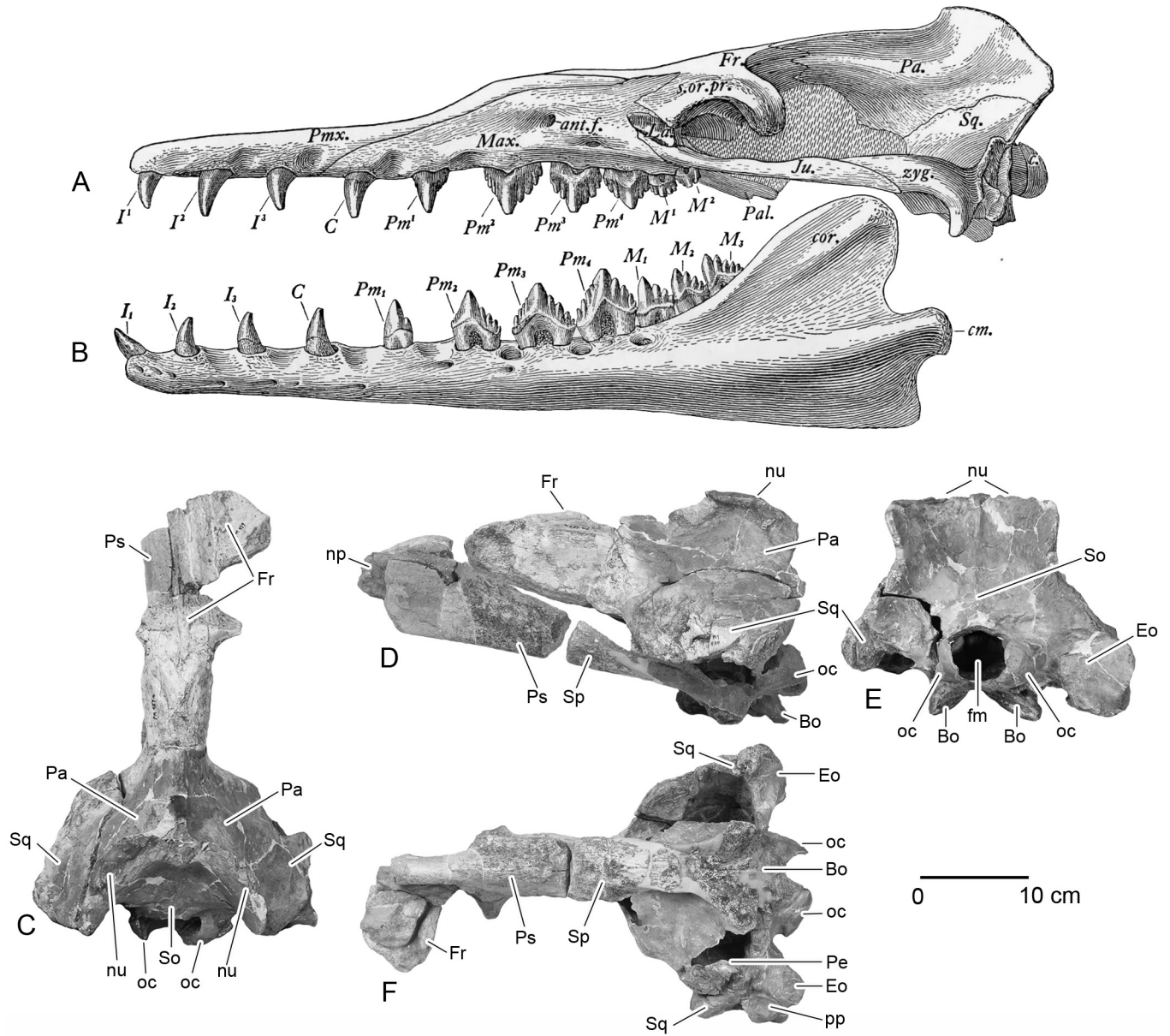


FIGURE 3 — Cranium of *Zygorhiza kochii*. A–B, cranium and dentary of USNM 11962 in left lateral view, from Kellogg (1936). C–F, partial cranium of FMNH PM-459, in dorsal, left lateral, posterior, and ventral view. Note that the right side of the PM-459 cranium is better preserved than the left side. Comparable parts of PM-459 are very similar in size and form to those of USNM 11962 described by Kellogg. Abbreviations: *ant. f.*, antorbital foramen; *Bo*, basioccipital; *c.*, condyle; *C*, canine tooth; *cm*, mandibular condyle; *cor.*, coronoid process of dentary; *Eo*, exoccipital; *fm*, foramen magnum; *Fr*, frontal; *I*, incisor; *Ju*, jugal; *La*, lacrimal; *M*, molar; *Max*, maxilla; *np*, nasal passage (stone endocast); *nu*, nuchal crest; *oc*, occipital condyle; *Pa*, parietal; *Pal*, palatine; *Pe*, periotic; *Pm*, premolar; *Pmx*, premaxilla; *pp*, posterior process of periotic; *Ps*, presphenoid; *s. or. pr.*, supraorbital process of frontal; *So*, supraoccipital; *Sp*, sphenoid; *Sq*, squamosal; *zyg.*, zygomatic process of squamosal.

The braincase of PM-459 is approximately 320 mm long, as preserved, and includes the posterior portion of the left and right frontal bones at its anterior end. These are fused at the midline, but sutures between the frontals and parietals are well marked dorsally and on the left side of the midcranial pons or intertemporal constriction. The surface of the midcranial

pons is less well preserved on the right side. Left and right supraorbital processes that formed the frontal shield are not preserved. Impressions of the olfactory stalk and of the left and right optic nerves are present on the ventral surface of the frontals. Left and right parietal bones form much of the dorsolateral surface of the braincase of PM-459, as in

other basilosaurids, extending back from the frontal suture anteriorly to the nuchal crest posteriorly, and extending down from the poorly preserved sagittal crest dorsally to the frontals and squamosals ventrolaterally. Intervening dorsal extensions of the sphenoid (left and right alisphenoids) are not preserved.

The braincase of PM-459 is floored anteriorly by the basisphenoid and posteriorly by the basioccipital. These bones are fused and the position of the suture between them is obscured. The basisphenoid has a rounded, more or less hexagonal cross section anteriorly, measuring approximately 35 mm high \times 55 mm wide, for its cartilaginous connection with the presphenoid. The basisphenoid becomes thinner and wider posteriorly where it merges with the basioccipital. Together these bones underlie the space that housed the brain. The basioccipital has a prominent basilar or falcate process on the left and right side, which is best preserved on the right side.

The occipital condyle is well preserved on the right side, where it measures approximately 49 mm high and 40 mm wide. Doubling the distance from the lateral margin of the right occipital condyle to the midline of the skull (and the midline of the foramen magnum, 60 mm) indicates that the distance across the lateral surfaces of the left and right condyles was

approximately 120 mm (similar to that in the type specimen MNB Ma 43248 illustrated by Müller, 1849, plate 3). The foramen magnum is elliptical, and measures approximately 65 mm wide and 40 mm high. The nuchal surface of the supraoccipital rises 145 mm above the foramen magnum to the apex of the nuchal crest. The nuchal crest is 155 mm wide at its widest, and rectangular when viewed posteriorly. The exoccipital portion of the occiput is well preserved on the right side, missing only its ventral process. Again measuring to the midline, the width across both exoccipitals appears to have been about 270 mm. All occipital bones, basioccipital, supraoccipital, and exoccipital, are solidly fused into one element.

Both squamosals are damaged ventrally and laterally, and both glenoid fossae for articulation with the dentaries are missing. The petrosal or periotic is present on the right side, but this too is broken, exposing calcite filling part of one turn of the cochlea (compare with cochleae in Ekdale and Racicot, 2014). The posterior process of the periotic is present on the right side of the braincase where it is wedged between the squamosal and exoccipital.

Dentary.— The left dentary, illustrated in Figure 4, is reasonably well preserved, although the teeth are all damaged

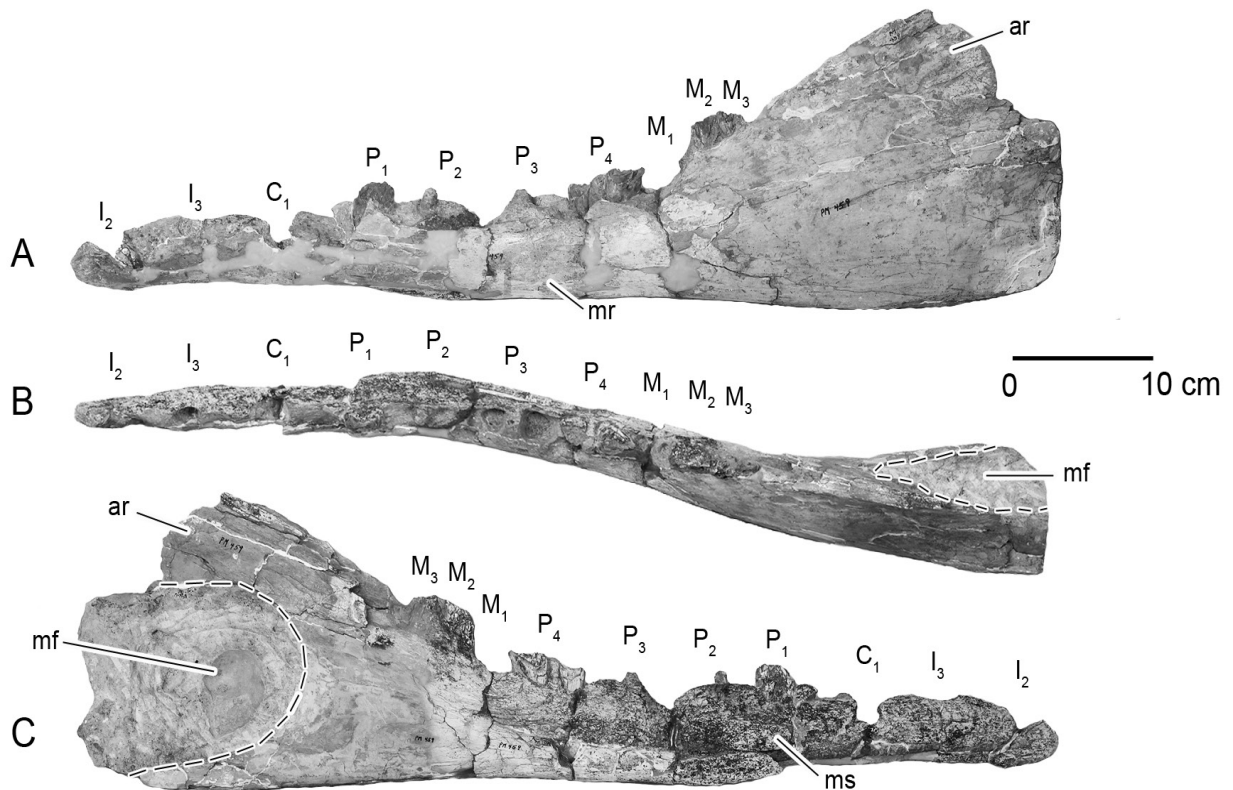


FIGURE 4 — Left dentary of *Zygorhiza kochii*, FMNH PM-459, in lateral (A), occlusal (B), and medial view (C). Alveoli, roots, or bases of tooth crowns are present representing the positions of incisor I₂ through molar M₃. Note the presence of a double-rooted P₁, a mandibular symphysis extending posteriorly to a point below P₂, and a very large mandibular foramen (dashed line) on the medial side of the dentary. Abbreviations as in figure 3, plus: *ar*, ascending ramus; *mf*, mandibular foramen; *mr*, mandibular ramus; *ms*, mandibular symphysis.

or missing. It measures 710 mm long as preserved, including an impression of the mandibular condyle (the condyle itself is missing). There is a small amount of mandibular ramus missing at its anterior end. The mandibular ramus is shallow, measuring only about 58 mm in depth below P₁, and measuring about 75 mm in depth below M₁. Left and right dentaries were unfused, and the mandibular symphysis extended back to a point under P₂, some 260 mm from the front of the jaw. The dentary has no alveolus for I₁, probably because this was a small tooth that was only shallowly embedded in bone and the occlusal surface of the dentary here is damaged. Alveoli are present for single-rooted I₂₋₃ and C₁. P₁ and all following teeth are double-rooted. The crown of P₁ measures about 30 mm in length × 15 mm in width. The anterior root of P₂ remains, but the rest of the tooth is missing. P₃ is represented by alveoli only. P₄ retains both roots and the base of the crown, which measures about 56 × 19 mm in length and width. M₁ is missing and alveoli remaining for this tooth are very small. M₂ and M₃ are represented by roots only. Diastemata separate all teeth anterior to P₃, but teeth following P₃ were all closely appressed.

The mandibular foramen, on the medial surface of the dentary below the ascending ramus, is very large, measuring approximately 115 mm dorsoventrally. This is sediment-filled, and the sediment preserves a natural mold of the posterior surface of a left tympanic bulla. The bulla itself is not with the specimen.

Discussion.— There is little about the FMNH PM-459 cranium that differs from USNM 11962, the cranium of *Zygorhiza kochii* illustrated by Kellogg (1936, pp. 107–108, figs. 29–31a). The nuchal crest of PM-459 is broader and possibly higher. Broken as it is, PM-459 reveals details of internal architecture of the cranium not seen in USNM 11962. PM-459 is also important in revealing the size and form of the endocranium, enabling estimation of the volume and weight of the brain, and estimation of brain weight relative to body weight (see below).

The PM-459 dentary is important in showing that all permanent teeth were fully erupted, meaning that the individual represented was fully adult. The PM-459 dentary shows that teeth anterior to the lower first premolar were single rooted, whereas P₁ itself and all following teeth were double-rooted (Kellogg, 1936, p. 121).

