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STROMERIUS NIDENSIS, NEW ARCHAEOCETE (MAMMALIA, CETACEA) FROM THE UPPER EOCENE QASR EL-SAGHA FORMATION, FAYUM, EGYPT

BY

PHILIP D. GINGERICH[1]

Abstract — A new basilosaurid archaeocete, *Stromerius nidensis*, is described on the basis of an articulated series of thoracic, lumbar, and caudal vertebrae. The type specimen was collected in the Temple Member of the Qasr el-Sagha Formation in northern Fayum. The type locality is on the Qasr el-Sagha escarpment near Garet el-Esh, in strata of middle Priabonian (middle late Eocene) age. *Stromerius* differs from all known archaeocetes in having much longer and more anteriorly oriented metapophyses on lumbar vertebrae. It is larger than contemporary *Saghacetus osiris*, and smaller than older *Dorudon atrox* and, if valid, *Dorudon stromeri*. *Stromerius* differs from other late Eocene archaeocetes in retaining a distinct anticlinal vertebra (the penultimate thoracic), and it differs in having twelve lumbars, the last four of which retain vestiges of homology with sacral vertebrae. *Stromerius* is the type of a new subfamily Stromeriinae of the family Basilosauridae.

Masracetus markgrafi is a new genus and species of basilosaurid with large lumbar centra that are distinctive in being relatively short anteroposteriorly. Finally, a lectotype is designated for '*Zeuglodon*' *brachyspondylus* Müller (1849).

INTRODUCTION

The first fossil whale known from the upper Eocene Qasr el-Sagha Formation of Egypt was found by explorer Georg Schweinfurth in January, 1886 (Schweinfurth, 1886). This is a well preserved dentary of a small archaeocete described and named *Zeuglodon osiris* by Dames (1894). '*Zeuglodon*' *osiris* Dames is in turn the type and only known species of the genus *Saghacetus* (Gingerich, 1992: 73). *Zeuglodon zitteli* Stromer (1903), *Zeuglodon sensitivus* Dart (1923), and *Zeuglodon elliotsmithii* Dart (1923) are all synonyms of *Saghacetus osiris* (see Gingerich, 1992: 73). *Saghacetus osiris* is common in the middle part of the Qasr el-Sagha Formation (Stufe II 5a of Blanckenhorn,1902; Temple Member of Bown and Kraus, 1988).

The only additional archaeocete species described from the Qasr el-Sagha Formation is *Prozeuglodon stromeri*, named by Remington Kellogg (1928). The species has always been dif-

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ficult to interpret. The type specimen, BSPM 1904.XII.134e, was collected by Richard Markgraf from an unknown locality and stratigraphic level. Ernst Stromer referred to this specimen as Mn. 9 (München 9; Stromer, 1908: 110), recognized it as immature, identified it as *Zeuglodon osiris*, and reported that it came from a fine-grained, gray-green, soft sandstone of the '*Saghastufe'* (Qasr el-Sagha Formation). He then combined Mn. 9 with another specimen, St. 11 (SMNS 11237a), in a much-reproduced skeletal composite (Stromer, 1908, Pl. I [IV]: 1).

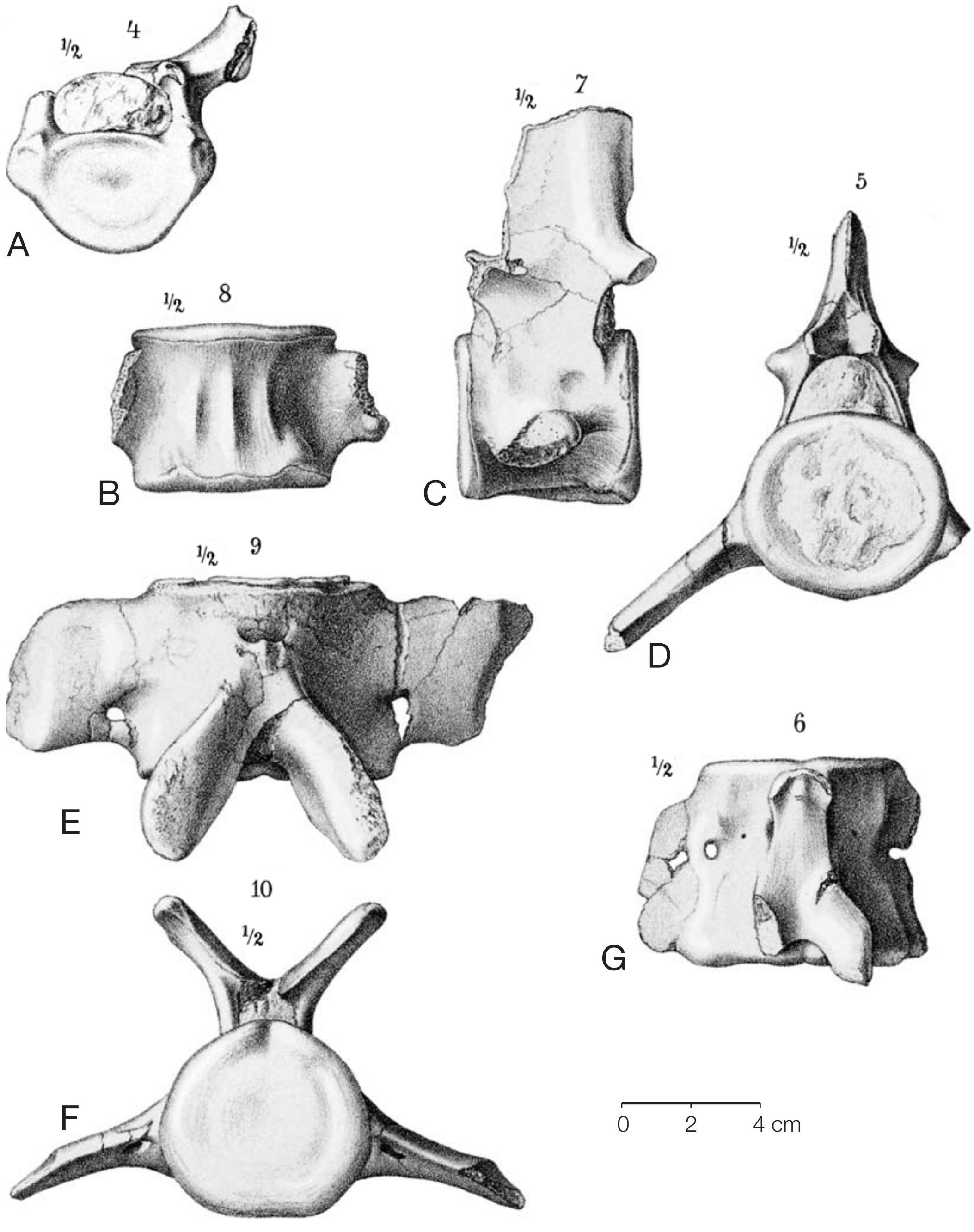
Kellogg (1928: 40), working from Stromer's report, called BSPM 1904.XII.134e a "fairly complete skeleton," applied the name *Prozeuglodon stromeri*, and wrote little else about it. Later, in 1930, Kellogg traveled to Germany where he was able to study Mn. 9. In his 1936 monograph on Archaeoceti, Kellogg (1936: 203) designated BSPM 1904.XII.134e (Mn. 9) as the type of *Dorudon stromeri*, but he left the rest of the composite reconstruction, SMNS 11237a (St. 11), in *'Dorudon' osiris*. Kellogg (1936) omitted any explicit diagnosis of *D. stromeri*, and never explained how *Dorudon stromeri* differs from archaeocete species named previously, including *D. atrox*. Adding to the difficulty of interpreting this species, the type, BSPM 1904.XII.134e, was destroyed when Munich was bombed during World War II. Uhen (2004: 15) regarded the description and measurements of the type specimen of *Dorudon stromeri* as fully consistent with assignment to *D. atrox*.

