

PYGMY SPERM WHALES (ODONTOCETI, KOGIIDAE) FROM THE PLIOCENE OF FLORIDA AND NORTH CAROLINA

JORGE VÉLEZ-JUARBE,^{*1,2,3} AARON R. WOOD,^{2,4} and CATALINA PIMIENTO^{2,5,6}

¹Department of Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A., jvelezjuar@nhm.org;

²Florida Museum of Natural History, University of Florida, 1659 Museum Road, Gainesville, Florida 32611, U.S.A.;

³Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.;

⁴Department of Geological and Atmospheric Sciences, Iowa State University, Ames, Iowa 50011, U.S.A., awood@iastate.edu;

⁵Paleontological Institute and Museum, University of Zurich, CH-8006, Switzerland, pimientoc@ufl.edu;

⁶Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama

ABSTRACT—We describe fossil kogiid periotics from the Lower Pliocene upper Bone Valley Formation in central Florida and the Lower to Upper Pliocene Yorktown Formation at Lee Creek Mine, North Carolina. The fossils show diagnostic characters that identify them as belonging to Kogiidae, such as three spines in the anterior process, presence of an incudal process, and a posterior process oriented along the long axis of the bone. Morphological comparisons and morphometric and statistical analyses of periotic proportions confirm the presence of a large and a small morphotype within the sample. The large morphotype (mean length = 39.76 mm) belongs to an unknown kogiid that occurs in both formations, whereas the small morphotype (mean length = 28.64 mm), referred to aff. *Kogia* sp., occurs only in the Yorktown Formation. The cooccurrence of two taxa in North Carolina may represent one of the earliest evidences of sympatry in kogiids and may demonstrate that this ecological behavior has been part of the natural history of this group at least since the deposition of the Yorktown Formation at Lee Creek (~4.8–3.1 Ma). In addition, the occurrence of the large morphotype in the upper Bone Valley Formation, herein reported for the first time, shows that we are still far from understanding the diversity of marine mammals of that formation and that revision of newly acquired material is necessary.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Vélez-Juarbe, J., A. R. Wood, and C. Pimiento. 2016. Pygmy sperm whales (Odontoceti, Kogiidae) from the Pliocene of Florida and North Carolina. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2016.1135806.

INTRODUCTION

The Palmetto Fauna of the upper Bone Valley Formation in Florida and the Yorktown Formation at Lee Creek Mine in North Carolina are considered two of the most diverse Pliocene marine mammal deposits (Morgan, 1994; Tedford et al., 2004; Ward and Bohaska, 2008). Identification of material from these formations is usually based on diagnostic cranial material, primarily skulls, mandibles, and ear bones (e.g., periotics), and, to a lesser extent, postcranial elements (e.g., Kazár and Bohaska, 2008). The marine mammal fauna of the upper Bone Valley Formation was reviewed by Morgan (1994), who listed a total of 17 taxa that included cetaceans, sirenians, and pinnipeds. In addition, Whitmore and Kaltenbach (2008), Kohno and Ray (2008), and Koretsky and Ray (2008) revised the cetaceans and pinnipeds of the Yorktown Formation at Lee Creek where they listed a total of 34 taxa.

The Bone Valley and Yorktown formations share taxa at a higher taxonomic level; however, they also present many unique occurrences (Appendix 1). Because of the inherent uncertainties of the fossil record, these unique occurrences could be either

true absences or the result of sampling bias. New discoveries and additions to these taxonomic lists will enhance our knowledge of early Pliocene marine mammal communities, ultimately allowing us to better understand changes in mammal diversity in deep-time and their biogeographic implications.

During a recent revision of the fossil material from the upper Bone Valley Formation at the Florida Museum of Natural History, the senior author of this work (JVJ) noted the presence of kogiid periotics, which have not been previously reported from this formation. Though kogiid periotics are known from the Yorktown Formation at Lee Creek (Luo and Marsh, 1996; Whitmore and Kaltenbach, 2008), they are in need of detailed revision. Here we describe kogiid periotics from both the Palmetto Fauna (5–4.7 Ma; Morgan, 1994; Webb et al., 2008) of the Lower Pliocene upper Bone Valley Formation in central Florida and from the slightly younger Lower to Upper Pliocene (~4.8–3.1 Ma; Snyder et al., 1983) Yorktown Formation at Lee Creek Mine, North Carolina. Furthermore, by using traditional morphological comparisons, morphometric observations, and statistical analyses, we identify two different cooccurring morphotypes at Lee Creek Mine. The presence and cooccurrence of these morphotypes potentially provide evidence of earliest record of sympatry in kogiids, showing that this type of biogeographic distribution has been part of the natural history of this group at least since the Pliocene.

*Corresponding author.

Color versions of one or more of the figures in this article can be found online at www.tandfonline.com/ujvp.

Institutional and Age Abbreviations—**ChM VP**, Charleston Museum, Charleston, South Carolina; **LACM**, Vertebrate Paleontology Collection, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; **NALMA**, North American Land Mammal Age; **UF**, Vertebrate Paleontology and Mammalogy Collections, Florida Museum of Natural History (FLMNH), University of Florida, Gainesville, Florida, USA; **USNM**, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Measurement Abbreviations—**LPP**, length of posterior process; **MLP**, maximum length of periotic; **MWP**, maximum width of periotic across cochlear portion; **PTA**, proximal thickness of the periotic anterior process.

Extant Specimens Examined—*Kogia breviceps* Blainville, 1838 (UF 13562, 14213, 14214, 17532, 18702, 18704, 19128, 25545; USNM 504902, 504921). *Kogia sima* Owen, 1866 (UF 18705, 18706, 24629, 25573, 25575–25578).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CETACEA Brisson, 1762

ODONTOCETI Flower, 1867

PAN-PHYSETEROIDEA Velez-Juarbe, Wood, De Gracia, and Hendy, 2015

PHYSETEROIDEA Gray, 1821

KOGIIDAE Gill, 1871

KOGIIDAE gen. et sp. indet.

(Figs. 1, 2; Tables 1, S2, 3)

Kogiinae incertae sedis, Whitmore and Kaltenbach, 2008:235 (in part).

Referred Specimens—Ninety-nine isolated left periotics: LACM 37258, 37260, 37262; UF 132958, 132967, 135934, 201842, 203144, 203164, 203525; USNM 26287, 182949, 182961, 251083, 251084, 251089, 251093, 251101–251103, 251105, 251109–251111, 251113, 251117, 251119, 251121, 251123, 251125, 251133, 251136, 251144–251147, 251149, 314779, 328219, 328222, 328223, 328225, 328238, 328240, 328241–328252, 328255, 328257, 328261, 328348, 328350, 347955, 357188, 357189, 364155, 364157, 364162, 364163, 364165, 364167, 364168, 364183, 364185, 364187, 364203, 364373, 447484, 447505, 452416, 452417, 452423, 452425, 452426, 452429, 454758, 454760, 457187, 457190, 457193, 508036; and 75 right periotics: LACM 37259, 37261, 37263, 135743; UF 132932, 135933, 135967, 203165, 203166, 203185, 203526, 209105; USNM 183010, 251081, 251085, 251087, 251088, 251092, 251094, 251096, 251099, 251104, 251112, 251114, 251115, 251124, 251128, 251142, 328221, 328225–328229, 328233–328237, 328239, 328254, 328256, 328349, 364153, 364156, 364158, 364160, 364164, 364166, 364169, 364171, 364184, 364186, 364204–364206, 364208, 364224, 364372, 447484, 452418, 452420, 452421, 452424, 454757, 454760, 454761, 457187, 457191, 457192, 457194, 457196, 508036.