Vertebral Column

Cervical vertebrae of the FMNH PM-459 specimen of *Zygorhiza kochii* include a well preserved atlas or C₁, portions of C₄, C₅, and C₆, and a well preserved C₇ (Fig. 5). Measurements of cervical vertebrae are given in Table 2. The axis, C₂, and the following cervical, C₃, are not represented here. Thoracic vertebrae include a complete series from T₁ through T₁₁ (Figs. 6–7). Thoracics T₁₂ through T₁₅ are not represented. Lumbar include L₁? and the neural spine of L₂? (identifications are uncertain; Fig. 8). Measurements of thoracic and lumbar vertebrae are listed in Table 3.

Vertebrae are identified to position from labels with the specimens, and from comparison with vertebrae of *Z. kochii* described and illustrated by Kellogg (1936). This does not mean that vertebral positions are known with certainty. The thoracic series for *Z. kochii* described by Kellogg (1936) may not be complete (Uhen, 2013a, p. 5; see below), and there is no complete series of lumbar or caudal vertebrae for *Z. kochii*.

Cervical C1.— The atlas is a complex and massive element in basilosaurids. The atlantal intercentrum is not developed to the extent of the postatlantal centra. The atlas is essentially a ring of bone surrounding the neural canal (Fig. 5A–B). This is surmounted dorsally by a curved neural arch. The neural canal is floored ventrally and anteriorly by articular facets for the occipital condyles of the skull, and ventrally and posteriorly by a curved surface for the dens of the axis. Below the facet for the dens, there is a well developed hypapophysis angled ventrally and posteriorly. The anterolateral margins of the neural canal bear extensions of facets for the occipital condyles, and the posterolateral margins bear oval facets for the anterior articular surfaces of the axis. There is a prominent transverse process on each side of C₁ lateral to these articular facets. This is best preserved on the right side in PM-459, where the dorsal angle of the transverse process bears a thickened boss. The ventral part of the transverse process is somewhat damaged, and it is not clear what this looked like. There is a 5 mm diameter vertebral foramen perforating the base of the transverse process on each side, which is a clear difference from atlantal vertebrae of *Dorudon atrox* (several of which retain, at most, a nutrient foramen in this position that does not penetrate the transverse process).

The maximum length of C₁ in PM-459 is 72 mm, the minimum length separating anterior and posterior articular facets is 40 mm, and the maximum width (doubling the width of the right half) was about 202 mm. The neural canal is hour-glass shaped, and the opening measures 56 mm dorsoventrally, 47 mm transversely in the dorsal part, and 39 mm transversely in the ventral part.

Cervical C4.— C₄ is represented by the dorsal left quarter or so of a centrum, part of the left neural arch, and a part of the left transverse process (Fig. 5G–H). The importance of this specimen is in showing that the neural canal is both wide and high, and in showing that the vertebral foramina of middle cervical vertebrae were very large (Fig. 5G). This partial vertebra could represent either C₃ or C₄, which, even when complete, are nearly identical.

Cervical C5.— The centrum is all that is known for C₅, and even this is incomplete (Fig. 5I–J). It is identified as C₅ because of the base for a relatively large, ventrally-projecting transverse process on the left side similar to, but smaller than, that seen on C₆. The centrum of C₅ is slightly wedge-shaped, with the anteroposterior length of the centrum being slightly greater ventrally than it is dorsally.

Cervical C6.— The sixth cervical vertebra is represented by a complete centrum lacking the neural arch and by most of each transverse process (Fig. 5K–L). C₆ has a notably longer centrum than C₅, and on the right side it retains the base of the more robust, ventrally-projecting transverse process

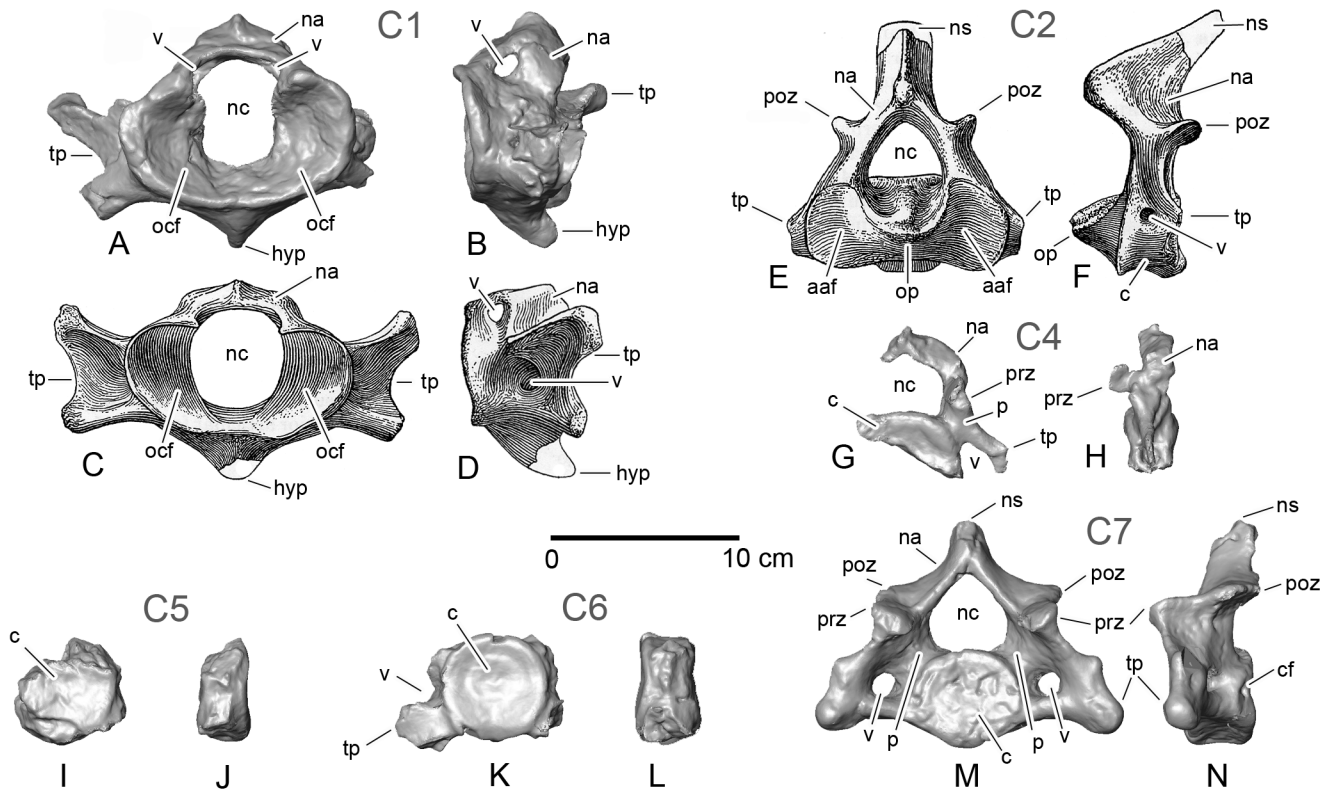


FIGURE 5 — Cervical vertebrae of *Zygorhiza kochii*. A–B, C1 (atlas) of FMNH PM-459 in anterior and left lateral view. C–D, C1 (atlas) of USNM 11962 in anterior and left lateral view (reversed from Kellogg, 1936, fig. 39). E–F, C2 (axis) of USNM 4679 in anterior and left lateral view (reversed from Kellogg, 1936, fig. 41). G–H, C4 of PM-459 in anterior and left lateral view. I–J, C5 of PM-459 in anterior and left lateral view. K–L, C6 of PM-459 in anterior and left lateral view. M–N, C7 of PM-459 in anterior and left lateral view. Images of PM-459 are orthographic laser scans. Note the similarity of C1 in PM-459 to that of USNM 11962, the vertebrarterial foramen perforating left and right transverse processes in PM-459, and evidence of a large vertebrarterial foramen on C4 in PM-459. C2 and C3 are not present in PM-459. Abbreviations: aaf, atlas articular facet; c, centrum; cf, capitular facet; hyp, hypophysis; na, neural arch; nc, neural canal; ns, neural spine; ocf, occipital condyle facet; op, odontoid process (dens); p, pedicle; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; v, vertebrarterial foramen perforating a neural arch or transverse process.

characteristic of C6 vertebrae. It is not possible to measure the width or height of the vertebrarterial canal, but this was large. The centrum of C6 is even more conspicuously wedge-shaped than that of C5.

Cervical C7.— This is the most complete of the cervical vertebrae, missing only the tip of the neural spine (Fig. 5M–N). The centrum is again notably longer than that of C6. It is almost circular in anterior view, but is shaped more like a dorsoventrally flattened ellipse when seen in posterior view. C7 has distinct demifacets for rib heads on the posterior surface of the centrum, which extend the lateral margins of the posterior surface. The neural canal is high and tear-shaped in cross section. Pre- and postzygapophyses are flat and slightly inclined ventromedially. Transverse processes are broad, with rounded bosses marking their ventrolateral corners, and smaller bosses higher on the lateral margins. The transverse processes have vertebrarterial foramina, but these are much smaller and more rounded than the one preserved on T4. The neural spine of C7 measures 23.7 mm anteroposteriorly at the

base. It is broken at the tip so its full dorsoventral length cannot be measured.

Measurements of cervical vertebrae are summarized in Table 2.

Thoracic T1.— The first thoracic vertebra is similar to the last cervical but differs in having a higher neural spine and in lacking transverse processes (Fig. 6A–B). Anterior and posterior surfaces of the centrum are dorsoventrally flattened ellipses, with demifacets for rib heads at their lateral margins. The anterior and posterior surfaces of the centrum are cancellous as if epiphyses are missing, but the surfaces of the demifacets are intact and smooth, and it is more likely that the anterior and posterior centrum surfaces were thin and, post mortem, have simply eroded through to cancellous bone in places. The neural canal is again high but oval in cross section, with the widest part of the oval being at about the level of the pre- and postzygapophyses. Pre- and postzygapophyses are flat and slightly inclined ventromedially. Tubercular facets are not well preserved, but these too were at the level

of the zygapophyses. The neural spine measures 24.7 mm anteroposteriorly at the base. It is broken at the tip so its full length cannot be measured.

Thoracic T2.— The second thoracic is similar to T1 but larger and more robust (Fig. 6D–E). The anterior surface of the centrum is damaged and its shape cannot be determined. The posterior surface of the centrum is ‘D’-shaped, with the flat part of the ‘D’ being the dorsal margin. Capitular demifacets are large on the posterior surface. The neural canal is again high and oval in cross section, but the widest part of the oval is well below the zygapophyses. The prezygapophyses are missing, but the postzygapophyses are well preserved, flat, and directed ventrally with only slight inclination toward the midline. The tubercular facet for the second rib is well preserved on the right side. It forms the end of a relatively long diapophysis, with a flat oval articular surface facing laterally and only slightly ventrally. This tubercular surface measures 30 mm dorsoventrally and 24 mm anteroposteriorly. A distinct metapophysis rises some 12–14 mm above the tubercular surface. The diapophysis and tubercular facet are high on the neural arch, emerging from the base of the vertebral lamina. The neural spine measures 34.0 mm anteroposteriorly at the base. Much of the dorsal part of the spine is missing so its full length cannot be measured.

Thoracic T3.— T3 is generally well preserved, but anterior and posterior surfaces of the centrum are eroded, and the dorsal end of the neural spine is missing (Fig. 6G–H). The anterior surface of the centrum is broadly oval in shape, with the widest portion just below the capitular facets. The posterior surface is ‘D’-shaped, with capitular facets at the apices of the ‘D,’ as on T2. The neural canal is high and wide, with a rounded pentagonal cross section. The widest part of the canal is at the junction between the vertebral laminae and pedicles, well below the level of the zygapophyses and just below the bases of the diapophyses. Pre- and postzygapophyses are well preserved, flat, and dipping slightly anteriorly. Tubercular facets are at the ends of diapophyses emerging from the bases of the vertebral laminae. The diapophyses are long, but shorter than those on T2. Tubercular facets are almost circular, with a diameter of 28 mm. Metapophyses rise approximately 12 mm

above the tubercular facets. The neural spine measures 37.0 mm anteroposteriorly at the base. The dorsal end of the spine is missing so its full length cannot be measured.

Thoracic T4.— T4 is well preserved, missing only a part of the tubercular facet and metapophysis on the right side, and the end of the neural spine dorsally (Fig. 6J–K). The anterior surface of the centrum is intact and triangular in shape, with corners rounded for each capitular facet and rounded ventrally. The posterior surface is slightly eroded and ‘D’-shaped, with large capitular facets at the apices as on the the posterior surfaces of T2 and T3. The neural canal is high and wide, with a rounded triangular cross section. The widest part is at the level of the pedicles, well below the prezygapophyses and diapophyses. Pre- and postzygapophyses are well preserved, flat, and dipping very slightly anteriorly. Tubercular facets are again at the ends of diapophyses arising high on the pedicles. The diapophyses are long but shorter than those on T2 and T3. Tubercular facets are slightly elliptical, with the long 28 mm axis being almost dorsoventral and the shorter 26 mm axis being anteroposterior. Metapophyses rise approximately 15 mm above the tubercular facets. The neural spine measures 38.3 mm anteroposteriorly at the base. The dorsal end of the spine is missing so its full length cannot be measured. The neural spine shows a small but distinct change of orientation, with the dorsal part of the spine being more vertical than the base.