Stromer collected a number of associated, well-preserved vertebrae when he worked in Fayum in February, 1902. These were found while traveling by camel from Cairo to Qasr el-Sagha. The vertebrae were first cataloged as BSPM 1902.XI.60a, and have since been recataloged as BSPM 1902.XI.504-510. They were collected in Blanckenhorn's interval II 5a of the Saghastufe (Qasr el-Sagha Formation), in a Tamarisk thicket within a plateau 'embayment' at a locality called Tamariskenbucht ('Tamarisk embayment'), a half-day's march (ca. 11-15 km) NNE of Qasr el-Sagha temple (Blanckenhorn, 1902: 381). The vertebrae of BSPM 1902.XI.504-510 were described, and most were illustrated, in Stromer (1903: 65, 76; Pl. IV (XI): 4-10; see Fig. 1 here). Stromer considered this specimen to be a larger species of archaeocete than his *Zeuglodon zitteli*, possibly representing a large specimen of *Zeuglodon osiris* (Stromer, 1903: 83). Kellogg (1936: 213), on the other hand, included BSPM 1902.XI.60a in *Dorudon zitteli* (synonym of '*Zeuglodon' or Saghacetus osiris)*.

In 1991, I collected an unusually well preserved series of thoracic, lumbar, and caudal vertebrae, UM 100140, near Garet el-Esh west of Qasr el-Sagha temple. The vertebrae came from a hard sandstone in Blanckenhorn's interval II 5a of the Temple Member of the Qasr el-Sagha Formation. UM 100140 is virtually identical in comparable parts to Stromer's BSPM 1902.XI.504-510. Both appear to represent a new archaeocete that is different from contemporary *Saghacetus osiris* and from older *Dorudon atrox* and/or *D. stromeri*. UM 100140 and BSPM 1902.XI.504-510 are important in showing a unique combination of primitive and advanced characteristics not seen in any other basilosaurid.

→

FIG. 1 — Five vertebrae included in *Stromerius nidensis*, BSPM 1902.XI.504-510, as illustrated by Stromer (1903, Pl. XI [IV]). All illustrations were reversed when originally printed; they are reprinted correctly here. Stromer's original figure numbers 4-10 and indications of reproduction at ½ natural size are included. A, BSPM 1902.XI.505; thoracic T5 in anterior view. B-C, BSPM 1902.XI.507, T(n-1) in ventral (ant. facing upward) and left lateral view. D, BSPM 1902.XI.506, L2 in posterior view. E-F, BSPM 1902. XI.504; mid-caudal vertebra Ca(p)1 in dorsal (ant. facing down) and anterior view. Note foramen near the anterior margin of the base of each transverse process. G, BSPM 1902.XI.508; mid-caudal vertebra Ca(p)2 in dorsal view (ant. facing down). Note the short transverse process with rib articulation (Fig. 1B) and vertical neural spine (Fig. 1C) on penultimate thoracic T(m). Note also perforating foramina near the center of the base of each transverse process on Ca(p)1 (Fig. 1E) and Ca(p)2 (Fig. 1G).



A
1/2
4
B
1/2
8
C
1/2
7
D
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E
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9
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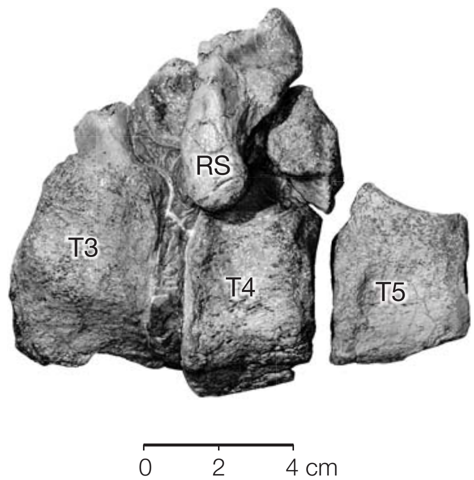

FIG. 2 — Anterior thoracic vertebrae T3, T4, and T5 of *Stromerius nidensis*, UM 100140 (holotype), viewed from the left side with the head of the fifth rib, R5, partially articulated. The right sides of these vertebrae were weathered away before they were collected.

INSTITUTIONAL ABBREVIATIONS

SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
BSPM — Ludwig-Maximilians-Universität und Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich (Germany)
UM — University of Michigan Museum of Paleontology, Ann Arbor, Michigan (U.S.A.)