Locality—Fifteen isolated periotics were recovered from the following phosphate mines in the Bone Valley region in central Florida (Morgan, 1994). Hardee County: Fort Green Mine (UF 201842, 203144, 203164, 203165, 203166, 203525, 203526, 209105); Hillsborough County: Four Corners Mine (UF 203185); Polk County: Fort Green Mine (UF 132958), Four Corners Mine (UF 132967), Payne Creek Mine (AGRICO; UF 135933, 135934), Phosphoria Mine (IMC; UF 132932), Tencor Mine (UF 135967). For a more detailed map of the region and location of the mines, see Morgan (1994:fig. 3). All of the fossils from North Carolina (158 periotics) were collected from spoil piles at Lee Creek Mine, located on the south side of Pamlico River, Aurora, Beaufort County, North Carolina (see location of mine in Ward and Blackwelder, 1987:fig. 1).

Formations and Age—Upper Bone Valley Formation; Palmetto Fauna, Lower Pliocene (5–4.7 Ma; early Zanclean [late

Hemphillian NALMA]). Yorktown Formation; Lower–Upper Pliocene (~4.8–3.1 Ma; middle Zanclean–early Piacenzian [Blancan NALMA]).

Description—Anterior process very short, relative to pars cochlearis; its apex or distal end consists of a pair (anterodorsal and anteroventral) of low, usually blunt spines (Figs. 1, 2), which together with the dorsal spine are typically found in kogiids (Muizon, 1988). The dorsal surface of the anterior process is rugose and, when viewed anterolaterally, it has a square outline. A large, fused, accessory ossicle occupies a concavity (fovea epitympanica) on the medial surface of the anterior process (Figs. 1, 2). An anteroexternal sulcus is absent.

The lateral (ventrolateral) tuberosity is located lateral to the malleolar fossa; it is low (~2 mm), blunt, and subtriangular to oval in outline; its smooth surface indicates that the lateral tuberosity did not contact the sigmoid process of the tympanic bulla as it does in *Physeter* and *Zarhachis* (Luo and Marsh, 1996). The hiatus epitympanicus is short and shallow, with some specimens showing little to no break between that surface and the posterior bullar facet. The articulation with the incus is marked by a raised circular area, the incudal process (Fig. 1E–H), located toward the medial extent of the hiatus epitympanicus; this raised area contrasts with the fossa observed in other odontocetes but is typical of kogiids (Luo and Marsh, 1996). A deep (~2 mm), round (~4 mm in diameter) malleolar fossa is located posterior to the accessory ossicle and medial to the lateral tuberosity. A shallow groove extends along the posterior and posteromedial borders of the malleolar fossa in some specimens (e.g., UF 203525). The pars cochlearis has a rounded outline in ventral view. The fenestra rotunda is located on the posteroventral surface of the pars cochlearis; it is large (~5 mm high by 3 mm wide) and separated by 4 mm from the small (~2 mm in diameter), posterodorsally located perilymphatic foramen (= cochlear aqueduct).

The posterior process is oriented posteriorly along the long axis as the rest of the bone; it is large relative to the total size of the periotic, with a posterior bullar facet that is, on average, about 40% of the total length of the periotic and has a total width that equals about 70% of the maximum width of the periotic (Table 1). The posterior process has a ventromedially oriented convex posterior bullar facet, with its medial edge upturned, thus differing from other physeteroids displaying a more posteroventrally oriented posterior bullar facet; fine grooves are present posteriorly on this otherwise smooth surface. In some specimens the length and width of the posterior bullar facet are subequal, giving it a plate-like shape (Fig. 1), similar to the periotics referred to *Scaphokogia cochlearis* (Muizon, 1988:fig. 37; Fig. 4A, C, E) and some of the periotics described from the Yorktown Formation (Whitmore and Kaltenbach, 2008:fig. 80). These rounded, plate-like posterior bullar facets are unlike the shorter, more rectangular surfaces seen in *Kogia* and the Yorktown periotic described by Luo and Marsh (1996:fig. 1). The dorsolateral and dorsal surfaces of the posterior process are relatively smooth and flat, in contrast to the more recurved and rugose surface in physeteroids (e.g., *Aulophyseter morricei* Kellogg, 1927). The rim of the internal acoustic meatus is raised and the meatus is somewhat funnel shaped. The height of the transverse septum within the internal acoustic meatus is variable, in some specimens being lower (e.g., UF 135933) or nearly as high (e.g., UF 203525) as the rim of the meatus; nonetheless, it clearly separates the facial canal from the cochlear foramina (Fig. 1A–D). The ventral foramen of the facial canal is round (<3 mm in diameter) and continuous, with a groove whose medial edge forms a ridge that separates these from the stapedial fossa. The fenestra ovalis is located medial to the ventral foramen of the facial canal, has smooth rounded edges, and its long axis is oriented anteromedial to posterolateral. The stapedial fossa is rounded in outline (~5 mm in diameter) and deep, with