Thoracic T5.— The fifth thoracic is generally well preserved, but the tubercular facet and metapophysis are missing on the left side, anterior and posterior surfaces of the centrum are eroded, and the dorsal end of the neural spine is missing (Fig. 6M–N). Both anterior and posterior surfaces of the centrum are ‘D’-shaped, like posterior surfaces of preceding centra, with again capitular facets at the apices. The neural canal is high and wide, with a rounded triangular cross-section like that of T4. The widest part of the neural canal is at the level of the pedicles, below the prezygapophyses and diapophyses. Prezygapophyses are well preserved, flat, and dipping very slightly anteriorly. Postzygapophyses are eroded but can be seen to face ventrally and slightly posteriorly. Tubercular facets are at the ends of diapophyses

TABLE 2 — Measurements of cervical vertebrae of *Zygorhiza kochii*, FMNH PM-459. Measurements are in mm. Abbreviations: *ant.*, anterior; *for.*, foramen; *hgt.*, height; *post.*, posterior; *vertebrart.*, vertebrarterial; *wid.*, width.

Vertebra	Centrum length	Centrum ant. wid.	Centrum ant. hgt.	Centrum post. wid.	Centrum post. hgt.	Neural canal wid.	Neural canal hgt.	Vertebrart. for. wid.	Vertebrart. for. hgt.
C1	—	—	—	—	—	47.0	39.0	5.0	5.0
C2	—	—	—	—	—	—	—	—	—
C3	—	—	—	—	—	—	—	—	—
C4	26.8	—	—	—	—	20.0	31.5	17.0	—
C5	27.1	—	—	—	—	—	—	—	—
C6	33.3	55.3	55.0	55.6	52.0	—	—	—	—
C7	35.4	58.0	51.3	63.5	49.2	42.7	42.0	17.5	14.0

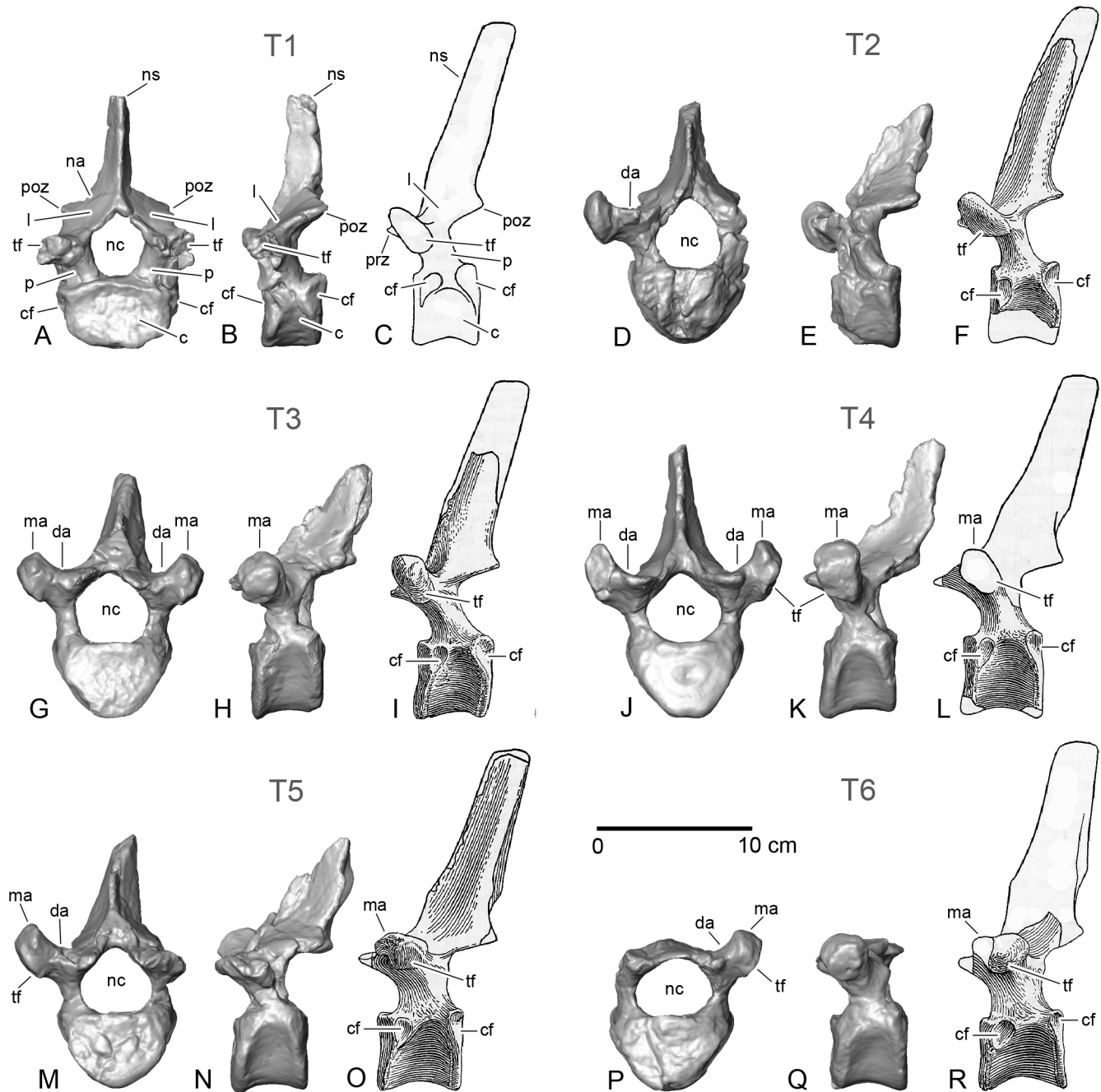


FIGURE 6 — Anterior thoracic vertebrae of *Zygohiza kochii*. **A–B**, T1 of FMNH PM-459 in anterior and left lateral view. **C**, T1 of USNM 11962 in left lateral view (reversed from Kellogg, 1936, fig. 42). **D–E**, T2 of PM-459 in anterior and left lateral view. **F**, T2 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 43). **G–H**, T3 of PM-459 in anterior and left lateral view. **I**, T3 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 44). **J–K**, T4 of PM-459 in anterior and left lateral view. **L**, T4 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 45). **M–N**, T5 of PM-459 in anterior and left lateral view. **O**, T5 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 46). **P–Q**, T6 of PM-459 in anterior and left lateral view. **R**, T6 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 47). Images of PM-459 are orthographic laser scans. Note similarity of anterior thoracics of PM-459 to those described by Kellogg. Note also the large and relatively high neural canals of *Z. kochii* anterior thoracics. Abbreviations: *c*, centrum; *cf*, capitular facet; *da*, diapophysis; *l*, lamina; *ma*, metapophysis; *na*, neural arch; *nc*, neural canal; *ns*, neural spine; *p*, pedicle; *poz*, postzygapophysis; *prz*, prezygapophysis; *tf*, tubercular facet.

arising from the junction of vertebral laminae and pedicles. The diapophyses are long, but shorter than those on preceding vertebrae. The right tubercular facet is slightly elliptical, with the long axis measuring 25.5 mm and the shorter axis measuring 22.6. This tubercular facet faces laterally but more ventrally than those on preceding thoracics. The metapophysis rises approximately 12 mm above the tubercular facet. The neural spine measures 44.9 mm anteroposteriorly at the base. The dorsal end of the spine is missing so its full length cannot be measured and it is difficult to determine whether there is a change of orientation of the dorsal part of the spine.

Thoracic T6.— T6 has an intact centrum and neural arch but is missing zygapophyses, the right diapophysis, and the whole neural spine (Fig. 6P–Q). The anterior surface of the centrum is eroded, but the posterior surface is intact. Both are ‘D’-shaped as are preceding centra. The neural canal appears more elliptical than triangular in cross section, but this is probably due to improper reconstruction of the dorsal surface of the neural canal filling some of its dorsal projection. The widest part of the canal is at the level of the middle of the pedicles. The diapophysis is shorter than that on preceding thoracics. The left tubercular facet is circular in outline, 25.5 mm in diameter, and distinctly folded, with the dorsal half facing laterally and the ventral half facing ventrolaterally. The metapophysis rises only about 5 mm above the tubercular facet.

Thoracic T7.— The seventh thoracic is generally well preserved, but the tubercular facet and metapophysis are missing on the left side, anterior and posterior surfaces of the centrum are eroded, and much of the neural spine is missing (Fig. 7A–B). Anterior and posterior surfaces of the centrum are ‘D’-shaped if capitular facets are included, forming the apices, but more elliptical in cross section if capitular facets are excluded. The neural canal is high and wide, with a rounded triangular cross section like that of T4 and T5. The widest part of the neural canal is at the level of the pedicles, below the prezygapophyses and diapophyses. Prezygapophyses are poorly preserved, but these appear to be narrow and closer to the midline than those on more anterior thoracics. Postzygapophyses are badly eroded. The tubercular facet on the right side is at the end of a short and robust diapophysis arising from the junction of the vertebral laminae and pedicles. The right tubercular facet is circular, with both axes measuring about 24.0 mm. This tubercular facet is flat, and faces laterally and ventrally. The metapophysis rises little above the tubercular facet. It is broken but appears to have projected more anteriorly than metapophyses on preceding thoracics. The neural spine measures 44.5 mm anteroposteriorly at the base. Much of the spine is missing so its full length cannot be measured.

Thoracic T8.— T8 is a well preserved centrum and neural arch, with diapophyses, tubercular facets, and metapophyses intact, lacking the neural spine (Fig. 7D–E). The anterior surface of the centrum is shaped like a rounded triangle with capitular facets at the dorsolateral apices. The posterior surface is similarly shaped without the capitular facets. The neural canal is high and wide, with a more rounded and less

triangular cross section than those of preceding thoracics. Zygapophyses are too poorly preserved to be informative. Diapophyses are short and robust with relatively small tubercular facets and much more massive metapophyses than those of preceding thoracics. Tubercular facets are elliptical surfaces facing ventrolaterally, with a long axis of 28 mm inclined anteromedially and ventrally, and a short axis of 18 mm oriented perpendicular to this. Metapophyses rise 25 mm anterodorsally and medially relative to the tubercular facets. Nothing can be said about the neural spine.

Thoracic T9.— The ninth thoracic vertebra is intact except for the prezygapophyses and metapophyses (Fig. 7G–H). Anterior and posterior surfaces of the centrum are dorsoventrally flattened ellipses. Capitular facets are on incipient parapophyses or transverse processes and no longer part of the anterior or posterior centrum surface. Tubercular facets are on diapophyses arising from the base of the pedicles, with metapophyses now arising from laminae of the neural arch. The neural canal is high and wide, and even more rounded in cross section than that of T8. Nothing can be said about the prezygapophyses but the postzygapophyses are long anteroposteriorly and narrow mediolaterally, with articular surfaces separated by a gap of 20.5 mm. Articular surfaces of the postzygapophyses face ventrally and slightly posteriorly and laterally. Capitular and tubercular facets are close to each other, circular in outline, and similar in size at 20 mm diameter. Both face laterally. T9 is the only thoracic with a nearly intact neural spine. This is inclined slightly posteriorly. The base of the spine is 44.7 mm long anteroposteriorly, and it rises 110 mm high above the top of the neural canal (some 206 mm above the base of the centrum).

Thoracic T10.— T10 is preserved like T9 except that most of the neural spine is missing (Fig. 7J–K). Anterior and posterior surfaces of the centrum are again shaped like dorsally-flattened ellipses. Capitular and tubercular facets for rib articulation are on common 19 mm long parapophyses, and the facets themselves, similar in size to those on T9, are here confluent. The neural arch is high and wide like that of T9. Postzygapophyses are like those on T9 but even closer to the midline. This vertebra, for whatever reason, is much more densely mineralized than preceding vertebrae.

Thoracic T11.— The eleventh thoracic is basically a centrum with parapophyses and the bases of pedicles (Fig. 7M–N). Anterior and posterior surfaces of the centrum are shaped like dorsally-flattened ellipses. Both are somewhat damaged, making them difficult to measure. Capitular and tubercular facets, now merged, are on 26 mm long parapophyses that are some 33 × 25 mm in diameter. T11 is the only PM-459 thoracic that lacks a neural arch. T11 is densely mineralized like T12.

Measurements of thoracic vertebrae are listed in Table 3.