SYSTEMATIC PALEONTOLOGY

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

Stromerius nidensis, new genus and species
Figs. 1-3

Zeuglodon osiris (in part), Stromer, 1903, p. 65, 76; Pl. IV (XI): 4-10.
Dorudon zitteli (in part), Kellogg, 1936, p. 212.

Holotype.— UM 100140, a well preserved series of 15 thoracic, lumbar, and caudal vertebrae, plus four additional vertebrae (three anterior thoracics and one middle caudal) and fragmentary ribs. All 19 vertebrae were found in association. Twelve of the series of 15 were found in articulation. The series of 15 vertebrae includes parts of one last thoracic, 12 lumbars, an anterior-most caudal, and part of a second caudal.

Type locality.— UM 100140 was found at 29.57195 N latitude, 30.56637 E longitude. This is approximately 11 km WSW of Qasr el-Sagha temple, and about 300 m SW of Garet el-Esh.

Referred specimen.— BSPM 1902.XI.504-510, renumbered from 1902.XI.60a; includes seven vertebrae: two thoracics, two lumbars, and three caudal vertebrae. Five of these are illustrated in Figure 1. All were found as parts of one associated skeleton at a locality called Tamariskenbucht(see above). Geographic coordinates of the locality are, approximately, 29.7 N latitude and 30.8 E longitude.

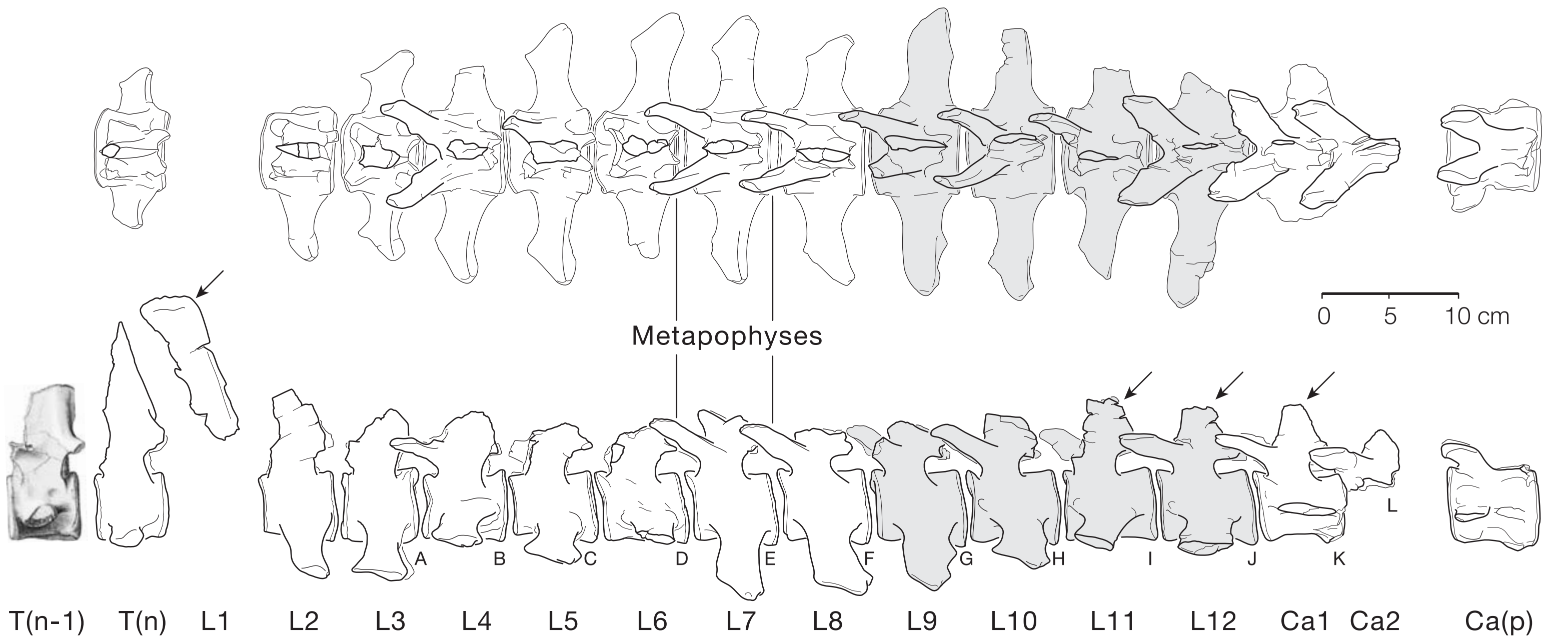

FIG. 3 — Associated vertebrae of *Stromerius nidensis*, UM 100140 (holotype), seen in dorsal and lateral view. T(n), L2, and Ca(p) were found on the weathered surface of the outcrop at the type locality, while the neural spine of L1 and Ca(p)2 were excavated in situ but out of sequence with the rest of the vertebrae. Vertebrae L3 through Ca2 (A through L here and in Table 2) were found and excavated in articulation. Deflection of transverse processes due to burial has not been corrected: this is particularly noticeable in lateral view. Note long, anteriorly-inclined metapophyses on lumbar vertebrae; and four posterior lumbars interpreted as homologous with sacral vertebrae of protocetids (L9-L12; shaded). Arrows mark complete neural spines. T(n-1) is referred specimen BSPM 1902.X1.507 (Fig. 1B,C).