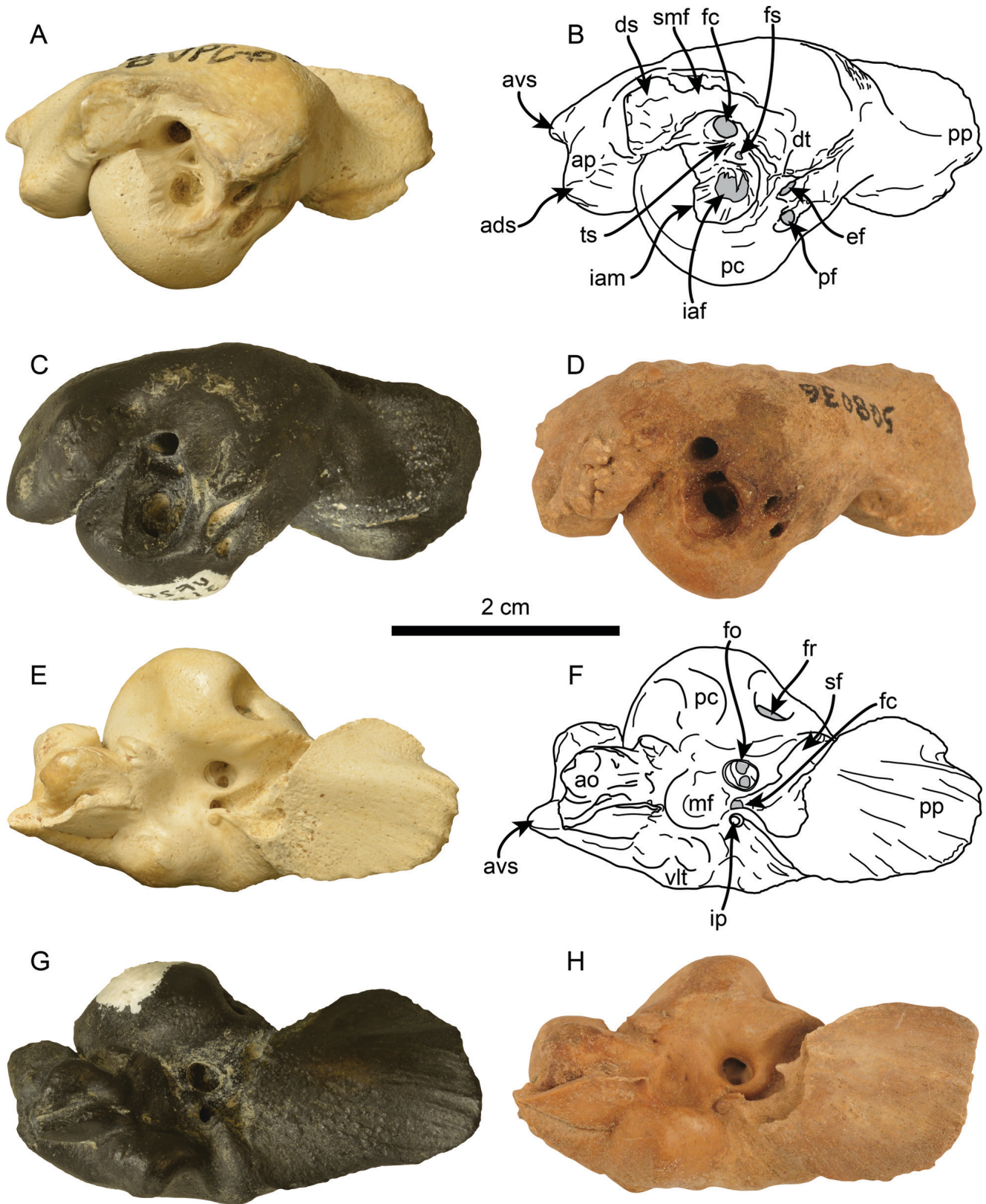


FIGURE 1. Periotics of *Kogiidae* gen. et sp. indet. from the Bone Valley and Yorktown Formations, in dorsal (A–D) and ventral (E–H) views. A, B and E, F, UF 135933, right periotic, Bone Valley Formation; C and G, UF 203185, left periotic (reversed for ease of comparison), Bone Valley Formation; D and H, USNM 508036, right periotic, Yorktown Formation. **Abbreviations:** ads, anterodorsal spine; ao, accessory ossicle; ap, anterior process; avs, anteroventral spine; ds, dorsal spine; dt, dorsal tuberosity; ef, endolymphatic foramen; fc, facial canal; fo, fenestra ovalis; fr, fenestra rotunda; fs, foramen singulare; iaf, inferior acoustic foramen; iam, internal acoustic meatus; ip, incudal process; mf, mallear fossa; pc, pars cochlearis; pf, perilymphatic foramen; pp, posterior process; sf, stapedia muscle fossa; smf, suprameatal fossa; ts, transverse septum; vlt, ventrolateral tuberosity.

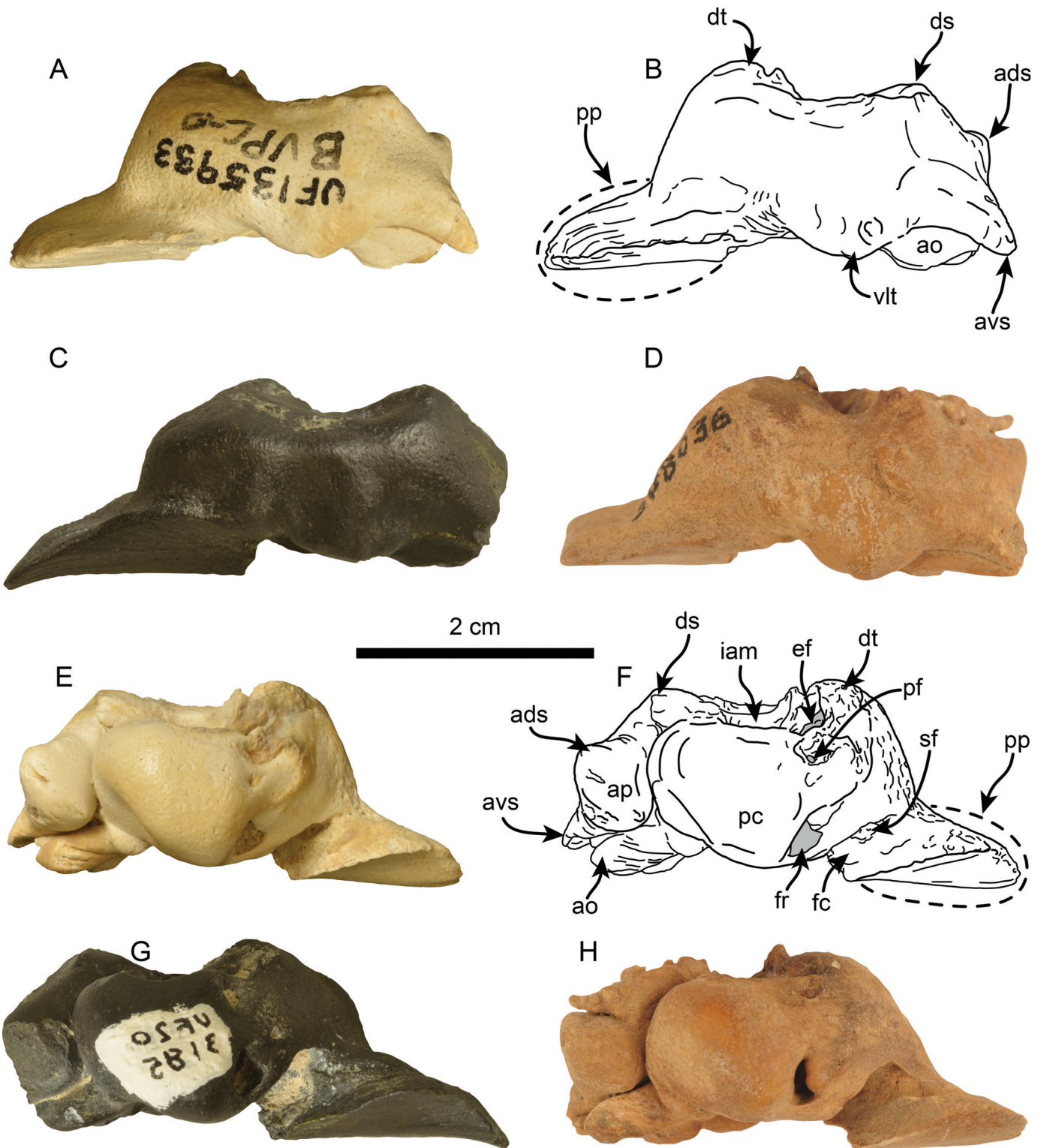


FIGURE 2. Periotics of *Kogiidae* gen. et sp. indet. from the Bone Valley and Yorktown Formations, in lateral (A–D) and medial (E–H) views. A, B and E, F, UF 135933, right periotic, Bone Valley Formation; C and G, UF 203185, left periotic (reversed for ease of comparison), Bone Valley Formation; D and H, USNM 508036, right periotic, Yorktown Formation. **Abbreviations:** ads, anterodorsal spine; ao, accessory ossicle; ap, anterior process; avs, anteroventral spine; ds, dorsal spine; dt, dorsal tuberosity; ef, endolymphatic foramen; fc, facial canal; fr, fenestra rotunda; iam, internal acoustic meatus; pc, pars cochlearis; pf, perilymphatic foramen; pp, posterior process; sf, stapedial fossa; vlt, ventrolateral tuberosity.

well-demarcated edges, and is located posterior to the fenestra ovalis and posterolateral to the fenestra rotunda, separated from the latter by a low caudal tympanic process.

Both the perilymphatic and endolymphatic foramina are close to the internal acoustic meatus, being separated from each other by an approximately 1-mm bony septum. The endolymphatic

TABLE 1. Mean and median values (in mm) of kogiid periotics. Individual measurements in Supplementary Material 1 (modified from Kasuya, 1973:table 3).

		MLP	PTA	MWP	DFE	DFP	LPP	WPP	DCP
Kogiidae ¹	Mean	41.99	15.57	24.25	1.82	3.69	18.15	16.44	15.43
	Med.	40.58	15.60	23.76	1.71	3.67	18.03	16.41	15.70
Kogiidae ²	Mean	39.76	11.55	21.97	1.41	3.17	16.39	15.62	14.98
	Med.	39.00	11.50	22.00	1.50	3.00	16.00	15.85	15.00
aff. <i>Kogia</i>	Mean	28.64	9.08	18.50	0.63	1.55	12.67	8.68	11.14
	Med.	28.50	8.75	18.50	0.50	1.75	12.50	8.00	10.50
<i>K. sima</i>	Mean	26.16	12.09	17.64	0.91	2.04	10.84	8.95	10.87
	Med.	26.26	12.05	17.99	0.87	2.02	10.85	8.70	10.96
<i>K. brev.</i>	Mean	28.62	14.18	19.84	0.83	2.64	11.38	8.78	12.04
	Med.	28.68	14.21	19.99	0.81	2.65	11.38	8.92	12.03
<i>S. cochlearis</i> ³		37.00	13.50	21.00	2.50	3.50	14.00	19.50	13.00
Tirabuzon kogiid ⁴		43.10	11.50	24.60	1.80	2.90	17.80	13.70	16.10

¹Bone Valley.²Yorktown.³MNHN PPI 240.⁴LACM 143481.