Lumbar L1?— This vertebra is identified as L1 (Fig. 8B–C), but it could be a posterior thoracic. It is identified as L1 because it has the bases of robust transverse processes and because it is similar in size to T11 described here (more posterior lumbar would be larger). Anterior and posterior surfaces of the centrum are circular in outline, with the outline

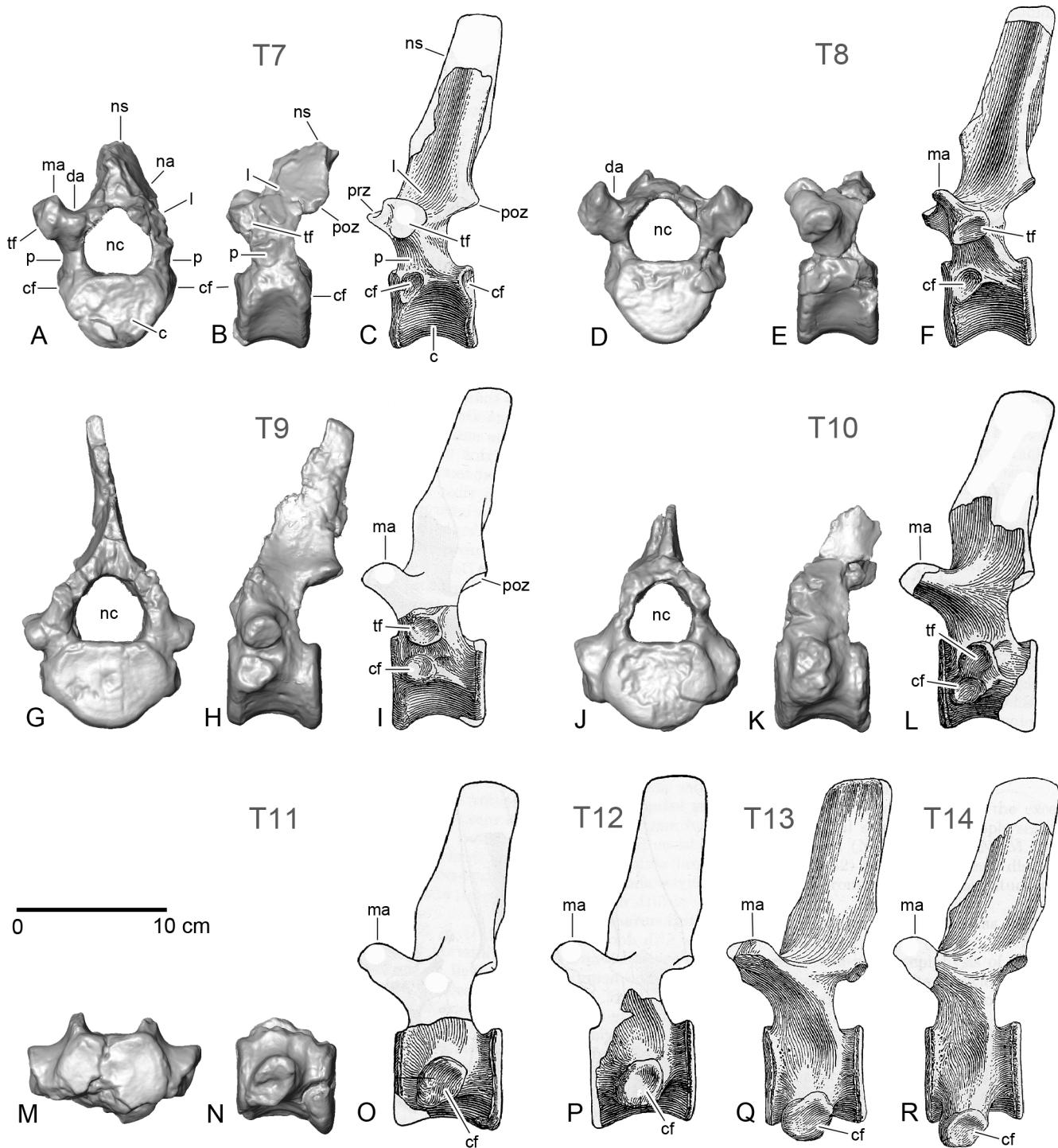


FIGURE 7 — Middle and posterior thoracic vertebrae of *Zygorhiza kochii*. **A–B**, T7 of FMNH PM-459 in anterior and left lateral view. **C**, T7 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 48). **D–E**, T8 of PM-459 in anterior and left lateral view. **F**, T8 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 49). **G–H**, T9 of PM-459 in anterior and left lateral view. **I**, T9 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 50). **J–K**, T10 of PM-459 in anterior and left lateral view. **L**, T10 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 51). **M–N**, T11 of PM-459 in anterior and left lateral view. **O**, T11 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 52). **P–R**, T12, T13, and T14 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, figs. 53–55). Images of PM-459 are orthographic laser scans. Note similarity of middle and posterior thoracics of PM-459 to those described by Kellogg. Note also the large and relatively high neural canals of *Z. kochii* middle thoracics. Abbreviations: *c*, centrum; *cf*, capitular facet; *da*, diapophysis; *l*, lamina; *ma*, metapophysis; *na*, neural arch; *nc*, neural canal; *ns*, neural spine; *p*, pedicle; *poz*, postzygapophysis; *prz*, prezygapophysis; *tf*, tubercular facet.

flattened dorsally and slightly flattened ventrally. The neural canal, like those of preceding thoracics, is high and wide. Prezygapophyses arise from the neural laminae high on the neural arch, and their articular surfaces are small and slope ventrally, medially, and slightly anteriorly. There is a small but prominent pit for a connective ligament at the posterior margin of the articular surface. Postzygapophyses are broken and missing. The neural spine measures 43.8 mm long anteroposteriorly at the base, making it similar in size to preceding thoracics. The neural spine is inclined slightly posteriorly. Its tip is missing, so the total length cannot be measured.

Lumbar L2?— All that remains of the vertebra identified as L2 is the left prezygapophysis on a portion of the neural arch and an intact neural spine (Fig. 8D–E). The dorsal surface of the neural canal is preserved, showing that this was large. The prezygapophysis is like that on L1?, but there is no associated ligamentous pit. The neural spine measures 57.3 mm anteroposteriorly at the base and 48.5 mm anteroposteriorly at the top, and it rises 112 mm above the top of the neural canal. An anteroposterior length of the neural spine so different from that of L1? makes it likely that this neural arch and spine came from a lumbar vertebra more posterior than L2.

Measurements of lumbar vertebrae are included in Table 3.

Discussion.— A vertebral centrum length profile for *Zygorhiza kochii* is illustrated in Figure 9. Parallel gray lines show an expected profile for the species, based on measurements of USNM specimens reported in Kellogg (1936). The central gray line is the average profile (sample size at a vertebral

position is often one), and flanking lines are expectations of plus and minus two standard deviations, plotted to give some idea of the expected range of variability. Kellogg assumed a vertebral count of 58 vertebrae, partitioned into 7 cervical, 15 thoracic, 15 lumbar, and 21 caudal vertebrae. Uhen (2013a, p. 5) mentioned, without documentation, that *Zygorhiza* had 17 thoracic vertebrae (this is based on RMM 2739/AUMP 2368, Mark D. Uhen, pers. comm., 2015). The profile here, based on measurements in Kellogg (1936), shows that the total numbers for lumbar and caudal vertebrae are also questionable.

The solid circles and heavier black line in Figure 9 show the profile of centrum length for FMNH PM-459 reported in Tables 2 and 3. Abrupt increase in centrum length between vertebrae labeled 15 and 16 (between T8 and T9) suggests that one or more vertebrae may be missing in PM-459, but centrum shape and the conformation of rib facets on T8 through T11 in PM-459 match those of Kellogg's specimens closely (Fig. 7), so no simple adjustment will explain the discrepancy. The vertebral column of *Zygorhiza kochii* is surprisingly poorly studied considering the number of specimens known that preserve vertebrae.

A salient feature of cervical C1 in PM-459 is retention of a vertebral foramen perforating the base of the transverse process on each side. These are relatively small in PM-459 and hidden by facets for articulation with the cranium and C2 in anterior and posterior view, respectively, but they are nevertheless well developed. Kellogg (1936, p. 131) wrote that the atlas vertebrae available to him (USNM 4678 and 11962) are “perforated at the base by a large vertebral foramen,”

TABLE 3 — Measurements of thoracic and lumbar vertebrae of *Zygorhiza kochii*, FMNH PM-459. Measurements are in mm. Abbreviations: *ant.*, anterior; *cent.-cent.*, center-to-center; *hgt.*, height; *len.*, length; *post.*, posterior; *wid.*, width.

Vertebra	Centrum length	Centrum ant. wid.	Centrum ant. hgt.	Centrum post. wid.	Centrum post. hgt.	Neural canal wid.	Neural canal hgt.	Neural spine base len.	Rib facet separation cent.–cent.
T1	38.1	65.3	45.0	68.2	45.0	36.6	41.4	24.7	38.8
T2	42.5	68.0	—	63.8	47.5	42.8	48.2	34.0	47.5
T3	45.2	61.6	48.3	67.1	43.7	48.1	48.7	37.0	52.5
T4	47.7	61.5	48.9	63.2	45.9	50.0	47.8	38.3	53.6
T5	48.6	62.5	47.0	66.8	47.0	47.1	44.9	40.2	50.0
T6	49.1	63.1	47.1	71.2	48.7	50.8	—	—	50.5
T7	50.0	66.3	47.6	67.5	48.7	47.2	48.2	44.5	44.4
T8	53.2	66.8	53.7	65.0	53.6	48.5	45.1	—	39.0
T9	62.4	81.2	56.7	70.2	56.3	49.9	48.5	44.7	28.7
T10	63.1	75.1	57.6	69.8	58.9	43.4	41.3	—	18.4
T11	65.8	73.8	—	67.6	59.7	39.9	—	—	12.1
T12	—	—	—	—	—	—	—	—	—
T13	—	—	—	—	—	—	—	—	—
T14	—	—	—	—	—	—	—	—	—
T15	—	—	—	—	—	—	—	—	—
L1	66.0	72.6	66.7	73.4	58.7	36.8	39.8	43.8	—
L2	—	—	—	—	—	—	—	57.3	—

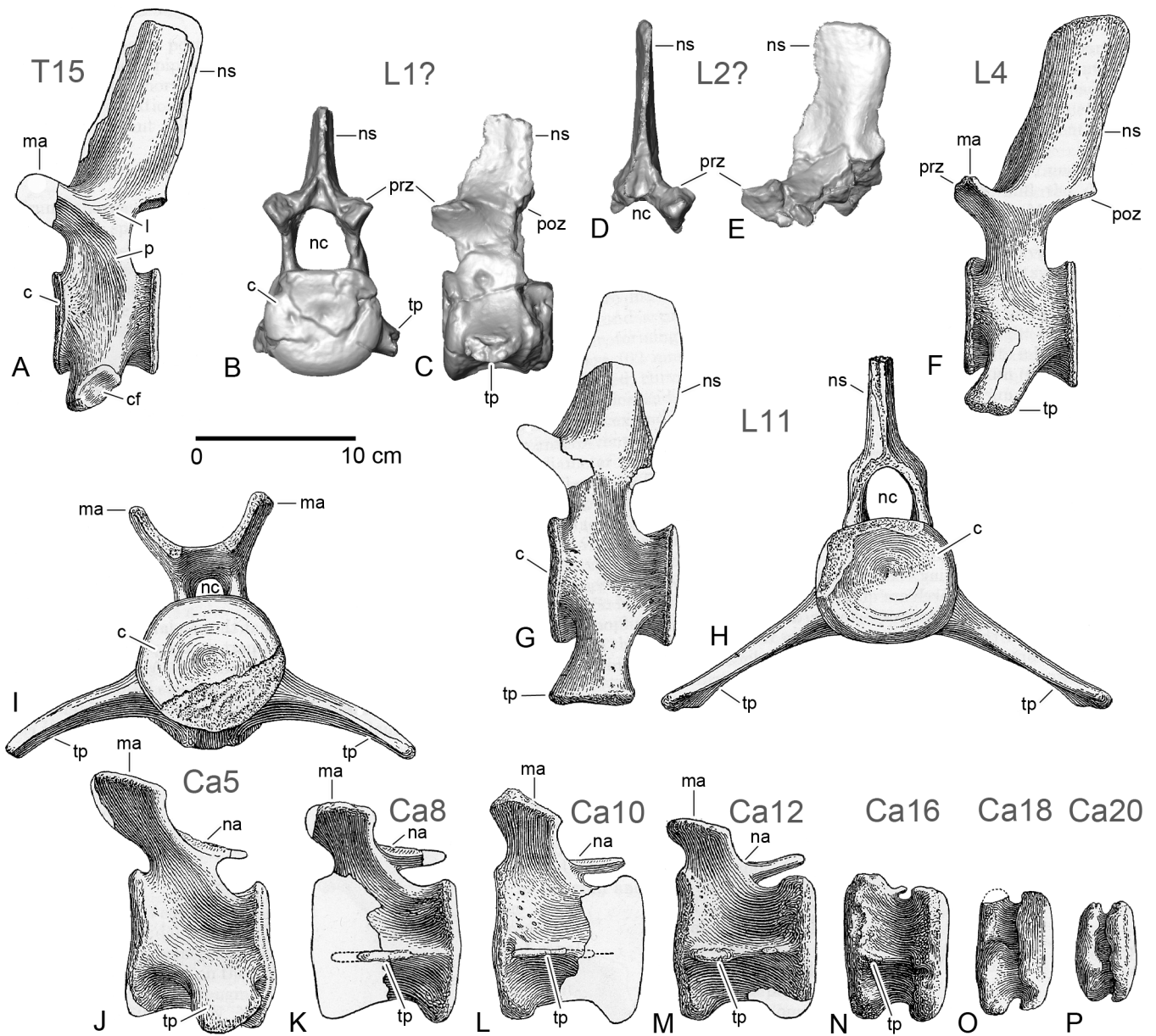


FIGURE 8 — Posterior thoracic, lumbar, and caudal vertebrae of *Zygohiza kochii*. A, T15 of USNM 4679 in left lateral view (reversed from Kellogg, 1936, fig. 56). B–C, L1? of FMNH PM-459 in anterior and left lateral view. D–E, L2? Neural arch and spine of PM-459 in anterior and left lateral view. F, L4 of USNM 12063 in left lateral view (reversed from Kellogg, 1936, fig. 49). G–H, L11 of USNM 4679 in left lateral and posterior views (reversed from Kellogg, 1936, figs. 58–59). I–J, Ca5 of USNM 4679 in anterior and left lateral views (reversed from Kellogg, 1936, fig. 60). K–P, Ca8, Ca10, Ca12, Ca16, Ca18, and Ca20 of USNM 4679 in left lateral views (reversed from Kellogg, 1936, figs. 61–63, 66–68). Images of PM-459 are orthographic laser scans. Note the large and relatively high neural canal of L1? in PM-459. Abbreviations: *c*, centrum; *cf*, capitular facet; *l*, lamina; *ma*, metapophysis; *na*, neural arch; *nc*, neural canal; *ns*, neural spine; *p*, pedicle; *poz*, postzygapophysis; *prz*, prezygapophysis; *tp*, transverse process.