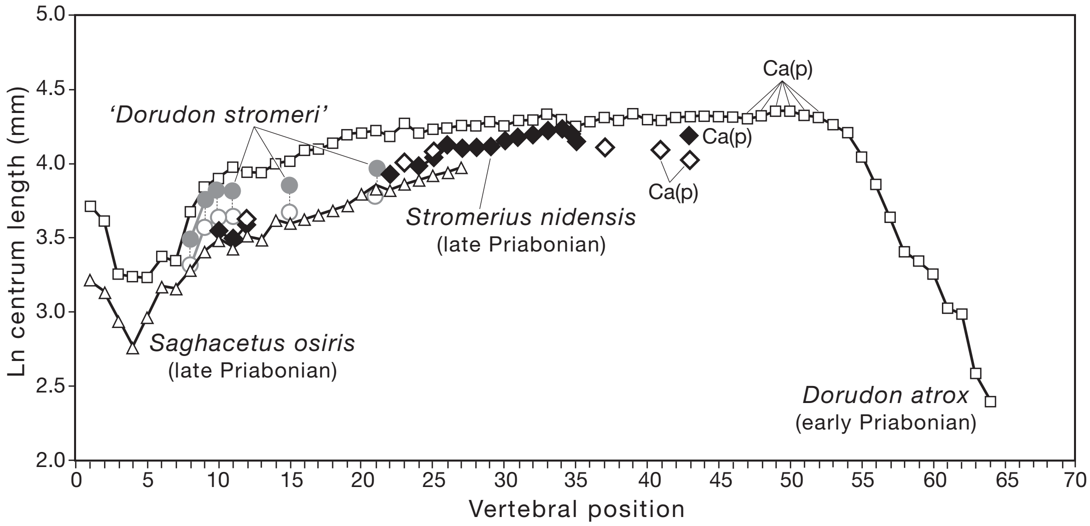

FIG. 4 — Vertebral profiles comparing lengths of vertebral centra for *Stromerius nidensis*, UM 100140 (holotype; Table 2, solid diamonds) and BSPM 1902.XI.504-510 (Table 1, open diamonds). Profiles for *Saghacetus osiris* (open triangles; UM 97550); type specimen of *Dorudon stromeri* (open circles are centrum length without epiphyses; solid circles are augmented 20% to estimate the length with epiphyses); and an average of four *Dorudon atrox* specimens (open squares; measurements from Uhen, 2004) are shown for context. Note that *Stromerius nidensis* has vertebrae intermediate in centrum length between those of *Saghacetus osiris* and *Dorudon atrox* (possibly = *D. stromeri*). Ca(p) indicates a caudal vertebra or series of caudals with a perforated transverse process or processes.

Diagnosis.— *Stromerius* is distinctive among basilosaurids in having unusually long and forwardly-directed metapophyses on lumbar vertebrae (Fig. 3). In addition, *Stromerius* retains an anticlinal-like penultimate thoracic vertebra with a vertical neural spine (Fig. 1C), which differs from the anteriorly directed spine of L2 in the same specimen. *Stromerius* retains a relatively short lumbus seemingly comprising only 12 vertebrae, the last four of which are identifiable as sacral homologs (Fig. 3). In addition, *Stromerius nidensis* differs from contemporary *Saghacetus osiris* in being larger, and from older *Dorudon atrox* and/or *D. stromeri* in being smaller (Fig. 4). *Stromerius nidensis* is the only species of the genus known to date.

Age and distribution.— The type and referred specimens were both found in Blanckenhorn's interval II 5a of the Saghastufe, in the Temple Member of the Qasr el-Sagha Formation. These beds are in the middle part of the Qasr el-Sagha Formation, and they are middle Priabonian or middle late Eocene in age. *Stromerius nidensis* is at present known only from the northern Fayum Province of Egypt, but it probably ranged more widely.

Etymology.— *Stromerius*, masc., named for Ernst Stromer von Reichenbach [1871-1952], esteemed paleontologist of Munich, in recognition of his important contributions to understanding the evolution of whales in Egypt. Species name nidensis comes from *nidus,* L., nest, and refers to the type locality, Garet el-Esh ('hill of the nest').

DESCRIPTION

Two specimens of *Stromerius nidensis* are known. The first, BSPM 1902.XI.504-510 (renumbered from 1902.XI.60a), includes seven vertebrae, five of which are illustrated in Figure 1. Each vertebra has been given a separate catalog number, 504 through 510, irrespective of its position in

TABLE 1 — Measurements of vertebrae *Stromerius nidensis* in BSPM 1902.XI.504-510. Specimen is illustrated in Figure 1. Positions of individual vertebrae in the vertebral column are uncertain because gaps between preserved vertebrae are large. Width and height of each vertebral foramen provide an estimate of neural canal width and height along the vertebral column. Most measurements are those of the author. Stromer (1903: 81) provides an independent set of measurements. All measurements are in mm. Asterisks denote estimates. Abbreviations: *Ca*, caudal vertebra; *Ca(p)*, caudal with perforated transverse process; *L*, lumbar vertebra; *T*, thoracic vertebra; *T(n-1)*, penultimate thoracic; *vert. foram.*, vertebral foramen.

Vertebra	No.	Centrum length	Centrum anterior width	Centrum anterior height	Centrum anterior height	Centrum posterior height	Vert. foram. width	Vert. foram. height
T5	505	38.0	50.0	35.0	60.0	35.0	35.0	15.0
T(n-1)	507	46.0	55.0	45.0	56.0	46.0	29.0	12.5
L2	506	55.0*	57.0	50.0*	60.0	51.0	28.0	13.5
L3	509	59.0*	58.0	53.0	60.0	54.0	25.0	11.5
Ca	510	61.0	62.0	54.0	60.0*	50.0*	12.0	10.0
Ca(p)1	504	60.0	60.0	55.0	60.0	50.0	12.0	10.0*
Ca(p)2	508	56.0	60.0*	52.0	55.0	51.0	11.5	3.0

the vertebral column. As noted above, Stromer found the vertebrae of BSPM 1902.XI.504-510 in association. Measurements of each vertebra of BSPM 1902.XI.504-510 are given in Table 1.

The second specimen, UM 100140 (holotype), includes 19 partial or complete vertebrae (Figs. 2 and 3) and numerous pieces of ribs. UM 100140 was found by the author in October, 1991, while prospecting near Garet el-Esh. It was found weathering out of an indurated sandstone bed. Articulated lumbar and caudal vertebrae were removed in blocks of sandstone that were subsequently prepared in the laboratory. Notes made at the time of excavation indicated that the whale was distinctive in having unusually long and anteriorly-directed metapophyses, and removal in blocks enabled these to be preserved. Measurements of vertebrae of UM 100140 are given in Table 2.

In the following description, vertebrae of both specimens are described in the order of their position in the vertebral column. All vertebrae of both specimens have anterior and posterior epiphyses solidly fused, and both specimens were fully adult.