Abbreviations: **DCP**, diameter of cochlear portion; **DFE**, least distance between fundus of internal auditory meatus and aperture for endolymphatic duct; **DFP**, least distance between fundus of internal auditory meatus and aperture for perilymphatic duct; **LPP**, length of articular surface of posterior process; **MLP**, maximum length of periotic; **MWP**, maximum width of periotic; **PTA**, proximal thickness of anterior process; **WPP**, width of articular surface of posterior process.

foramen has an oval outline (~4 mm wide by ~2 mm long) and is located between the perilymphatic foramen and the internal acoustic meatus. The dorsal tuberosity is prominent (being the highest point on the dorsal surface), blunt, and located posterolateral to the internal acoustic meatus and endolymphatic foramen (Figs. 1A–D, 2). A concave area just lateral to the internal acoustic meatus is likely the suprimeatal fossa (Luo and Marsh, 1996).

Remarks—Whitmore and Kaltenbach (2008) described, in part, the large morph from the Yorktown Formation at Lee Creek Mine. The overall morphology of the Yorktown periotics does not differ markedly from those of the upper Bone Valley. However, we do note that mean and median values (Table 1) and the results of our morphometric analyses (see below) indicate slight differences between periotics from the respective formations, potentially representing distinct but closely related (congeneric) species.

KOGIA Gray, 1846

aff. *KOGIA* sp. indet.

(Fig. 3A, B, D, E, G, H, J–K; Tables 1, S4)

Kogiinae genus indeterminate, Luo and Marsh, 1996:331.

Kogiinae incertae sedis, Whitmore and Kaltenbach, 2008:235 (in part).

Referred Specimens—Seven left periotics: ChM VP4994, USNM 251148, 364172, 364173, 364175, 364177, 364179; and five right periotics: USNM 328315 (two specimens), 364176, 457197, 457198.

Locality—The material was collected from spoil piles at Lee Creek Mine, located on the south side of Pamlico River, Aurora, Beaufort County, North Carolina (see location of mine in Ward and Blackwelder, 1987:fig. 1).

Formation and Age—Yorktown Formation; Lower Pliocene (~4.8–3.1 Ma: middle Zanclean–early Piacenzian [Blancan NALMA]; Snyder et al., 1983).

Remarks—Luo and Marsh (1996) provided a very thorough description of this morphotype. The specimens differ from the other kogiid periotics from the Yorktown and Bone Valley by their smaller size (Table 1, Fig. 5), being on average about 10 mm shorter, and the more rectangular and mediolaterally narrower outline of the posterior bullar facet. Most of the characteristics that make this morphotype unique are shared with *Kogia breviceps* and *K. sima* and are why we tentatively refer it to aff. *Kogia* sp.

COMPARISONS

Morphological Comparison

Both periotic morphotypes studied show several characteristics diagnostic of kogiids, such as the presence of three spines, dorsal, anterodorsal, and anteroventral, on the anterior process; a raised incudal process; and a posterior process that is oriented along the long axis of the bone and is not recurved ventrally (Muizon, 1988; Luo and Marsh, 1996; Lambert, 2008). The large morphotype from Bone Valley and Yorktown compares best with the referred periotic of *Scaphokogia cochlearis* in size and overall morphology (Muizon, 1988; Table 1, Fig. 4A, C, E). Though differing from Yorktown aff. *Kogia* sp., *K. sima*, and *K. breviceps* in its larger size (Figs. 1–4; Tables 1, S1; Kasuya, 1973:99), the large morphotype further differs by exhibiting a disproportionately larger posterior process with an oval or rounded outline of the posterior bullar facet and, with respect to *Kogia sima* and *K. breviceps*, has a less triangular outline of the cochlear portion in ventral view (Figs. 1E–H, 3F). A recently described kogiid periotic from the late Tortonian of Malta (Bianucci et al., 2011) differs from the Bone Valley material in the unique morphology of the posterior process, which is shallowly concave and posterolaterally directed relative to the long axis of the rest of the periotic.

The second periotic morphotype, found only in the Yorktown Formation, resembles those of *Kogia sima* and *K. breviceps* in its small size and overall morphology (Fig. 3; Luo and Marsh, 1996). However, the Yorktown aff. *Kogia* differs by having a less recurved and dorsoventrally thinner anterior process, more inflated body of the periotic, and more rounded pars cochlearis (= more inflated pars cochlearis sensu Luo and Marsh, 1996; Fig. 3).

There are other records of *Kogia* from Pliocene deposits. Pilleri (1986, 1987) described several periotics from the Pliocene of Italy and referred them to extant taxa. Some of these periotics and a tympanic bulla were later restudied by Bianucci (1996), who referred to them only as *Kogia* sp. Based on their larger size, some of these Italian periotics are more similar to the large morph from Bone Valley and Yorktown but do share morphological similarities with *Kogia* as reported by Bianucci (1996: fig. 2). In addition to the periotics, there is a skull from Piacenzian-age deposits that represents an extinct species, *Kogia pusilla* (Pilleri, 1987); it is the earliest record of the genus known from cranial material (Bianucci and Landini, 1999). Unfortunately, no periotics were associated with the skull.