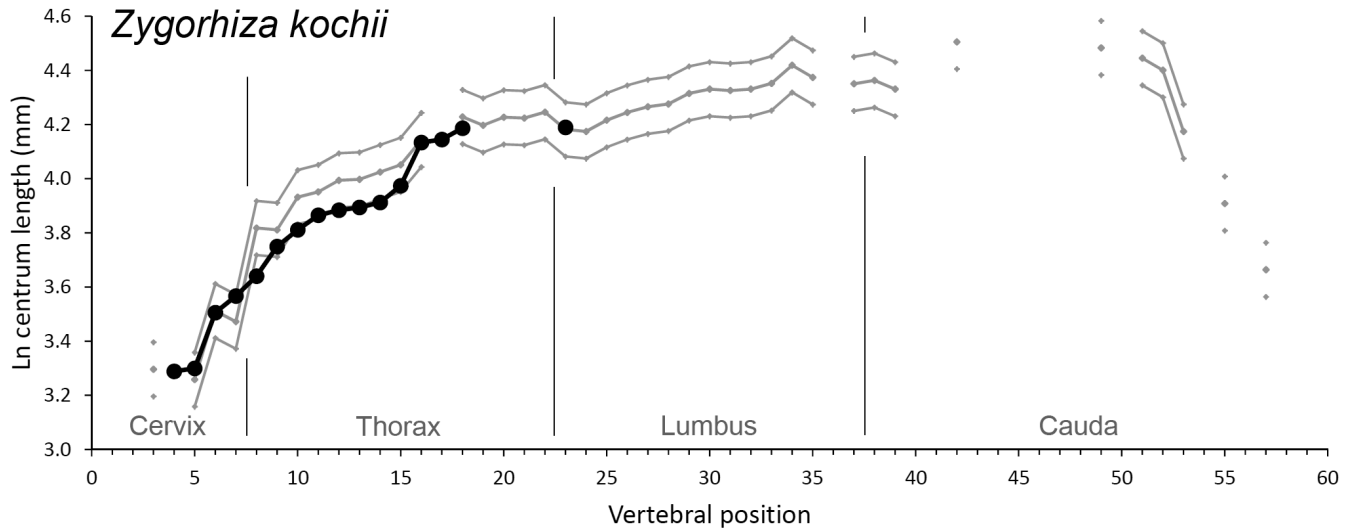


FIGURE 9 — Profile of vertebral centrum length for *Zygorhiza kochii*. Abscissa is position in the vertebral column. Ordinate is the natural logarithm of centrum length measured in mm. Parallel gray lines represent the average length of centra reported by Kellogg (1936) plus and minus two standard deviations (± 0.1 natural log unit on ordinate; sample size is often one). Kellogg assumed a vertebral count of 7 cervicals, 15 thoracics, 15 lumbar, and 21 caudals, for a total of 58 vertebrae. Solid circles and heavier black line show the profile for centrum length of FMNH PM-459 reported in Tables 2 and 3. The abrupt increase in centrum length between vertebrae labeled 15 and 16 (T8 and T9) in PM-459 suggests that one or more vertebrae may be missing, however the vertebrae at positions 16–18 match those at T9–T11 described by Kellogg (1936; see Fig. 7). The vertebral column of *Zygorhiza kochii* is surprisingly poorly studied considering the number of known specimens that preserve vertebrae.

but he did not illustrate this nor give any measurements. The vertebrarterial foramen of C1 measures only about 5 mm in diameter where this has been fully prepared on PM-459, so it appears that the size of the vertebrarterial canal is variable in *Zygorhiza kochii*.

Vertebrarterial foramina perforating the transverse processes of C1 are a common trait in protocetids, and hence probably a primitive retention in *Zygorhiza*. Vertebrarterial foramina perforating the transverse processes are not present on C1 in either *Dorudon atrox* or *Basilosaurus isis*, but Kellogg (1936, p. 40, fig. 11) illustrated a specimen identified as *B. cetoides* (USNM 4675) that does have vertebrarterial foramina well developed on C1.

A general feature of thoracic vertebrae of *Zygorhiza kochii* is the similarity of neural canal heights and widths. Vertebrae of *Z. kochii* differ in this respect from vertebrae of *Dorudon atrox* (Uhen, 2004, pp. 72–78), *Basilosaurus isis*, and *B. cetoides* (Kellogg, 1936, p. 46), which have much lower and wider neural canals. The presence of larger and more circular neural canals in vertebrae of *Z. kochii* may indicate the presence of a substantial epidural (spinal) rete mirabile (McFarland et al., 1979; Rommel et al., 2006), or may indicate greater flexibility of the vertebral column.

Scapula

The scapula of FMNH PM-459 is almost complete, missing only the cranial angle and parts of the blade that are now filled with plaster (Fig. 10B). The scapular blade is minimally 285

mm long anteroposteriorly, but the cranial angle of the blade is missing and so the length may have been a little greater. The blade measures 220 mm high dorsoventrally, measured along the scapular spine from the glenoid fossa to the dorsal border of the blade. The scapular spine of PM-459 is weakly developed, barely rising above the lateral surface of the blade, and it is not raised like the spine shown in Kellogg's illustration (Kellogg, 1936, fig. 71). The spine is only evident at all in the middle one-third of the scapular blade. Anterior to the scapular spine the anterior spinous fossa is narrow, and posterior to this the posterior spinous fossa is broad.

The glenoid fossa for articulation with the humerus forms a shallowly concave surface perpendicular to the much larger blade of the scapula. The glenoid fossa is oval in outline, with the anterior portion being narrower than the posterior portion. The anteroposterior axis of the fossa is 54 mm long, and the fossa is 45 mm wide at its widest point. The coracoid process for origin of biceps musculature is well developed just above the anterior apex of the glenoid fossa. Above this there is a relatively robust and long acromion, curving anteriorly and providing an extensive surface for the origin of deltoideus musculature along its ventral border.

Discussion.— The scapula of PM-459 differs from USNM 4673 as reconstructed and illustrated by Kellogg (1936, p. 160, fig. 71) in being longer anteroposteriorly and shorter dorsoventrally. Both are fan-shaped, but PM-459 spans a broader angular range. Cranial and caudal borders of the scapula can be projected to intersect at an oblique angle of about 110°. This angle is only about 80° and acute in Kellogg's

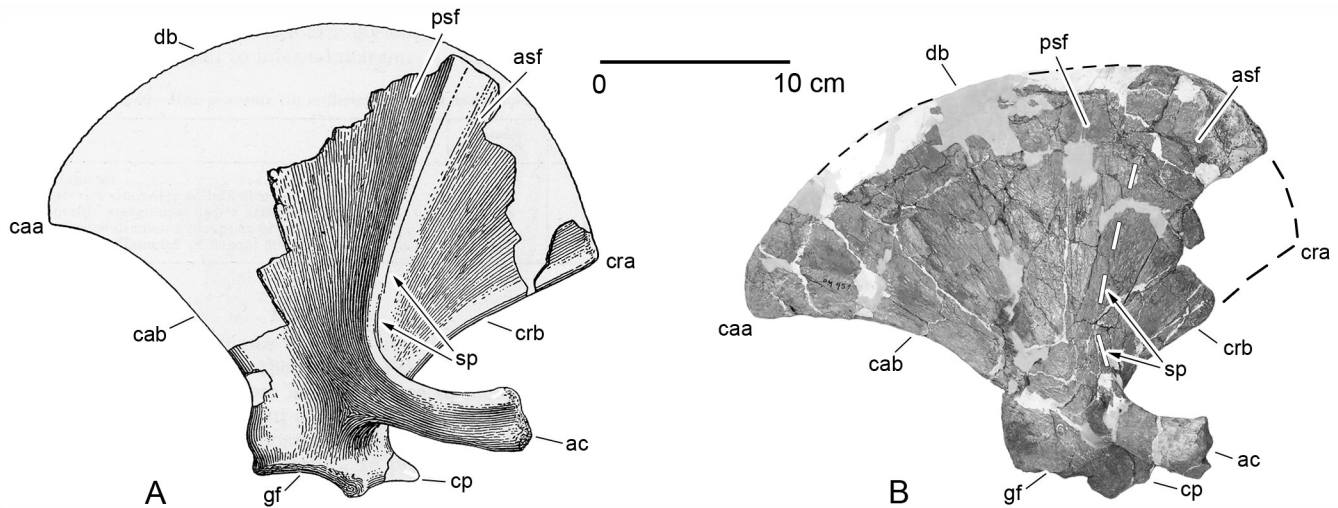


FIGURE 10 — Scapula of *Zygorhiza kochii*. **A**, right scapula of USNM 4673 in right lateral view (reversed from Kellogg, 1936, fig. 71). **B**, right scapula of FMNH PM-459 in right lateral view. Note greater cranial-caudal length of the PM-459 scapula, the lower dorsal-ventral profile, and the oblique rather than acute angle formed by intersection of the cranial and caudal borders. Note also the much weaker scapular spine (white dashed line). Abbreviations: *ac*, acromion; *asf*, anterior spinous fossa; *caa*, caudal angle; *cab*, caudal border; *cp*, coracoid process; *cra*, cranial angle; *crb*, cranial border; *db*, dorsal border; *gf*, glenoid fossa; *psf*, posterior spinous fossa; *sp*, spine.

illustration. A greater angular range of the scapular blade indicates a greater angular range of muscles stabilizing the shoulder and forelimb. Greater stability of the forelimb may be a correlative of tail-powered swimming in basilosaurids.

ENDOCRANIAL CAST AND RELATIVE BRAIN SIZE IN *ZYGORHIZA*

The endocranial cast of *Zygorhiza kochii* prepared from the FMNH PM-459 cranium is illustrated in Figure 11 (one copy is archived with FMNH PM-459 and another as UM 116960). The new endocast is one of the best known for an archaeocete, comparable to endocasts of *Saghacetus osiris* and *Dorudon atrox* described by Dart (1923) and endocasts of *D. atrox* described by Uhen (2004). However, in spite of this excellent preservation, the endocast reveals few details of morphology of the brain itself. An endocast provides a surface impression of everything filling a braincase in life, including arteries and veins as well as brain tissue. In *Zygorhiza* much of the surface of the brain was covered by massive dorsal and rostral cranial retia mirabilia. These elaborate vascular networks functioned to cool arterial blood reaching the brain through counter-current heat exchange with the returning venous drainage (Breathnach, 1955; Baker, 1979; McFarland et al., 1979).

Some landmarks of the brain can be identified on the endocast. The most obvious is the medulla oblongata leading to the foramen magnum and spinal cord. Additional landmarks are provided by the olfactory (I), optic (II), trigeminal (V), and vestibulocochlear (VIII) cranial nerves. A portion of the surface of the cerebrum is visible on the left and right anterolateral surfaces of the endocast between the midline

dorsal sagittal sinus and the more lateral rostral retia mirabilia. This surface of the cerebrum is smooth, with no suggestion of the cortical folding characteristic of modern cetacean brains. The largest surface of the brain preserved in the endocast is the ventral surface. This is broad and smooth, with impressions of cranial nerves II and V at the rostral pole and the impression of the medulla oblongata at the caudal pole. Between rostral and caudal poles the endocast has a slightly extruded midline hypophysis representing the depression in the basisphenoid that accommodated the pituitary gland. Finally, near the right lateral pole the cranial hiatus, evident on the cranium itself, is represented by an impression of filler inserted when the endocast was made. The ventral surface near the left pole reflects an area of damage on the left side of the basicranium, and the cranial hiatus includes a larger area of damage.

Asymmetry is a salient feature of the dorsal retia mirabilia, where the right rete rises higher and is more massive than the left. This can be seen looking at the endocast in anterior, posterior, or dorsal view (Fig. 11B, C, and E). Asymmetry of retia within the braincase means that the internal surface of the braincase was asymmetrical, but this does not necessarily mean that the brain was asymmetrical, nor does it mean that the external surface of the cranium was asymmetrical. Subtracting the retia, the shape of the underlying brain is approximately that of an equilateral triangle 18.4 cm on a side forming the base, with a smoothly-curving cerebral cortex rising only some six cm above the base.

Relative Brain Size

Relative brain size in fossils is quantified by comparing 'observed' endocranial volume and estimated brain weight for

a specimen or species to the ‘expected’ brain weight for an average living mammal of the body weight estimated for the fossil. The density of brain tissue is very near that of water, so the weight of a brain in grams is, to a good approximation, the volume of the brain in cubic centimeters. Brain weight increases proportionally, allometrically, with body weight, and expected brain weight is calculated from a regression of log brain weight on log body weight. The theory here is explained and applied in Jerison (1973) and a large subsequent literature.

I differ from Jerison (1973) and subsequent authors in comparing observed and expected in terms of encephalization residuals rather than encephalization quotients, in employing log base-2 rather than log base-10 units, and in the choice of a reference sample (Gingerich, 2015b). Log base-2 units are intuitive because they represent halvings and doublings, and the resulting encephalization residuals span a range from about -3 to $+3$. Log base-10 units represent orders of magnitude, and use of the resulting encephalization residuals, while legitimate, would span an inconvenient fractional range from about -0.9 to $+0.9$. Terrestrial mammals as a class are an excellent reference sample because mammals were initially terrestrial and because brain and body weights are known for many terrestrial mammal species. Regression of \log_2 brain weight in grams on \log_2 body weight in grams for terrestrial mammals as a class yields a slope coefficient of 0.740 and an intercept of -4.004 . These can be used to calculate expected

brain weight using $\log_2 E_e = 0.740 \cdot \log_2 P - 4.004$, where E_e is expected brain weight (in g) and P is body weight (in g) estimated for the fossil. Finally, relative brain size is calculated as an encephalization residual or difference $ER_{TC} = \log_2 E - \log_2 E_e$, where E is the weight (g) of the brain equivalent to the volume (cc) observed in the fossil.