T3, T4, and T5. — UM 100140 includes the left halves of two vertebral centra preserving facets for articulation of rib capitula, and parts of the left neural arches of two vertebrae, which are all preserved together in a block with the head of a left rib adhering (Fig. 2). There is also an isolated partial centrum that fits behind the more posterior of the centra in the block. The anterior centrum is slightly longer than the middle centrum, and centrum height appears to have been substantially less than centrum width for each. The tubercular facet on each vertebra for articulation with the corresponding rib appears to have been positioned about halfway up the neural arch. Hence the centra involved are interpreted as T3, T4, and T5. One left neural arch is that of T4, and the other represents T5. The attached rib head is interpreted as that of left R5. T3 and T4 are separated by rock matrix representing their separation by an intervertebral disk of connective tissue in life.

BSPM 1902.XI.505 (Fig. 1A) is part of an anterior thoracic vertebra similar to T3, T4, and T5 described above. This includes a relatively short, broad, low centrum, with distinct facets for articulation with rib capitula, and one remaining well-separated facet for articulation with a rib tuberculum. The tubercular facet is on a distinct tubercular process arising from the left neural arch, and the facet itself is surmounted by a small metapophysis. The centrum is a little higher relative

TABLE 2 — Measurements of vertebrae in UM 100140, *Stromerius nidensis.* Letters A-L denote vertebrae preserved in articulation. Specimen is illustrated in Figure 3. Width and height of each vertebral foramen provide an estimate of neural canal width and height along the vertebral column. All measurements are in mm. Asterisks denote estimates. Abbreviations: *ant*., anterior; *Ca*, caudal vertebra; *Ca(p)*, caudal with perforated transverse process; *centr*., centrum; *L*, lumbar vertebra; *metap*., metapophysis; *T*, thoracic vertebra of uncertain position; *T(n)*, last thoracic; *post*., posterior; *thick*., thickness; *trans. proc.*, transverse process; *vert. foram.*, vertebral foramen.

Vertebra	Centr. length	Centr. ant. width	Centr. ant. height	Centr. post. width	Centr. post. height	Vert. foram. width	Vert. foram. height	Trans. proc. length	Trans. proc. A-P	Trans. proc. thick.	Metap. length
T3	35.0	—	35.0*	—	—	—	—	—	—	—	—
T4	33.0	—	35.0*	—	—	—	—	—	—	—	—
T5	36.3	—	34.0*	—		—	—	—	—	—	—
T(n)	51.3	59.3	50.0	59.6	48.2	31.4	17.0	40.5	22.9	11.0	—
L1	—	—	—	—	—	—	—	—	—	—	—
L2	54.1	58.0	48.0*	62.3	52.9	30.5	17.5	69.1	21.8	10.9	—
L3 A	56.9	59.8	49.4	65.2	54.5	28.8	19.3	73.6	23.8	10.3	—
L4 B	62.1	63.5	47.9	64.2	54.3	31.3	18.0	79.5	26.2	11.3	40.7
L5 C	61.0	63.4	47.1	64.0	52.7	30.2	17.4	81.5	25.1	9.1	—
L6 D	61.2	62.7	52.9	65.0	53.6	27.0	16.6	80.4	25.3	9.5	—
L7 E	61.5	63.5	53.4	64.5	54.0	26.6	16.9	90.6	26.1	9.4	42.2
L8 F	64.1	64.2	54.1	65.2	56.0	26.0	13.5	90.2	28.9	9.2	39.7
L9 G	65.9	65.7	50.9*	65.4	57.5	22.6	13.6	93.8	29.9	9.1	33.0
L10 H	66.3	67.0	53.6	65.7	55.0	22.6	13.0	95.8	27.9	8.8	35.3
L11 I	68.5	66.9	52.0	67.2	54.1	20.5	11.8	—	26.8	9.5	27.2
L12 J	69.2	67.0	50.7	68.6	56.3	18.1	12.2	89.4	33.9	9.2	35.2
Ca1 K	63.5	66.9	51.8	70.6	—	18.6	10.5	—	—	—	35.2
Ca2 L	—	—	—	—	—	—	—	—	—	—	27.8
Ca(p)2	66.2	63.7	54.4	61.7	56.6	8.5	3.0	17.1	—	4.9	25.5

to its width than is seen in T3 and T4, and hence it is identified as T5. The vertebral foramen is large, and broad relative to its height.

T(n-1).— BSPM 1902.XI.507 (Fig. 1B-C) is a well preserved posterior thoracic vertebra with short transverse processes bearing a rib articulation at the end. The neural arch supports the lower part of the neural spine, which appears to have been nearly vertical. The vertebral foramen is large and relatively high compared to that of more posterior vertebrae. Prezygapophyses and metapophyses are broken, and the length of the latter cannot be determined. There do not appear to be any nutrient foramina on the ventral surface of the centrum.

The vertical neural spine indicates that T(n-1) was the anticlinal vertebra in the thoracolumbar series. Vertebrae anterior to the anticlinal vertebra would have had posteriorly-inclined neural spines, and vertebrae posterior to it have anteriorly-inclined neural spines. Retention of a distinct anticlinal vertebra is a primitive characteristic not seen in more advanced basilosaurids like *Dorudon* (Uhen, 2004).

T(n).— UM 100140 includes a thoracic vertebra similar to BSPM 1902.XI.507 but with longer transverse processes. These too bear rib articulations, but for smaller ribs. The neural spine is high, relatively long at the base, and anteriorly inclined. As in BSPM 1902.XI.507, the vertebral foramen is large and high relative to that of more posterior vertebrae. Prezygapophyses and metapophyses are broken, and the length of the latter cannot be determined on this vertebra. Postzygapophyses face ventrolaterally and are definitely post-diaphragmatic (if there was a distinct diaphragmatic vertebra). There is a single very small nutrient foramen on the left side of the ventral surface of the centrum.

L1.— UM 100140 includes a long, anteriorly-inclined neural spine. This is very similar to the neural spine preserved on T(n), but does not fit onto any of the following lumbar vertebrae. Hence it is almost certainly from a first lumbar vertebra for which the centrum was not preserved. The neural spine is bilaterally compressed and broadest closer to its posterior margin. The posterior border of the spine has a sharp keel, and the dorsal surface of the spine is rugose where it was undoubtedly attached to a dorsal ligament. This dorsal surface forms an oblique angle with the posterior keel, indicating that the spine itself was anteriorly inclined. The spine is very similar to that preserved on T(n), but seemingly about the anteroposterior length of the neural spine on what is identified as L2. It is possible that the vertebra identified as L1 here is really L2, and the vertebra identified as L2 is really L1.