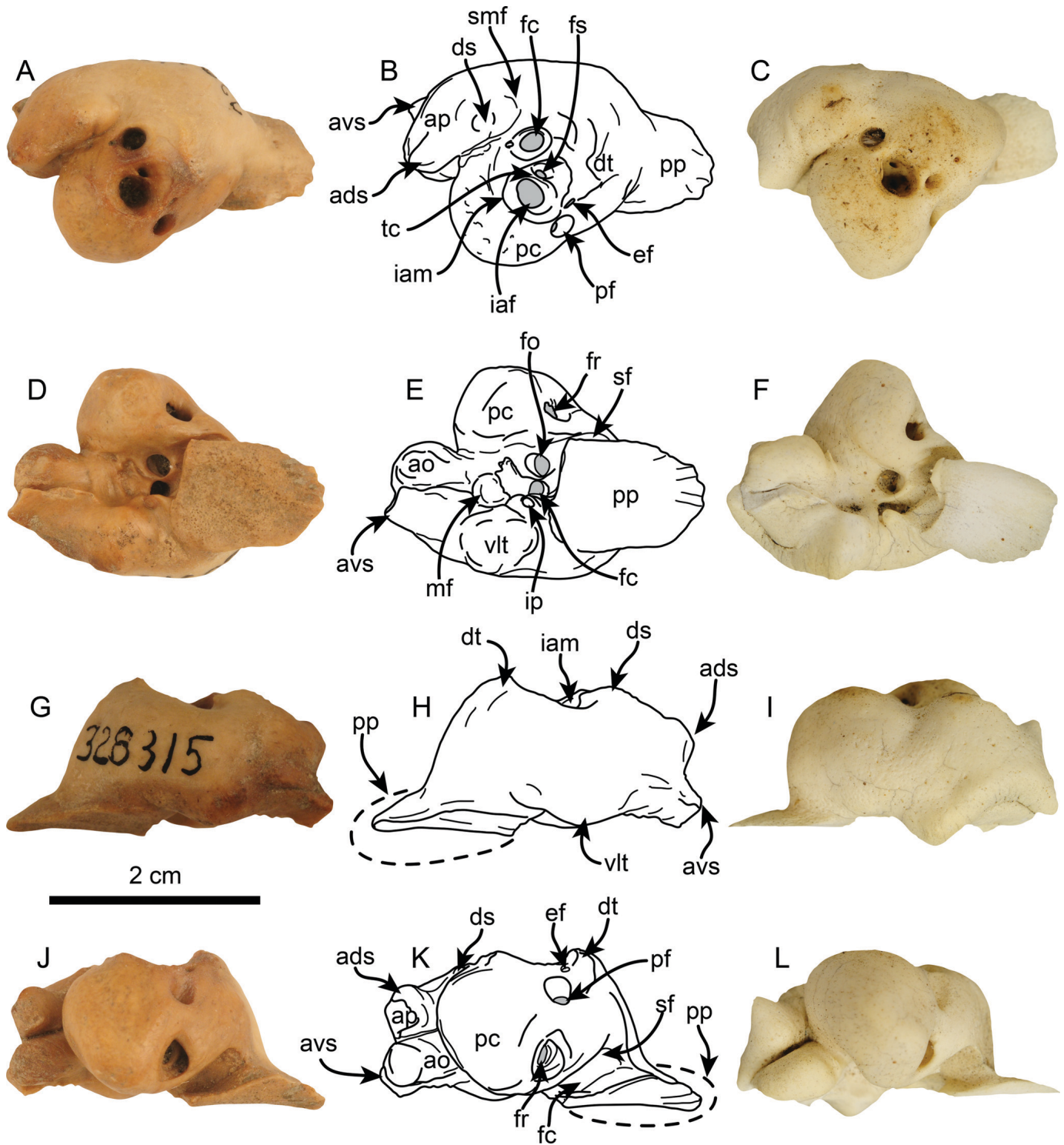


FIGURE 3. Periotics of aff. *Kogia* sp. from the Yorktown Formation and *Kogia sima*, in dorsal (A–C), ventral (D–F), lateral (G–I), and medial (J–L) views. A, B, D, E, G, H, and J, K, aff. *Kogia* sp. (USNM 328315), right periotic, Yorktown Formation; C, F, I, and L, *Kogia sima* (UF 24629), right periotic. **Abbreviations:** ads, anterodorsal spine; ao, accessory ossicle; ap, anterior process; avs, anteroventral spine; ds, dorsal spine; dt, dorsal tuberosity; ef, endolymphatic foramen; fc, facial canal; fo, fenestra ovalis; fr, fenestra rotunda; fs, foramen singulare; iaf, inferior acoustic foramen; iam, internal acoustic meatus; ip, incudal process; mf, malleolar fossa; pc, pars cochlearis; pf, perilymphatic foramen; pp, posterior process; sf, stapedial fossa; smf, suprameatal fossa; tc, transverse crest; vlt, ventrolateral tuberosity.

The third Pliocene record of *Kogia* comes from the late Zanclean Tirabuzon Formation in Baja California Sur. Barnes (1998) mentioned the presence of periotics representing aff. *Kogia* and cf. *Scaphokogia* sp. as part of his Santa Rosalia Local Fauna. Upon

reexamination of the material by one of us (JVJ), it is evident that all of the Tirabuzon material represents a single large morph (e.g., LACM 143481:Fig. 4B, D, F). In general, the morphology and size of the Tirabuzon kogiid periotics cannot be readily differentiated

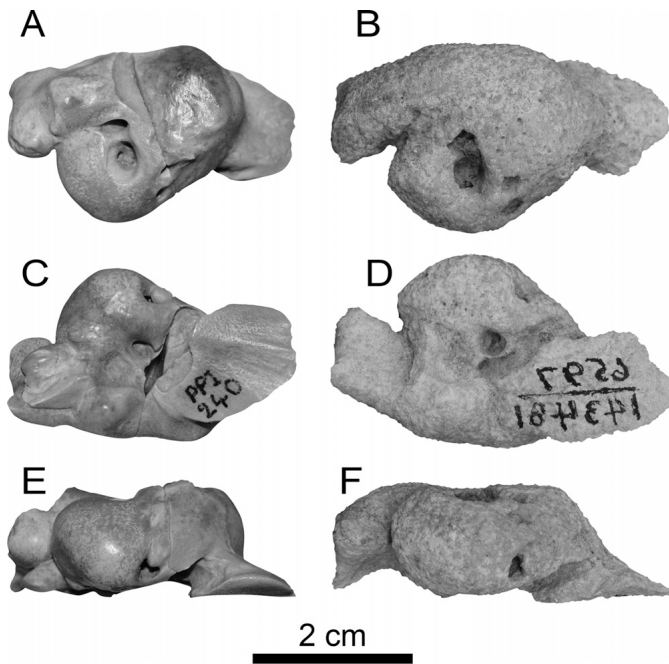


FIGURE 4. Periotics of *Scaphokogia cochlearis* (MNHN PPI 240). **A**, **C**, and **E**, from the late Miocene Pisco Formation of Peru and Kogiidae gen. et sp. indet. (LACM 143481: reversed); **B**, **D**, and **F**, from the early Pliocene Tirabuzon Formation of Baja California Sur, in dorsal (**A–B**), ventral (**C–D**), and medial (**E–F**) views.

from the referred periotic of *S. cochlearis* or from any of the large morphs from the Bone Valley or Yorktown formations examined in this study and is better referred to Kogiidae gen. et sp. indet.

Other fossil kogiids from the Bone Valley and Yorktown localities include *Kogiopsis floridana* Kellogg, 1929 and *Aprixokogia kelloggi* Whitmore and Kaltenbach, 2008. Although fragmentary, the type material of *K. floridana* (cast LACM 123975) represents a taxon of a size larger than any known kogiid and more consistent with physeterids. Therefore, we agree with other workers (e.g., Barnes, 1973; de Muizon, 1988) who consider *K. floridana* a physeterid instead. The stem kogiid *Aprixokogia kelloggi* was described based on a nearly complete skull, with no periotics associated with it, which limits our comparison with this species. Additional fossil kogiids, such as *Thalassocetus antwerpensis* Abel, 1905, *Praekogia cedrosensis* Barnes, 1973, and *Nanokogia isthmia* Velez-Juarbe et al., 2015, are known only from cranial material lacking associated periotics.

Morphometric Analysis

Qualitative comparisons of the Bone Valley and Yorktown kogiid periotics ($n = 178$) and assessment of the measurements presented in Table 1 and complete measurements of each periotic reported in the Supplementary Material (Tables S2–S4, Fig. S1) conservatively indicate the presence of two morphotypes in the sample. We conducted morphometric analyses, using the statistical software R (R Development Core Team, 2012) to further test whether the fossil periotics actually reflect the presence of two distinct taxa. First, we performed principal component analysis on linear measurements (centered and geometrically scaled) from the 172 complete fossil periotics and 16 periotics from extant taxa to detect groupings along statistically significant principal component (PC) axes. Results from pair-wise Anderson tests (Zelditch et al., 2012) show that the eigenvalues associated with the first two PC axes are significantly greater than subsequent eigenvalues ($\chi^2 = 158.06$, $df = 2$, $P < 0.001$ and $\chi^2 = 27.17$, $df = 2$,

$P < 0.001$), indicating that PC1 and PC2 are aligned along biologically significant dimensions of variance.

Along PC1, the periotics separate into a group with highly negative values (i.e., small morphotype and *Kogia* spp.) and a group of more positive values (large morphotype; Fig. 5A). The highest PC1 loadings correspond to the width and length of the posterior process (0.64 and 0.47, respectively), indicating that the large morphotype differs significantly from the small morphotype by exhibiting a disproportionately larger posterior process. The grouping of taxa along the PC2 axis is based primarily on the proximal thickness of the anterior process (proximal thickness of the periotic anterior process loading = 0.93). The noticeable separation of extant *Kogia* spp. along PC2 suggests that the morphological variation represented by this axis is restricted to the species level.