Relative Brain Size in PM-459

The volume of the three-dimensional digital image of the laser-scanned endocast of PM-459 was measured using the MeshLab measuring tool (MeshLab is free and open-source software from the Visual Computing Lab, ISTI-CNR; <http://meshlab.sourceforge.net/>). The endocast illustrated in Figure 11 has a bounding box of $18.3 \times 18.4 \times 11.6$ cm, a surface area of 749 cm² and a volume of 1189 cm³ including both the dorsal and rostral retia mirabilia. Marino et al. (2000) and Uhen (2004, p. 126) estimated that retia mirabilia constitute about 19.5% of endocranial volume, meaning the brain fills about 80.5% of endocranial volume. Using these numbers, the volume of the brain in the PM-459 *Zygorhiza kochii* endocranial volume is estimated to have been about 957 cm³. A brain volume of 957 cm³ is equivalent to a brain weight of 957 g or, rounding, 960 g.

The body weight of *Zygorhiza kochii* can be estimated from the size of its thoracic and lumbar vertebrae compared to

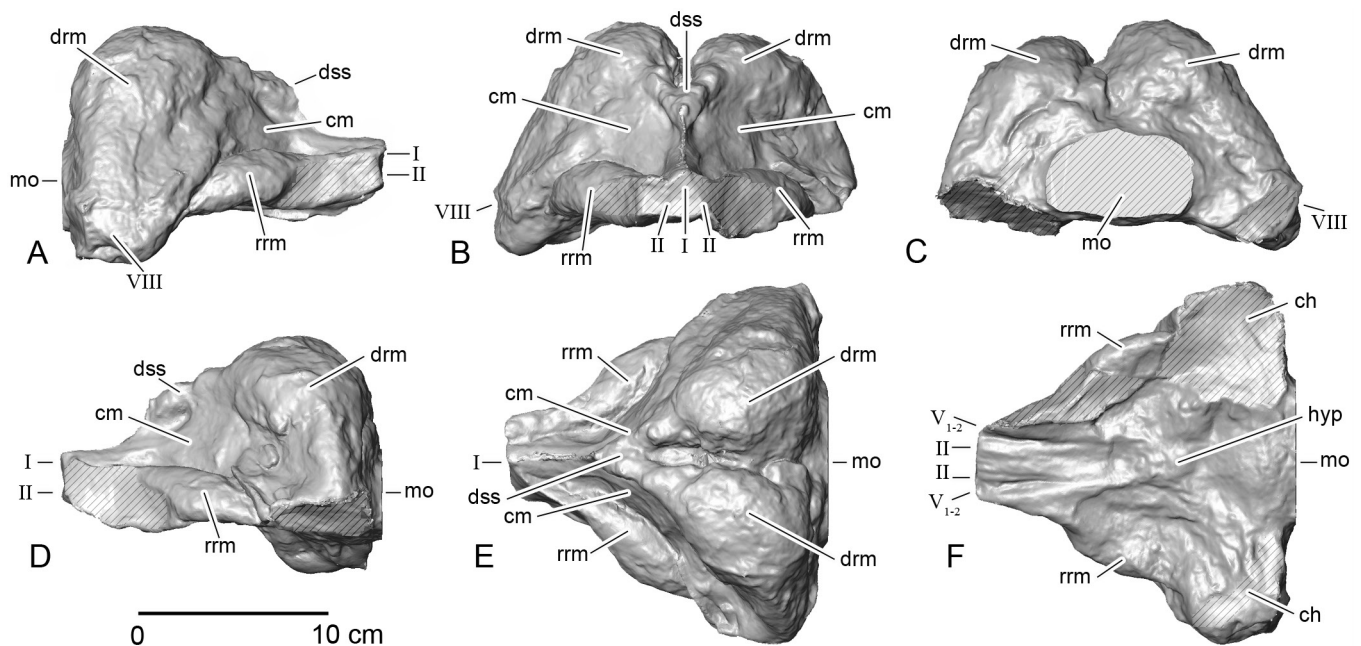


FIGURE 11 — Endocranial cast of *Zygorhiza kochii*, FMNH PM-459. **A**, right lateral view. **B**, anterior view. **C**, posterior view. **D**, left lateral view. **E**, dorsal view. **F**, ventral view. Images are orthographic laser scans. Note that relatively few landmarks can be interpreted reliably, and the brain itself is largely hidden under massive dorsal and rostral retia mirabilia. Abbreviations: *ch*, cranial hiatus; *cm*, cerebrum; *drm*, dorsal rete mirabile; *dss*, dorsal sagittal sinus; *hyp*, hypophysis; *mo*, medulla oblongata; *rrm*, rostral rete mirabile; I, first cranial nerve (olfactory nerve); II, second cranial nerve (optic nerve); V, fifth cranial nerve (trigeminal nerve); VIII, eighth cranial nerve (acoustic or vestibulocochlear nerve).

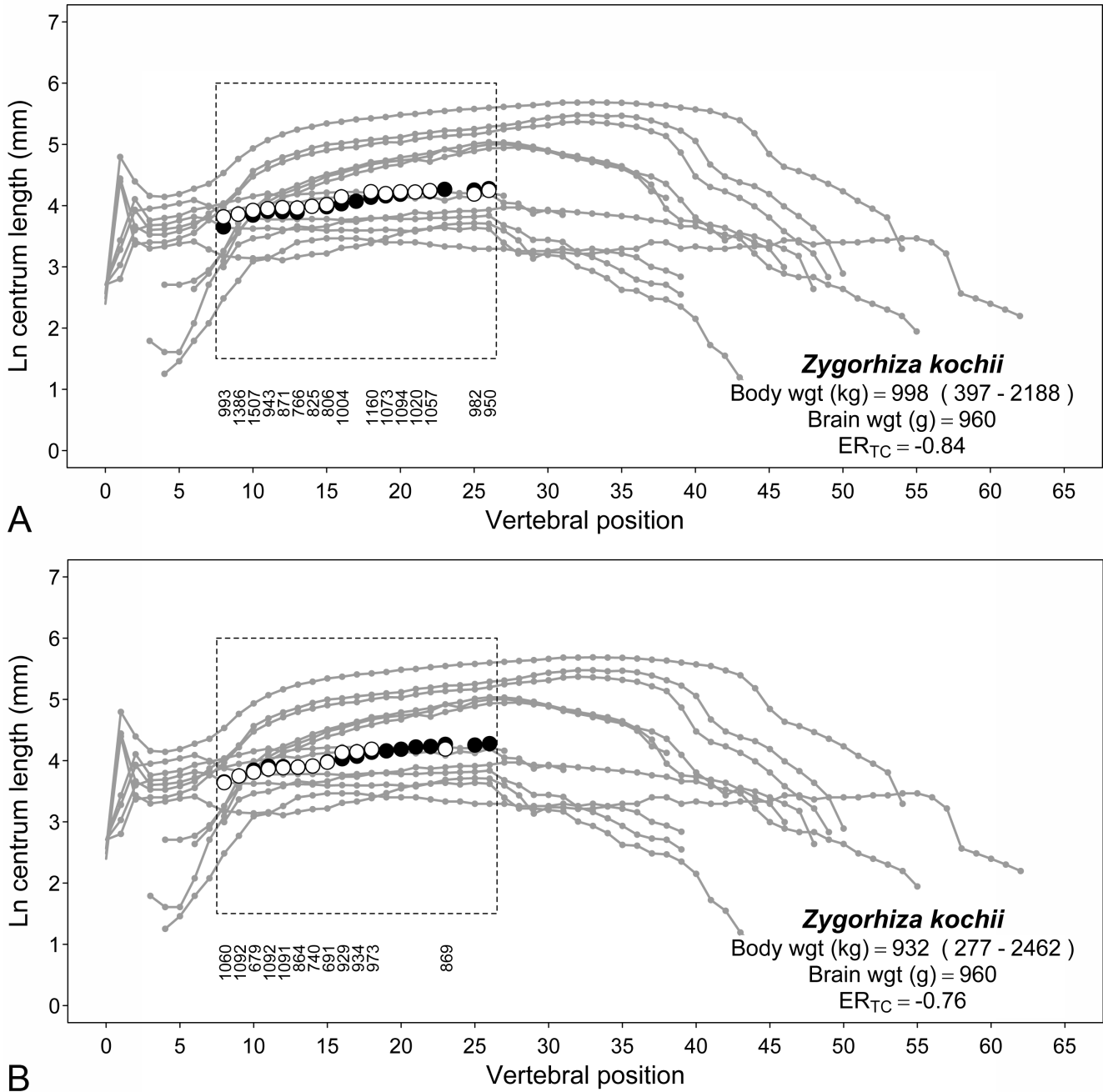


FIGURE 12 — Body weight estimates for *Zygorhiza kochii* based on **A**, vertebral measurements reported by Kellogg (1936); and **B**, vertebral measurements reported here. The preferred estimate of 998 kg in panel A is the median of 16 independent multiple regressions for vertebrae 8–26 (numbers written vertically), while that in panel B is the median of 12 independent multiple regressions. Weights in parentheses are a 95% confidence interval for the overall estimate of 998 kg or 932 kg. Gray lines are traces of vertebral centrum length for each of the 11 cetacean and pinniped species used as a reference set (corresponding centrum width and height are not shown). White solid circles are vertebral lengths for *Zygorhiza kochii* (centrum width and height are not shown). These are superimposed on black solid circles representing vertebral lengths for *Dorudon atrox*. Dashed rectangle encloses core vertebrae of interest for body weight prediction. *Zygorhiza* vertebrae at positions 8–22 are thoracics and 23–26 are lumbar. One or more centrum length, width, and height measurements are missing for *Zygorhiza* vertebrae 10, 16, and 17 in panel A, and for *Zygorhiza* vertebrae 19–22 in panel B). Note that the ordinate is on a natural logarithmic scale, and vertebral measurements are in mm. See Gingerich (2015b) for further explanation and documentation.

those in a reference set of eight cetaceans and five pinnipeds (Fig. 12; Gingerich, 2015b). Estimation of body weight from vertebral measurements reported by Kellogg (1936; Fig. 12A) yields 16 independent estimates with a median of 998 kg. Combining this median body weight with a brain weight of 960 g, yields an encephalization residual $ER_{TC} = -0.84$ on a \log_2 doubling scale ($ER_{TC} = -0.84$ is equivalent to an encephalization quotient $EQ_{TC} = 0.56$ or 56% of expectation for an average living terrestrial mammal of the same size; see Gingerich, 2015b).

The body weight of *Zygorhiza kochii* can also be estimated from the vertebral measurements reported here (Fig. 12B), but now there are only 12 estimates with a median of 932 kg. Combining this median body weight with a brain weight of 960 g yields a larger encephalization residual $ER_{TC} = -0.76$. The latter has the advantage of being estimated from the same skeleton that yielded the brain size estimate, but the disadvantage of being based on fewer vertebrae, which provide fewer individual body size estimates and a less constrained median.

Figure 13 shows where the brain weight and body weight of *Zygorhiza kochii* fall relative to brain weights and body weights of living terrestrial mammals, living toothed whales (Odontoceti), and living baleen whales (Mysticeti). Odontocetes generally have brains larger than expected for their body size, and mysticetes have brains smaller than expected for their body size. The Eocene archaeocete *Zygorhiza kochii* has a brain smaller than expected for a living terrestrial mammal of the same weight, but intermediate between the sizes expected for living odontocetes and mysticetes.

VALIDITY OF THE GENUS *PONTOGENEUS*

The first archaic fossil whale known to science was found in 1832 in what is today the Jackson Formation or Jackson Group of geological formations. It was found on the west side of the Ouachita River in what is now Caldwell Parish in the U. S. state of Louisiana. This large-bodied species with elongated lumbar vertebrae was named *Basilosaurus* (without a species name) by Richard Harlan (Harlan, 1834), and first recognized as a cetacean by Richard Owen, who named related remains *Zeuglodon cetoides* (Owen, 1841). *Zeuglodon* is a synonym of *Basilosaurus*, and the large species described by Harlan and later named by Owen is now called *Basilosaurus cetoides* (Owen, 1841).

Albert Koch collected a substantial number of archaeocetes in the Yazoo Formation of Alabama in 1845, and his specimens were studied by Johannes Müller (1849). In describing these, Müller wrote (p. 21):

Unter den Zeuglodon-Knochen der Kochschen Sammlung giebt es eine große Anzahl von Lenden- und Schwanzwirbeln von zwei ganz verschiedenen Arten derselben Gattung, welche sich in Hinsicht der Stelle, welche sie in der Wirbelsäule einnehmen, ganz gleich, von einander nur unterscheiden,

dafs die Wirbelkörper in der einen Art, die ich Zeuglodon macrospondylus nannte, fast doppelt so lang als breit sind, während sie in der andern Art Zeuglodon brachyspondylus nur so lang als breit sind.

Among the *Zeuglodon* bones in Koch's collection are a great number of lumbar and tail vertebrae of two very different species of the same genus, which in terms of location in the spine are all the same. These only differ from each other in that vertebral bodies I call *Zeuglodon macrospondylus* are almost twice as long as they are wide, whereas those in the other species *Zeuglodon brachyspondylus* are only as long as they are wide. (author's translation)

Müller distinguished *Z. macrospondylus* from *Z. brachyspondylus* based on vertebral shape. He later distinguished *Zeuglodon brachyspondylus minor* from *Z. brachyspondylus* based on size (Müller 1851). Müller's *Zeuglodon macrospondylus* was and is a junior synonym of *Basilosaurus cetoides*, but his *Zeuglodon brachyspondylus* was new and different, and has been widely accepted as valid. Müller's *Z. b. minor* was and is a junior synonym of both *Z. kochii* (Reichenbach in Carus, 1847) and *Z. hydrarchus* (Carus, 1849). So in the end Koch's collection included a large species with unusually elongated vertebral centra, a medium-sized species with normally-proportioned centra, and a relatively small species with normally-proportioned centra.