L2.— UM 100140 includes a relatively complete lumbar vertebra lacking the dorsal end of the neural spine, articular surfaces of zygapophyses, metapophyses, and the right transverse process. As on the posterior thoracics, the vertebral foramen is large and high relative to that of more posterior vertebrae. This vertebra preserves the articular surface of the right postzygapophysis, which faces ventrolaterally. There is a single nutrient foramen on the ventral surface of the centrum, again on the left side.

BSPM 1902.XI.506 (Fig. 1D) is a similar vertebra that is almost identically preserved, It too has a slightly forwardly inclined neural spine.

L3.— L3 is represented by two specimens, UM 100140 (A) and BSPM 1902.XI.509 (not illustrated). The former is the first of the series labeled A-L and excavated in articulation in the field (Table 2). This vertebra is a typical basilosaurid lumbar, with a cylindrical centrum only slightly shallower dorsoventrally than broad bilaterally. The vertebral foramen is large and more rectangular in cross-section than those on more anterior vertebrae. The neural arch is more than half the length of the centrum, with pedicles positioned closer to the anterior surface of the centrum than to the posterior surface.

Prezygapophyses and metapophyses of UM 100140 (A) are broken, but both of the postzygapophyses are well preserved. The ventral surfaces of these are smooth and flat, and as such they might be mistaken for ventrally-facing articular surfaces. However, articulation of several successive vertebrae indicates that the postzygapophyses of one vertebra here have limited contact with prezygapophyses of the following vertebra. Articular surfaces on postzygapophyses are small and lateral to the postzygapophyseal processes, facing ventrolateally rather than ventrally.

The base of the neural spine of UM 100140 (A) is robust, but the spine itself is not preserved. Left and right transverse processes are well preserved, and each has a relatively delicate, sharp, and flat anterodistal projection distinct from a more robust and rounded posterodistal projection at the end of each transverse process. There is a well developed nutrient foramen on the right side of the midline on the ventral surface of the centrum.

L4.— UM 100140 (B) is a little larger than UM 100140 (A), and it has transverse processes oriented a little less ventrally than those of UM 100140 (A). UM 100140 (B) is the first of the series to have the metapophyses well preserved and these extend well past the prezygapophyseal articular surfaces, which are themselves positioned anterior to the anterior face of the centrum.

Measurements in Table 2 indicate how far these project anteriorly from the anterior surface of the base of the neural spine. UM 100140 (B) is the first of the series to have a well developed pair of nutrient foramina on the ventral surface of the centrum.

L5-L8.— UM 100140 (C), UM 100140 (D), UM 100140 (E), and UM 100140 (F) are very similar to UM 100140 (B) in most characteristics, including the orientation of the transverse processes. The pedicles of the neural arch are a little shorter, and end farther from the posterior margin of the centrum on the more posterior of these lumbars. Where preserved, on UM 100140 (E) and UM 100140 (F), the metapophyses are anteriorly elongated like those of UM 100140 (B). There is considerable space between the postzygapophysesal facets of the former and the prezygapophyseal facets on the medial sides of the metapophyses of the latter, and it is doubtful that these could have articulated directly. These facets are small, but they are nevertheless well formed even if they did not articulate. Each of these vertebrae, L5-L8, have a relatively delicate, sharp, and flat anterodistal projection on each transverse process that is distinct from the thicker and rounded posterodistal projection of the main body of the transverse process. All have paired nutrient foramina on the ventral surface of the centrum, as do most of the following lumbars.

L9.— UM 100140 (G) is the first vertebra to differ conspicuously from those that precede it. The difference is principally in the shape of the transverse processes, but the neural spine is also narrower, and it was evidently shorter and more delicate. L9, like the vertebrae that precede it, has a relatively delicate, sharp, and flat projection in addition to the longer, thicker, and more rounded posterodistal projection of the transverse process, but in L9 the delicate, sharp, and flat accessory process is a posterodistal projection rather than an anterodistal one. This posterodistal projection appears to match a correspondingly delicate and sharp anterodistal projection on L10, and these together define an opening that is much larger but nevertheless reminiscent of the pleurapophyseal foramina separating centra of a sacrum. The right metapophysis is elongated anteroposteriorly like those preceding it, and in other respects L9 resembles L5-L8 very closely.

L10-11.— UM 100140 (H) and UM 100140 (I) are very similar to UM 100140 (F), and these again have a delicate and sharp anterodistal projection on left and right transverse processes. L10 has the longest transverse processes of any of the vertebrae. The principal differences of note in UM 100140 (H) and UM 100140 (I) are the somewhat shorter and more dorsally directed metapophyses, and the narrower, shorter, and more triangular neural spines. The vertebral foramina are smaller than that of UM 100140 (F) but still fairly large.

L12.— UM 100140 (J) has a number of differences from the vertebrae that precede it. The most conspicuous is in the anteroposteriorly shorter, mediolaterally expanded metapophyses, which resemble those of following vertebrae and are much broader than the metapophyses of preceding vertebrae. The prezygapophyses of L12 articulate directly with the postzygapophyses of L11, as do the postzygapophyses of L12 with prezygapophyses of the following vertebra. Here again the articular surfaces of the postzygapophyses face ventrolaterally. The transverse processes of L12 are broad anteroposteriorly for more of their length than is seen in preceding vertebrae. Another conspicuous difference from L11 is a pair of distinct swellings at the posteroventral margin of the centrum of L12, where articulations for hemal arches or chevron bones would be expected on an anterior caudal vertebra. However, these are only swellings and there are no facets for articulation of a chevron bone or bones.

Ca1-2.— UM 100140 (K) and UM 100140 (L) have the anteroposteriorly shorter and mediolaterally expanded metapophyses of L12. Pre- and postzygapophyses articulate directly. Neural spines are narrow, short, and triangular in shape. Vertebral foramina are conspicuously smaller than those of the lumbar vertebrae (L12 is transitional). Transverse processes appear less robust (but only the bases are preserved). The centrum of UM 100140 (K) has the posteroventral margin damaged to some extent. It is clear that Ca1 bore larger swellings for chevron facets, but the surface of the bone is damaged in UM 100140 (K) and hence the facets cannot be identified [this is different from the case in UM 100140 (J) where the swellings are smaller and the bone surface is well preserved]. All of these characteristics taken together indicate that UM 100140 (K) and UM 100140 (L) are anterior caudal vertebrae.