We also used a Welch's two-sample t -test ($\alpha = 0.05$) to compare ratios and measurements between the distinct morphotypes (large [Bone Valley and Yorktown combined] and small) of the Bone Valley and Yorktown formations and the periotics of extant *Kogia* spp. (Table 1, S1; Fig. 5B). We compared maximum length (MLP) to length of posterior process (LPP) ratio (MLP/LPP); width of periotic across cochlear portion (MWP) to length of posterior process (LPP) ratio (MWP/LPP); and the MLP and MWP measurements (Fig. 5B).

The differences observed among the fossil morphotype measurements are greater than those in the two extant *Kogia* spp. (MLP/LPP fossil morphotypes: $t = 2.71$, $P = 0.02$; *Kogia* spp.: $t = 2.30$, $P = 0.04$; MWP/LPP fossil morphotypes: $t = 1.94$, $P = 0.07$; *Kogia* spp.: $t = 2.52$, $P = 0.03$; MLP fossil morphotypes: $t = 7.32$, $P < 0.001$; *Kogia* spp.: $t = 3.99$, $P = 0.002$; MWP fossil morphotypes: $t = 3.90$, $P = 0.002$; *Kogia* spp.: $t = 1.53$, $P = 0.15$; LPP fossil morphotypes: $t = 7.16$, $P < 0.001$; *Kogia* spp.: $t = 0.35$, $P = 0.72$; Fig. 5B). Similarly, the Mahalanobis distance between the multivariate means of the two fossil morphotypes is greater than that of the extant species (3.51 and 1.76, respectively). Consequently, we hypothesize that the differences between the fossil morphotypes large and small from the Yorktown Formation do not reflect an ontogenetic series or sexual dimorphism within a single species. Instead, these morphotypes potentially indicate the presence of two sympatric species of kogiids during the early Pliocene.

DISCUSSION

Previous work had pointed out the presence of at least two kogiids in the Yorktown Formation at Lee Creek, based on periotics (Luo and Marsh, 1996; Whitmore and Kaltenbach, 2008) and postcranial elements (Kazár and Bohaska, 2008). Here, we have confirmed the presence of these two morphotypes in Lee Creek, as well as identified one of them (the large morph) in the Palmetto Fauna of the upper Bone Valley Formation in Florida. The Yorktown periotics represent two different taxa, potentially different genera (one referred to aff. *Kogia*), and is interpreted as one of the earliest evidences of sympatry in kogiids. However, because the fossils from Lee Creek Mine come from spoil piles and therefore lack a well-resolved stratigraphic context, we consider sympatry as a tentative scenario. The newly noted presence of kogiids in the upper Bone Valley shows that we are still far from understanding the diversity of marine mammals of the Palmetto Fauna and that a revision of material acquired in more recent years is needed. Unfortunately, until diagnostic cranial material associated with any of these morphotypes is collected, we cannot determine their true affinities and know whether they belong to any of the Pliocene kogiids known from more diagnostic cranial material, such as *Aprixokogia kelloggi* from the Yorktown Formation. Alternatively, it is possible that the large morph reported here actually represents *A. kelloggi*, because it is the largest of the two better known Pliocene-age kogiids from the Atlantic–Mediterranean regions, whereas the small morph

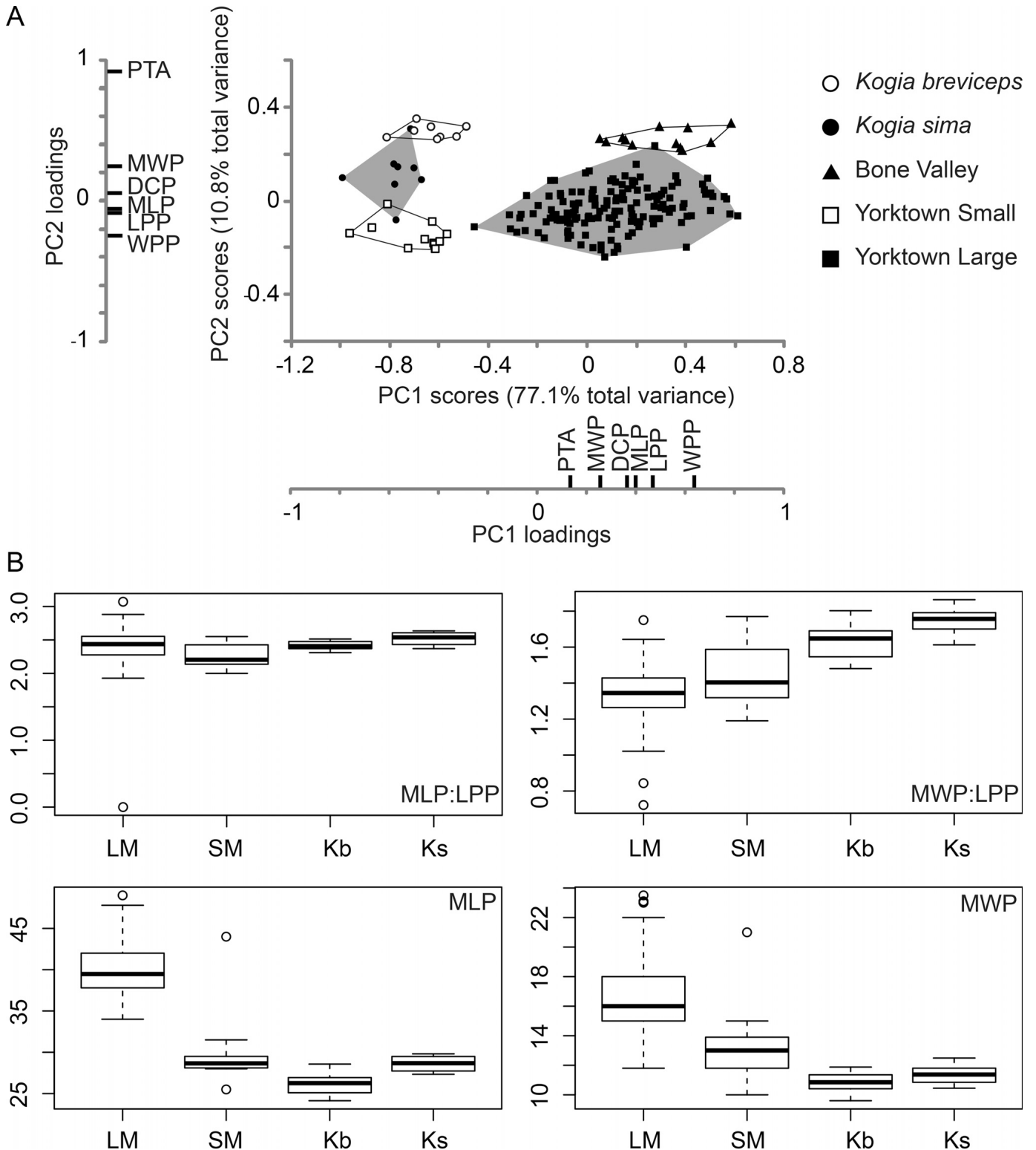


FIGURE 5. Results of morphometric analyses of the Bone Valley and Yorktown kogiid periotics. **A**, bivariate plot of principal component results showing the separation of the large Yorktown morphotype (solid squares) from the small morphotype (hollow squares) along the statistically significant PC1 axis. PC1 and 2 loadings of the original linear measurements are shown next to their respective axes; **B**, differences in proportions between fossil morphotypes large and small and between *Kogia breviceps* and *K. sima*. *P* values based on Welch's two-sample *t*-tests ($\alpha = 0.05$). **Abbreviations:** **DCP**, diameter of cochlear portion; **Kb**, *Kogia breviceps*; **Ks**, *Kogia sima*; **LM**, large morphotype (Bone Valley and Yorktown); **LPP**, length of posterior process; **MLP**, maximum length of periotic; **MWP**, maximum width of periotic across cochlear portion; **PTA**, proximal thickness of anterior process; **SM**, small morphotype (Yorktown); **WPP**, width of articular surface of posterior process.

represents *Kogia pusilla*. Nonetheless, our work highlights the importance of understanding morphological variation in less diagnostic and/or more fragmentary elements, such as periotics and postcranial elements, because they can uncover a greater degree of diversity than that represented by well-preserved cranial material (e.g., monodontids in the Yorktown Formation; Kazár and Bohaska, 2008; Vélez-Juarbe and Pyenson, 2012). Our methodology should provide a basis to study other taxa represented in collections by large numbers of periotics, such as other material from the Yorktown Formation or from the middle Miocene Sharktooth Hill Bonebed (Pyenson et al., 2009).