In 1852, Joseph Leidy named the new genus and species *Pontogeneus priscus* based on a medium-sized cervical vertebra, ANSP 13668, from the *Basilosaurus*-bearing Eocene of the Ouachita River, Louisiana (Fig. 14D). Leidy himself later determined that the cervical vertebra named *Pontogeneus priscus* appeared "to agree nearly in size, form, and construction with the cervicals described by Müller as those of *Zeuglodon brachyspondylus*" (Leidy, 1869, p. 430). Later Remington Kellogg (1936) synonymized Müller's *Zeuglodon brachyspondylus* and Leidy's *Pontogeneus priscus* and, recognizing that *Zeuglodon* is a junior synonym of *Basilosaurus* and therefore could not be used, combined these as *Pontogeneus brachyspondylus* (Müller, 1849). When Kellogg (1936) finished, there were still three contemporaneous species from the *Basilosaurus* beds of Louisiana, Mississippi, and Alabama, but these now bore different names: large *Basilosaurus cetoides*, medium-sized *Pontogeneus brachyspondylus*, and relatively small *Zygorhiza kochii*.

In 1997, Mark D. Uhen published an abstract on a new, relatively complete specimen of *Pontogeneus brachyspondylus*, MMNS VP 445, recovered from a Yazoo Formation clay pit near the Cynthia rail siding in Mississippi (Uhen, 1997). Writing about the specimen later, Uhen (2005, p. 158–159) dismissed *Zeuglodon brachyspondylus* and *Pontogeneus priscus* as 'nomina nuda,' and proposed a new genus and species, *Cynthiacetus maxwelli*, for the medium-sized Yazoo Formation archaeocete, with the type being MMNS VP 445.

Uhen (2005) regarded *Zeuglodon brachyspondylus* Müller (1849) as a nomen nudum because, as he wrote, the generic

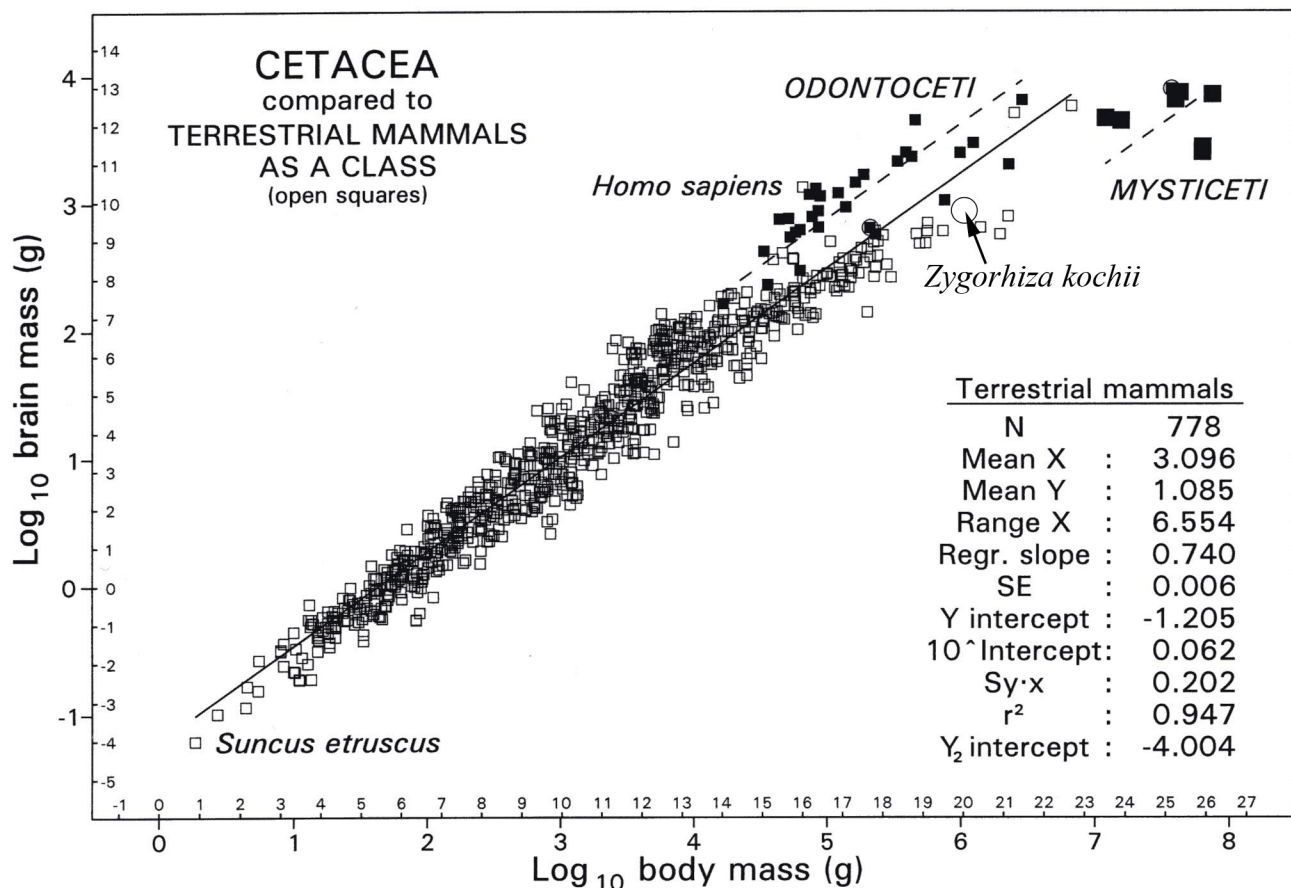


FIGURE 13 — Relative brain size of Eocene *Zygorhiza kochii* (open circle) in relation to that of extant Odontoceti (small solid squares) and Mysticeti (large solid squares). All are shown relative to the allometric scaling of brain weight and body weight in extant terrestrial mammals as a class (open squares). Abscissa and ordinate are shown on \log_{10} order-of-magnitude scales (outside the axes) and on \log_2 halving or doubling scales (within the axes). An encephalization residual ER_{TC} of -0.84 for *Zygorhiza kochii* means that the brain is a little greater than one-half the weight expected for an average living terrestrial mammal of the same body weight (0.00 represents the expected weight; and -1.00 , one halving, represents one half of the expected weight). Expected brain weight is based on a slope of 0.740 and an intercept of 4.004 for regression of \log_2 brain weight on \log_2 body weight. See Gingerich (2015b) for further explanation.

name *Zeuglodon* is a junior synonym of *Basilosaurus*, and because “the species referred to as *Zeuglodon brachyspondylus* never had a type specimen designated” (Uhen, 2005, p. 159). A nomen nudum is a scientific name that is not available in a technical sense because it is not properly published. For *Zeuglodon brachyspondylus*, published before 1931, calling this a nomen nudum means publication did not conform to Article 12 of the International Code of Zoological Nomenclature. Article 12.2.7 stipulates that evidence for a new species-level name can be a description, a definition, or an indication, and the latter can be as minimal as association of the name with an illustration.

Müller (1849) named *Zeuglodon brachyspondylus* on page 26 of his *Zeuglodonten von Nordamerika* monograph, in which he provided clear descriptions, measurements, and illustrations of the specimens involved. The most informative of Müller’s illustrations are on Plate XX, where three rows

of specimens are illustrated, the middle row being *Zeuglodon brachyspondylus*. Müller’s *Zeuglodon brachyspondylus* was properly published in 1849. It is available as a scientific name, and it is not a nomen nudum. Müller’s (1849) failure to designate a type specimen does not make *Zeuglodon brachyspondylus* a nomen dubium either; the bones indicated in his plate XX constitute the type series.

To resolve the type specimen question I designated the lumbar vertebra shown in Müller’s (1849) plate XX, row II, no. 6, illustrated in dorsal and posterior view, to be the lectotype of *Zeuglodon brachyspondylus* (Gingerich, 2007, p. 376). This is also shown in Müller’s plate XVIII, fig. 1–3, where it is illustrated in dorsal, lateral, and posterior view. Müller (1849, p. 26) and Kellogg (1936, p. 254) provided measurements of the chosen lectotype.

Uhen (2005, p. 158–159) regarded *Pontogeneus priscus* Leidy (1852) as a nomen nudum because of the limited nature

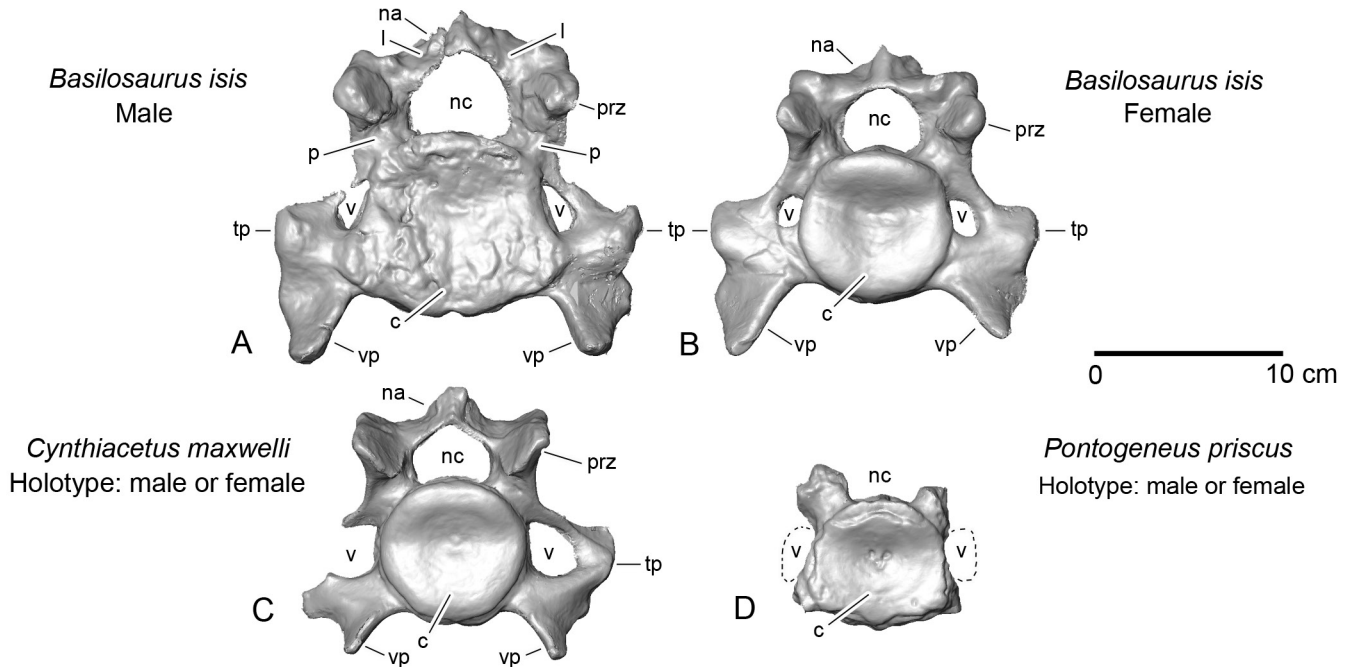


FIGURE 14 — Variation in C4 cervical vertebrae of *Basilosaurus isis*, *Cynthiacetus maxwelli*, and *Pontogeneus priscus*. **A**, *Basilosaurus isis* male, UM 97503 (WH-30), early Priabonian late Eocene, from the Birket Qarun Formation of Wadi Hitán in Egypt. **B**, *Basilosaurus isis* female, UM 97507 (WH-74), early Priabonian late Eocene, from the Birket Qarun Formation of Wadi Hitán in Egypt. **C**, *Cynthiacetus maxwelli* holotype, male or female, MMNH VP-445, late Priabonian, late Eocene, from the Yazoo Clay of Cynthia Clay Pit in Mississippi (U.S.A.). **D**, *Pontogeneus priscus* holotype, male or female, ANSP 13668, late Priabonian late Eocene, from the Jackson Group, possibly Yazoo Clay, where this intersects the Ouachita River in Louisiana (U.S.A.). Images are orthographic laser scans in anterior view. Note the small vertebral foramina (*v*) in *Basilosaurus* and the comparatively large vertebral foramina in *Cynthiacetus* and in *Pontogeneus* (dashed lines). Bases of the neural canals in *Cynthiacetus* and *Pontogeneus* are similar in transverse diameter. Note also the substantial difference in size between cervical centra of male and female *Basilosaurus isis*, and the nearly identical size of cervical centra in *Cynthiacetus maxwelli* and *Pontogeneus priscus*. Cervical vertebrae of male and female *Basilosaurus cetoides* contemporaneous with *C. maxwelli* and *P. priscus* are even larger than those of *B. isis* shown here. Abbreviations: *c*, centrum; *l*, lamina; *na*, neural arch; *nc*, neural canal; *p*, pedicle; *prz*, prezygapophysis; *tp*, transverse process; *v*, vertebral foramen; *vp*, ventral part of transverse process.

of the type specimen, a cervical vertebral centrum “larger than those of *Zygorhiza* ... and smaller than most cervical vertebral bodies from *Basilosaurus*.” When concluded “based on the limited nature of the type specimen and the similarity of the type specimen to cervical vertebral centra of *Basilosaurus*, *Pontogeneus priscus* is here designated a nomen nudum” (Uhen, 2005, p. 159). Leidy (1852) did not publish an illustration, but he gave a clear combined description of the nominal genus and its single nominal species, which made both names available (ICZN article 12.2.6). Leidy’s *Pontogeneus priscus* is properly published, and it is not a nomen nudum.