The centrum of UM 100140 (L) and any following vertebrae that may be present were left in the field in 1991, and unfortunately it has not been possible to revisit the locality near Garet el-Esh to collect additional parts of this specimen that may remain there.

Ca(p)1.— BSPM 1902.XI.504 (Fig. 1E-F) is a well preserved middle caudal vertebra with foramina perforating the base of each transverse process. Here the metapophyses are broad like those of UM 100140 (J), UM 100140 (K), and UM 100140 (L). The transverse processes are relatively short transversely and broad anteroposteriorly, and the perforating foramina are near the anterior margin of each transverse process.

Ca(p)2.— UM 100140 (Ca) and BSPM 1902.XI.508 (Fig. 1G) are two well preserved middle caudal vertebrae with foramina like those of BSPM 1902.XI.504 perforating the base of each transverse process. These vertebrae are a little different from each other, but both are similar in having even shorter transverse processes than those of BSPM 1902.XI.504. Both exhibit approximately the same stage of reduction of the metapophyses. UM 100140 (Ca) and BSPM 1902.XI.508 have a neural arch and vertebral foramen, but the latter is very small and very flat. Both lack any trace of a neural spine.

DISCUSSION

Stromerius nidensis is a small to medium-sized archaeocete interpreted as a member of Basilosauridae because of its geological age and because of the lumbarization of its sacral vertebrae. Protocetids are known from the Lutetian and Bartonian stages of the middle Eocene, but they have not been found in the succeeding Priabonian stage of the upper Eocene. As described above, the delicate, sharp, and flat accessory processes on the transverse processes of L9 are reversed to project posteriorly and thus match corresponding anterodistal projections on L10. Together these matching projections define an opening that is much larger but nevertheless reminiscent of a pleurapophyseal foramen separating centra of a sacrum. The neural spines of L9 through L12 are narrower and, where determinable, less high than those of preceding lumbars. Finally, L12 has expanded chevron-like processes on its posteroventral margin, but it lacks the facets that would indicate actual articulation with an ossified chevron. Expanded chevron-like processes lacking articular facets are common on last sacral vertebrae. Thus it appears that lumbars L9 through L12 are probably homologous with S1 through S4 of a former sacrum.

Loss of a functional sacrum is a derived characteristic diagnostic of Basilosauridae. By this criterion *Stromerius nidensis* is basilosaurid in morphology. However, retention of interpretable traces of a sacrum is a primitive difference from other basilosaurids (and these are no more than interpretable traces of a sacrum). Retention of a vertical neural spine on a vertebra in the penultimate thoracic vertebral position, where the anticlinal vertebra would be in a more primitive whale, is again a primitive difference from other basilosaurids. The neural spine of the penultimate thoracic is vertical, while vertebrae posterior to this have neural spines that are anteriorly inclined. *Stromerius* retains some primitive characteristics, but on balance it fits comfortably enough within a broadly conceived family Basilosauridae.

Stromerius nidensis differs from the best known basilosaurid species, the slightly older early Priabonian *Dorudon atrox* (Andrews, 1906; Uhen, 2004), in several ways. *D. atrox* has a lumbus of 20 vertebrae, and there is evidence for only 12 lumbars in *S. nidensis* (including, in each instance, vertebrae thought to be homologous with former sacrals). The presence of 12 lumbars is documented in UM 100140 (holotype), where a posterior thoracic and anterior lumbar were found on the surface, and a lumbar neural spine plus 10 additional articulated lumbars were excavated in situ before reaching the caudals. The confirmed presence of 12 lumbar vertebrae is a derived condition, as most protocetids have only six lumbars plus four sacrals. *Dorudon atrox* had 16-17 thoracic vertebrae (Uhen, 2004). Given that the number of lumbars in *S. nidensis* was less than that in *D. atrox*, the number of thoracics may have been smaller as well.

FIG. 5 — Comparison of atlas vertebrae of *Saghacetus osiris*. (A) UM 100140a found with UM 100140. (B) Atlas vertebra found with *S. osiris* skeleton UM 97550. Note that both are virtually the same size, and both have distinctive and similarly narrow transverse processes (arrows) unlike those of other basilosaurids. UM 100140a almost certainly represents the common species *S. osiris* found in the same strata, even though it was collected on the surface when the type specimen of *Stromerius nidensis* was collected (see text).

Stromerius nidensis differs from all known archaeocetes in the greater length of the anteriorly projecting metapophyses described here. This is, as far as can be determined, a uniquely derived characteristic in *S. nidensis.* Metapophyses are the sites of insertion of fibers of the deep tendon of dolphins, a broad curved tendon sheet that originates as fibers from the ventrolateral surface of the m. multifidus and medial surface of the m. semispinalis epaxial muscles (Strickler, 1980; Pabst, 1990; Uhen, 2004). More complete skeletons in which proportions of different parts of the axial skeleton can be compared will be required to determine the functional significance of the observed elongation of metapophyses in *Stromerius.*

The two whales most likely to be confused with *Stromerius nidensis* are contemporary *Saghacetus osiris* (Dames, 1894) and older *Dorudon atrox* and/or *D. stromeri* (Kellogg, 1928). The former is smaller (Fig. 4), and has lumbar and anterior caudal vertebrae with centra that are distinctly longer relative to their height and breadth (Gingerich, 1992: 73). *Dorudon atrox* and the type specimen of *D. stromeri* are larger (Fig. 4), and the latter immature specimen has thoracic centra that are longer, even lacking epiphyses, than mature thoracic centra of *Stromerius nidensis* that have epiphyses (Table 2).

There are now two archaeocete genera and species known from interval II 5a in the Temple Member of the Qasr el-Sagha Formation, *Saghacetus osiris* and *Stromerius nidensis*, and this number would increase to three if it could be shown that *Dorudon atrox* or *D. stromeri* came from this interval as well.