CONCLUSIONS

Our description and quantitative comparisons of the kogiid periotics from the early Pliocene Palmetto Fauna of the upper Bone Valley Formation, Florida, and Yorktown Formation, North Carolina, identify significant differences in morphology, size, and shape amongst the specimens and confirm the presence of two morphotypes. The large morphotype, which we designate as an indeterminate taxon of Kogiidae, is found in both Bone Valley and Yorktown, whereas the second, small morphotype is found only in the latter and represents an unknown species with similarities to *Kogia*. In addition, our reexamination of other published Pliocene kogiid periotics from North America revealed that previous reports of aff. *Kogia* and cf. *Scaphokogia* from the Tirabuzon Formation in Baja California Sur represent a single taxon, best considered as Kogiidae gen. et sp. indet.

The occurrence of kogiids in the Palmetto Fauna of the upper Bone Valley Formation represents a new record, expanding the diversity of marine mammals in the early Pliocene of Florida. The presence of two species of kogiids in the Yorktown Formation potentially represents the earliest evidence of sympatry in kogiids and indicates that this type of biogeographic distribution was likely present at least since the time of deposition of the Yorktown Formation at Lee Creek (~4.8–3.1 Ma) and thus is not restricted to extant taxa.

ACKNOWLEDGMENTS

We thank D. J. Bohaska, C. W. Potter, and N. D. Pyenson (USNM); R. C. Hulbert, Jr., and C. L. McCaffery (FLMNH); C. Argot, G. Billet, and C. de Muizon (MNHN) for providing access to specimens under their care. We are grateful to G. Bianucci, R. E. Fordyce, and Editor O. Lambert for their thorough and helpful review of our article. We extend our gratitude to J. E. Ranson, Jr., for collecting and kindly donating some of the Bone Valley material. The pictures of the UF material were taken by S. Moran as part of ongoing curatorial efforts sponsored by NSF CSBR grant#1203222. This project was funded by NSF PIRE grant #0966884 and NSF Earth Sciences Postdoctoral Fellowship grant #1249920.

LITERATURE CITED

- Abel, O. 1905. Les odontocètes du Boldérein (Miocène supérieur) des environs d'Anvers. Mémoires du Musée royal d'histoire naturelle de Belgique 3:1–155.
- Barnes, L. G. 1973. *Praekogia cedrosensis*, a new genus and species of fossil pygmy sperm whale from Isla Cedros, Baja California, Mexico. Contributions in Science 247:1–20.
- Barnes, L. G. 1998. The sequence of fossil marine mammal assemblages in Mexico. Avances en Investigación, Paleontología de Vertebrados, Publicación Especial 1:26–79.
- Berta, A., S. Kienle, G. Bianucci, and S. Sorbi. 2015. A reevaluation of *Pliophoca etrusca* (Pinnipedia, Phocidae) from the Pliocene of Italy: phylogenetic and biogeographic implications. Journal of Vertebrate Paleontology 35:1, e889144, DOI: 10.1080/02724634.2014.889144
- Bianucci, G. 1996. I Cetacei fossili del Museo di Storia Naturale Dell'Università di Pisa. Atti della Società Toscana di Scienze Naturali Memorie Serie A 103:63–68.
- Bianucci, G., and W. Landini. 1999. *Kogia pusilla* from the middle Pliocene of Tuscany (Italy) and a phylogenetic analysis of the family Kogiidae (Odontoceti, Cetacea). Rivista Italiana di Paleontologia e Stratigrafia 105:445–453.
- Bianucci, G., M. Gatt, R. Catanzariti, S. Sorbi, C. G. Bonavia, R. Curmi, and A. Varola. 2011. Systematics, biostratigraphy and evolutionary pattern of the Oligo–Miocene marine mammals from the Maltese Islands. Geobios 44:549–585.
- Blainville, H. de. 1838. Sur les cachalots. Annales Françaises et Étrangères d'Anatomie et de Physiologie 2:335–337.
- Brisson, M. J. 1762. Regnum Animale in Classes IX Distributum, Sive Synopsis Methodica Sistens Generalem Animalium Distributionem in Classes IX, et Duorum Primarium Classium, Quadrupedum Scilicet & Cetaceorum, Particulare Divisionem in Ordines, Sectiones, Genera, et Species. T. Haak, Paris, 296 pp.
- Domning, D. P., and O. A. Aguilera. 2008. Fossil Sirenia of the West Atlantic and Caribbean region. VII. *Nanosiren garciae*, gen. et sp. nov. and *Nanosiren sanchezi*, sp. nov. Journal of Vertebrate Paleontology 28:479–500.
- Flower, W. H. 1867. Description of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillii*, with remarks on the systematic position on these animals in the order Cetacea. Transactions of the Zoological Society of London 6:87–116.
- Gibson, M. L., and J. H. Geisler. 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae), from the Lee Creek Mine, North Carolina. Journal of Vertebrate Paleontology 29:966–971.
- Gill, T. 1871. The sperm whales, giant and pygmy. American Naturalist 4:723–743.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. London Medical Repository 15:296–310.
- Gray, J. E. 1846. On the cetaceous animals; pp. 13–53 in J. Richardson and J. W. Gray (eds.), The Zoology of the Voyage of H. M. S. Erebus and Terror under the Command of Captain Sir James Clark Ross, R. N., F. R. S., during the Years 1839 to 1843. Vol. 1 pt. 3 (Mammals). Longman, Brown, Green and Longmans, London.
- Kasuya, T. 1973. Systematic consideration of recent toothed whales based on morphology of tympano-periotic bone. Scientific Reports of the Whale Research Institute (Tokyo) 25:1–103.
- Kazár, E., and D. J. Bohaska. 2008. Toothed whale (Mammalia: Cetacea: Odontoceti) limb bones of the Lee Creek Mine, North Carolina; pp. 271–324 in C. E. Ray, D. J. Bohaska, I. A. Koretsky, L. W. Ward, and L. G. Barnes (eds.), Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication 14.
- Kellogg, R. 1927. Study of the skull of a fossil sperm-whale from the Temblor Miocene of Southern California. Contributions to Paleontology from the Carnegie Institution of Washington 346:1–23.
- Kellogg, R. 1929. A new fossil toothed whale from Florida. American Museum Novitates 389:1–10.
- Kohno, N., and C. E. Ray. 2008. Pliocene walrus from the Yorktown Formation of Virginia and North Carolina, and a systematic revision of the North Atlantic Pliocene walrus; pp. 39–80 in C. E. Ray, D. J. Bohaska, I. A. Koretsky, L. W. Ward, and L. G. Barnes (eds.), Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication 14.
- Koretsky, I. A., and C. E. Ray. 2008. Phocidae of the Pliocene of Eastern USA; pp. 81–140 in C. E. Ray, D. J. Bohaska, I. A. Koretsky, L. W. Ward, and L. G. Barnes (eds.), Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication 14.
- Lambert, O. 2008. Sperm whales from the Miocene of the North Sea: a re-appraisal. Bulletin de l'Institut royal des sciences naturelles de Belgique, Sciences de la Terre 78:277–316.
- Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus 1, Editio decima, reformata. Laurentii Salvii, Stockholm, Sweden, 823 pp.
- Luo, Z., and K. Marsh. 1996. Petrosal (periotic) and inner ear of a Pliocene kogiine whale (Kogiinae, Odontoceti): implications on relationships and hearing evolution of toothed whales. Journal of Vertebrate Paleontology 16:328–348.
- Morgan, G. S. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of Central Florida; pp. 239–268 in A. Berta and T. A. Deméré (eds.), Contributions in Marine Mammal