Kellogg (1936) recognized the distinctiveness and validity of Müller’s species *Zeuglodon brachyspondylus*, the synonymy of *Zeuglodon* with *Basilosaurus*, the synonymy of *Pontogeneus priscus* with *Zeuglodon brachyspondylus*, and the availability of *Pontogeneus* as a replacement for *Zeuglodon* in the new combination *Pontogeneus brachyspondylus* (Müller, 1849). The type specimen of *Pontogeneus priscus*, ANSP 13668, is illustrated in Figure 14, where it is compared to the fourth cervical vertebra of *Cynthiacetus maxwelli* and to the fourth cervical vertebrae of male and female

Basilosaurus isis, the *Basilosaurus* species most comparable in size. *Cynthiacetus* resembles *Zygorhiza* and differs from *Basilosaurus* in having large vertebral foramina, and the type specimen of *Pontogeneus priscus* shows that it too had large vertebral foramina (Fig. 14D). There is a substantial difference in size between cervical C4 in male and female *Basilosaurus isis*, but this vertebra is larger in both sexes than the comparable cervical in *Cynthiacetus maxwelli* or that in *Pontogeneus priscus* (C4 of *C. maxwelli* and *P. priscus* being similar in size). Cervical vertebrae of male and female *Basilosaurus cetoides* contemporaneous with *C. maxwelli* and *P. priscus* are even larger than those of *B. isis* shown here, so there is even less chance that the type of *Pontogeneus priscus* belongs to contemporaneous *Basilosaurus cetoides*.

I follow Uhen (1997) in identifying MMNS VP-445 as a specimen of *Pontogeneus brachyspondylus*, but I do not follow his later interpretation that MMNS VP-445 represents a new genus and species *Cynthiacetus maxwelli*. I regard *Cynthiacetus maxwelli* as a junior subjective synonym of both *Zeuglodon brachyspondylus* Müller (1849) and *Pontogeneus priscus* Leidy (1852), and I follow Kellogg (1936) in

combining the latter species as *Pontogeneus brachyspondylus* (Müller, 1849). This conservative taxonomic interpretation may be proven wrong by further preparation and description of MMNS VP-445, which could show it to be different from contemporaneous specimens referred to *Pontogeneus brachyspondylus*, but pending such a development there is presently no reason to support recognition of more than three basilosaurids from Yazoo Formation upper Eocene strata of the Gulf Coast. These are, from largest to smallest: *Basilosaurus cetoides* (Owen, 1841), *Pontogeneus brachyspondylus* (Müller, 1849), and *Zygorhiza kochii* (Reichenbach, 1847). If *Cynthiacetus peruvianus* Martínez-Cáceres and Muizon (2011) was correctly referred to *Cynthiacetus* before, then it should now be referred to *Pontogeneus* as *Pontogeneus peruvianus* (Martínez-Cáceres and Muizon, 2011).

Discussion.—Two principles related to these determinations are worth discussing. The first is the ‘Principle of Priority’ encoded in Article 23 of the International Code of Zoological Nomenclature to promote nomenclatural stability. A nomen nudum is a name that was never validly published. It is thus, objectively, not ‘available’ as a valid name. Such a name has no standing and no priority. However, a nomen dubium is a name validly published that is set aside, subjectively, by a subsequent author or authors as having uncertain application. A nomen dubium has priority and retains the priority of its original publication. Setting a name aside as a nomen dubium is generally a practice of last resort where there is insoluble ambiguity about the meaning of the name. There is no harm in declaring a name to be a nomen dubium, but this is an interpretation and subsequent authors may have a different interpretation.

The second principle might be called the ‘Principle of Taxa as Population Samples’: “the essential principle that taxa in modern evolutionary taxonomy are based on samples, not on types” (Simpson, 1961, p. 183). A type specimen is the tangible reference for a species-group name, but the type is usually, as here, only one of a sample of specimens representing a taxon. A type specimen has the morphology preserved in the specimen itself or, if lost, in its published descriptions and illustrations. A type specimen usually also has context: it came from some place, the type locality, and from some time in the past or present, which can be called its type age (e.g., here late Priabonian). Expanding from the type specimen of a species to the sample it represents, the sample always has, conceptually at least, variation in form, variation in place (geographic range), and variation in time (age range). To interpret the species is to document, and quantify if possible, its variation in form, place, and time. In the context of population samples, the type specimen of a species is just one specimen of the sample available for study, one member of the hypodigm no more important than any other. The value of a type specimen as a name-bearer comes in tying a name to the population sample representing one particular species and not to population samples representing other species.

In the case at hand, all authors agree that the Yazoo Formation and equivalents in Louisiana, Mississippi, Alabama, and Georgia yield three archaeocetes: the large *Basilosaurus*

cetoides, a medium-sized species, and the relatively small *Zygorhiza kochii*. Names for the medium-sized species, *Zeuglodon brachyspondylus* Müller (1849), *Pontogeneus priscus* Leidy (1852), and *Cynthiacetus maxwelli* Uhen (2005), are all validly published, and their type specimens tie all three names to the medium-sized species and not to the large or relatively small species. I interpret *Pontogeneus brachyspondylus*, as Kellogg (1936) did, to combine the priority of *Pontogeneus* as a generic name, with the priority of *brachyspondylus* as a species name for the medium-sized archaeocete. If in the future someone can show that there are two medium-sized species rather than one, then this interpretation will have to be reviewed and reassessed.

DISCUSSION

Zygorhiza kochii is part of a late Priabonian, latest Eocene, archaeocete fauna from the North American Gulf Coast that includes the larger species *Basilosaurus cetoides* and *Pontogeneus brachyspondylus*. The paleobiogeography of *Zygorhiza* is interesting, as is its relative brain size. Finally I end with an appeal for more and better documentation of known *Zygorhiza* specimens.

Paleobiogeography of *Zygorhiza*

Tew and Mancini (1995) developed the regional paleogeographic reconstruction shown as background in Figure 15. Superimposing the *Z. kochii* localities listed here in Table 1 shows that *Zygorhiza* is consistently found in shallow marine deposits paralleling the late Eocene shoreline. From this distribution we can infer that preservation of *Z. kochii* depended on the intersection of (1) a suitable living environment; (2) sediment accumulation and preservation in the area during the appropriate interval of time; and (3) evolutionary time in the sense that *Z. kochii* had a limited temporal range, marked at the beginning by its evolutionary origin and marked at the end by its continued evolution into one or more descendants or by its extinction. Note that *Z. kochii* specimens are all found near the late Eocene shoreline, but span a range of more clastic to more carbonate-rich depositional environments. The geographic range of *Zygorhiza* in life may have been substantially greater than the Gulf Coast of North America, but this range was possibly limited to nearshore environments.

Relative Brain Size

The body weight and endocranial volume determined here for *Zygorhiza kochii* are 998 kg and 1189 cm³, respectively. These are close to the body weight and endocranial volume for *Dorudon atrox*, but differ substantially from the body weight of 3351 kg and endocranial volume of 917 cm³ published by Marino et al. (2000, p. 90) for *Z. kochii*.

Marino et al. (2000) estimated body weight in *Zygorhiza kochii* by substituting a skeletal length of 520 cm into an

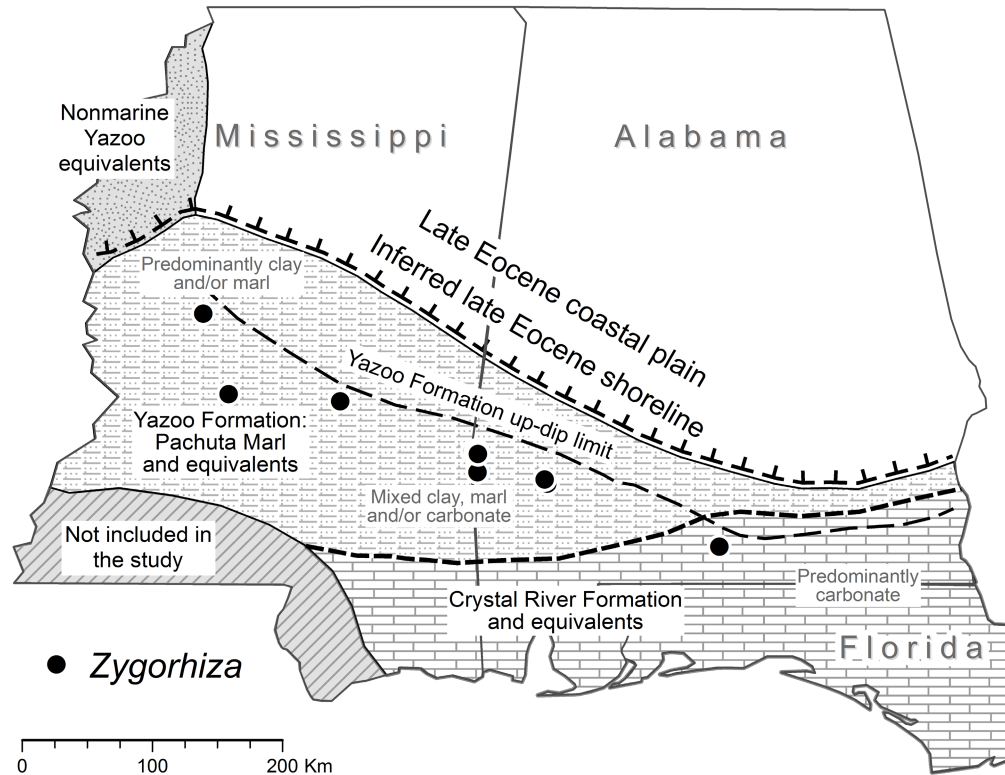


FIGURE 15 — Paleogeographic map of the Gulf Coast states of Mississippi, Alabama, and Florida during the time of deposition of the Pachuta Marl member of the Yazoo Formation (late Priabonian, very late Eocene). Map shows the late Eocene shoreline crossing Mississippi and Alabama diagonally; the geographic distribution of the Yazoo and Crystal River formations, and their equivalents, during Pachuta Marl time; and the general gradient of more clastic to more carbonate-rich depositional environments offshore farther from the shoreline. Superimposing the distribution of *Zygorhiza kochii* localities (solid circles) shows that these parallel the late Eocene shoreline near the up-dip limit of Yazoo Formation exposures, and the localities span a range of more clastic to more carbonate rich environments. Paleogeographic map is redrawn from Tew and Mancini (1995).

allometric regression of body weight (W in kg) on skeletal length (L in cm) for modern cetaceans, $\log W = 3.08 \cdot \log L - 4.84$, yielding a body weight estimate of 3351 kg. The resulting estimate is more than three times (336%) greater than the weight estimated here. There is no skeleton of *Z. kochii* described in the literature that would provide an estimate of length, and Marino et al. did not explain why the skeletal length of *Z. kochii* was estimated to be 520 cm when *Dorudon atrox*, with larger vertebrae, has a skeletal length of only 485 cm.

The difference between the endocranial volume of *Zygorhiza kochii* calculated here, 1189 cm³, and that calculated by Marino et al. (2000), 917 cm³, is less difficult to reconcile. The difference is in the range of 23–30% depending on how the comparison is made. The specimen studied here (FMNH PM-459) is fully adult, but so is the one (USNM 16638) that yielded the endocranial volume reported by Marino et al. (2000). We agree within 2% in calculating the endocranial volume of *Dorudon atrox* to have been 1200 cm³ (Gingerich, 1998) or 1173 cm³ (Marino et al., 2000), so it is doubtful that the problem is one of measurement. Brain size is variable,

like every other measure of size. A 95% confidence interval for endocranial volume, centered on the geometric mean of the two endocranial volumes observed for *Z. kochii*, would be expected to range from 774 cm³ to 1409 cm³. The two observed endocranial volumes, 1189 cm³ and 917 cm³, lie within this range.

Reduction of both endocranial volumes by 19.5%, as Marino et al. (2000) proposed, to remove the proportion of rete mirabile filling the braincase, leaves a brain volume of 957 cm³ for the FMNH PM-459 specimen of *Zygorhiza kochii*, corresponding to an estimated brain weight, rounded to the nearest 10 g, of 960 g (as was estimated for *Dorudon atrox* by Gingerich, 1998). The Marino et al. (2000) endocranial volume of 917 cm³ for USNM 16638 reduces to a brain volume of 738.2 cm³, corresponding to a rounded brain weight of 740 g. Comparing these observations to the brain weight expected for a body weight of 998 kg yields an encephalization residual, ER_{TC} , of -0.84 for FMNH PM-459, and an encephalization residual, ER_{TC} , of -1.22 for USNM 16638. Comparing these observations to the brain weight expected for a body weight of 932 kg yields an encephalization residual, ER_{TC} , of -0.76 for

FMNH PM-459. Such differences in relative brain size may be real, but it is worth studying additional crania of adult *Z. kochii* to test this.

Zygorhiza Morphology and Variation

FMNH PM-459 is one of a number of undescribed skeletons and partial skeletons of *Zygorhiza kochii* known in U. S. museums. Virtually everything written about *Zygorhiza* in the past 80 years is based on specimens described by Kellogg (1936). Kellogg's documentation of the specimens he had available is exemplary, but much remains to be learned. Figure 9 shows how poorly vertebral counts and basic measurements are known for the *Zygorhiza* skeleton. Without a complete skeleton or carefully constructed composite, it is not possible to determine the full length of the body. Without a series of specimens it is not possible to document variation or sexual dimorphism. Judging from vertebrae, *Zygorhiza kochii* is similar in size to the slightly older late Eocene species *Dorudon atrox*, but *Z. kochii* differs markedly in some aspects of postcranial morphology, both vertebral and appendicular, and these differences are worthy of better documentation and further analysis and interpretation.

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