- Paleontology Honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29.
- Muizon, C. de. 1988. Les Vertébrés fossiles de la Formation Pisco (Pérou) III. Les odontocètes (Cetacea, Mammalia) du Miocène. Editions recherche sur les civilisations, Mémoire 78:1–244.
- Owen, R. 1866. On some Indian Cetacea collected by Walter Elliot, Esq. Transactions of the Zoological Society of London 6:17–47.
- Pilleri, G. 1986. Pygmy sperm whales (*Kogia*) in the Italian Pliocene. Investigations on Cetacea 18:133–153.
- Pilleri, G. 1987. The Cetacea of the Italian Pliocene with a Descriptive Catalogue of the Species in Florence Museum of Paleontology. Vammalan Kirjapaino Oy, Vammala, Finland, 160 pp.
- Pyenson, N. D., R. B. Irmis, J. H. Lipps, L. G. Barnes, E. D. Mitchell, Jr., and S. A. McLeod. 2009. Origin of a widespread marine bonebed deposited during the middle Miocene Climatic Optimum. *Geology* 37:519–522.
- R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Snyder, S. W., L. L. Mauger, and W. H. Akers. 1983. Planktonic foraminifera and biostratigraphy of the Yorktown Formation, Lee Creek Mine. *Smithsonian Contributions to Paleobiology* 53:455–482.
- Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafraña, R. M. Hunt Jr., J. E. Storer, C. R. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene epochs); pp. 169–231 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York.
- Velez-Juarbe, J., and N. D. Pyenson. 2012. *Bohaskaia monodontoides*, a new monodontid (Cetacea, Odontoceti, Delphinoidea) from the Pliocene of the Western North Atlantic Ocean. *Journal of Vertebrate Paleontology* 32:476–484.
- Velez-Juarbe, J., A. R. Wood, C. De Gracia, and A. J. W. Hendy. 2015. Evolutionary patterns among living and fossil kogiid sperm whales: evidence from the Neogene of Central America. *PLoS ONE* 10(4): e0123909.
- Ward, L. W., and B. W. Blackwelder. 1987. Late Pliocene and early Pleistocene Mollusca from the James City and Chowan River at the Lee Creek Mine; pp. 113–283 in C. E. Ray (ed.), *Geology and Paleontology of the Lee Creek Mine, North Carolina, II*. Smithsonian Contributions to Paleobiology 61.
- Ward, L. W., and D. J. Bohaska. 2008. Synthesis of paleontological and stratigraphic investigations at the Lee Creek Mine, Aurora, N. C. (1958–2007); pp. 325–436 in C. E. Ray, D. J. Bohaska, I. A. Koretsky, L. W. Ward, and L. G. Barnes (eds.), *Geology and Paleontology of the Lee Creek Mine, North Carolina, IV*. Virginia Museum of Natural History Special Publication 14.
- Webb, S. D., R. C. Hulbert Jr., G. S. Morgan, and H. F. Evans. 2008. Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the central Florida phosphate district. *Natural History Museum of Los Angeles County Science Series* 41:293–312.
- Whitmore, F. C., Jr., and J. A. Kaltenbach. 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina; pp. 181–269 in C. E. Ray, D. J. Bohaska, I. A. Koretsky, L. W. Ward, and L. G. Barnes (eds.), *Geology and Paleontology of the Lee Creek Mine, North Carolina, IV*. Virginia Museum of Natural History Special Publication 14.
- Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. (eds.) 2012. *Geometric Morphometrics for Biologists: A Primer*, second edition. Elsevier Academic Press, New York, 488 pp.

Submitted September 29, 2015; revisions received December 17, 2015; accepted December 21, 2015.

Handling editor: Olivier Lambert.

APPENDIX 1. Marine mammal assemblages from the upper Bone Valley Formation Palmetto Fauna and Yorktown Formation at Lee Creek (compiled from Morgan, 1994; Domning and Aguilera, 2008; Kazár and Bohaska, 2008; Kohno and Ray, 2008; Koretsky and Ray, 2008; Whitmore and Kaltenbach, 2008; Gibson and Geisler, 2009; Velez-Juarbe and Pyenson, 2012).

		Palmetto Fauna	Lee Creek
Cetacea;	Physeteridae gen. et sp. indet. 1		X
Physeteridae	Physeteridae gen. et sp. indet. 1		X
	<i>Kogiopsis floridana</i>	X	
	<i>Physeterula</i> sp.	X	
Kogiidae	Kogiidae gen. et sp. indet.	X	X
	aff. <i>Kogia</i> sp.		X
	<i>Aprixokogia kelloggi</i>		X
Ziphiidae	<i>Mesoplodon</i> sp.	X	
	<i>Mesoplodon longirostris</i>		X
	<i>Ninziphius</i> cf. <i>N. platyrostris</i>		X
	<i>Ninziphius platyrostris</i>	X	
	<i>Ziphius</i> cf. <i>Z. cavirostris</i>		X
Iniidae	<i>Goniodelphis hudsoni</i>	X	
Pontoporiidae	Pontoporiidae gen. et sp. indet.	X	
	cf. <i>Pontoporia</i> sp.		X
	<i>Auroracetus bakerae</i>		X
Monodontidae	Monodontidae gen. et sp. indet.		X
	<i>Bohaskaia monodontoides</i>		X
Delphinidae	Delphinidae gen. et sp. indet.	X	
	<i>Delphinus</i> sp.		X
	<i>Globicephala</i> sp.		X
	<i>Lagenorhynchus</i> sp.		X
	<i>Lagenorhynchus harmatuki</i>		X
	<i>Pseudorca</i> sp.		X
	cf. <i>Stenella</i> sp.		X
	<i>Stenella rayi</i>		X
	<i>Tursiops</i> sp.		X
Mysticeti;	Cetotheriinae gen. et sp. indet.		X
Cetotheriidae	<i>Herpetocetus transatlanticus</i>		X
Balaenopteridae	<i>Balaenoptera</i> sp.	X	
	<i>Balaenoptera</i> cf. <i>B. acutorostrata</i>		X
	<i>Balaenoptera borealina</i>		X
	<i>Balaenoptera floridana</i>	X	
	<i>Megaptera</i> sp.		X
	<i>Plesiocetus</i> sp.		X
Eschrichtiidae	<i>Gricetoides aurorae</i>		X
Balaenidae	<i>Balaena</i> sp.		X
	<i>Balaenula</i> sp.		X
Carnivora;	<i>Enhydritherium terraenovae</i>	X	
Mustelidae			
Odobenidae	<i>Trichecodon huxleyi</i>	X	
	<i>Ontocetus emmonsii</i>		X
Phocidae	Phocinae gen. et sp. indet.	X	
	<i>Callophoca obscura</i>	X	X ¹
	<i>Homiphoca capensis</i>		X
	<i>Gryphoca similis</i>		X
	<i>Phocanella pumila</i>	X	X
	<i>Platyphoca vulgaris</i>		X
	<i>Pliophoca etrusca</i>		X ¹
Sirenia;	<i>Corystosiren varguezii</i>	X	
Dugongidae	<i>Nanosiren garciae</i>	X	

¹Lee Creek material referred to these taxa may actually represent different species according to Berta et al. (2015).