Note on an atlas vertebra.— A somewhat weathered and relatively small atlas vertebra (Fig. 5A) was found about one meter east of the main concentration of ribs and vertebrae excavated as UM 100140. This was initially thought to be part of the same specimen, however it was recognized to be unusually small, and its position one meter from the main specimen was noted in the field because its identification was questionable. Subsequent comparison indicates that the atlas is distinctive in morphology, and virtually identical to the atlas of *Saghacetus osiris* (specifically that of UM 97550; Fig. 5). The atlas found with UM 100140 is now numbered UM 100140a. Dribbles of plaster or a plaster-like substance were found near the atlas, and it is possible that a previous collector removed a skull or other parts of UM 100140 in a plaster jacket. The small atlas may have been picked up while prospecting nearby, and then abandoned at the site of the larger specimen. This interpretation involves some speculation, obviously, but (1) the atlas was found loose on the surface; (2) no other cervical vertebrae were found in the vicinity; (3) the atlas is the size and morphology expected for *S. osiris* (Fig. 5); (4) S. osiris is common in these beds (UM 97550 was found less than 500 meters from UM 100140); and (5) the atlas is smaller than expected for a whale the size of UM 100140. Hence, the atlas 100140a is not considered to be part of the skeleton represented by UM 100140.

ADDENDUM

A review of African Cetacea (Gingerich, 2008) made it clear that an important early Priabonian (early late Eocene) basilosaurid has been described in the literature, but never properly named. This comes from the Birket Qarun Formation, and it has been found both north of Birket Qarun in northern Fayum, and west of Birket Qarun at Wadi Hitan in western Fayum. Representative specimens are reviewed and the new archaeocete is named here.

Masracetus markgrafi, new genus and species

Zeuglodon isis (in part), Stromer, 1908, p. 128.
Zeuglodon cf. brachyspondylus (in part), Stromer, 1908, p. 136, Pl. V (II), fig. 27.
Prozeuglodon isis (in part), Kellogg, 1936, p. 76.
Zeuglodon cfr. brachyspondylus, Kellogg, 1936, p. 262.
Zeuglodon brachyspondylus (in part), Slijper, 1936, p. 319, fig. 179.

Holotype.— SMNS 11414, vertebral column mentioned by Stromer as part of specimen ‘St. 8’ (Stromer, 1908: 129). The associated skull is cataloged as SMNS 11413.

Type locality.— According to the label with the specimen, SMNS 11413-11414 was found by Markgraf near Dimeh in 1905. Stromer (1908) reported that this came from a yellow sandstone. Kellogg (1936) indicated that it came from the Birket Qarun Formation. Dimeh is at approximately 29.536 N latitude and 30.669 E longitude.

Referred specimens.— BSPM 1904.XII.135 includes a posterior thoracic (Mn. 19, studied and measured in 1990) and two caudal vertebrae (Mn. 17; not found in 1990). All were collected by Markgraf in 1904, and described by Stromer (1908: 136) and Slijper (1936).

UM 97535 from Wadi Hitan includes a weathered centrum of a posterior lumbar or anterior caudal vertebra, and UM 101221 from Wadi Hitan includes two centra of lumbar vertebrae representing this species.

Diagnosis.— *Masracetus markgraf*i is distinguished from other archaeocetes by the size and shape of its lumbar vertebrae. These are large, but relatively short compared to their width and height. Lumbar centra are nearly the diameter (width and height) of lumbar centra of *Basilosaurus isis*, but centra of *Masracetus* are less than half the length of the latter. *Masracetus markgrafi* lumbar centra are similar to those of *‘Zeuglodon’ brachyspondylus* Müller (1849: 26), but they are not as large. They also differ in being less wide relative to their length and height. *Masracetus* is larger than *Cynthiacetus* Uhen (2005), and it has a lower lumbar length-to-width ratio; *Cynthiacetus* is more like *Dorudon* than it is like *Masracetus* in both respects.

Age and distribution.— All specimens known to date are early Priabonian in age (early late Eocene), and all come from the Birket Qarun Formation of Fayum Province, Egypt.

Etymology.— *Masr*, Arabic, Egypt; and *cetos*, Gr., whale (masc.). Species name honors Richard Markgraf, who collected the type.

Description.— Little can be said about the skull (SMNS 11413), which is substantially reconstructed in plaster. The vertebral column (SMNS 11414) has been described by Slijper (1936: 319), who provided a good set of measurements for all of the known vertebral centra. Following Slijper, middle lumbar vertebrae of *Masracetus markgrafi* are on the order of 13-14 cm long, and have centra with length-to-width and length-to-height ratios of about 0.77 and 0.94, respectively. These vertebrae also have centrum width-to-height ratios of about 1.20, making them relatively wider than centra of *Zeuglodon brachyspondylus* reported by Müller (1849: 26).

Discussion.— Much of the skeleton of a new specimen of *Masracetus markgrafi* was collected from the Birket Qarun Formation in Wadi Hitan in February, 2006. Preparation and study of this has been delayed, but hopefully progress will be permitted in the future.

Uhen (2005) included SMNS 11413-11414, UM 97535, and possibly UM 101221 (as 101222) from Fayum in his list of specimens referred to North American *Cynthiacetus maxwelli*. These are larger than *Cynthiacetus*, and have a lower lumbar length-to-width ratio. *C. maxwelli* has not been fully prepared, but it appears to be more like *Dorudon* in terms of proportion than it is like *Masracetus*. The Fayum specimens as a group are comparable in size, form, and provenance, and are here separated from *C. maxwelli*.

'Zeuglodon' brachyspondylus

North American *'Zeuglodon' brachyspondylus* is similar to *Masracetus markgrafi*, and it may prove to be a species of *Masracetus*. *Z. brachyspondylus* was named more than 150 years ago by Müller (1849: 26) without designation of a holotype, and it has not been studied for many years. To clarify the meaning of the name, the lumbar vertebra illustrated as No. 6 of vertebral series II in Plate XX of Müller (1849) is designated the lectotype of *'Zeuglodon' brachyspondylus*. This was collected by Albert C. Koch in Alabama, and it is now in the collection of the Museum für Naturkunde in Berlin. Kellogg (1936: 254) identified the designated vertebra as lumbar L9, and transcribed Müller's measurements as 190.5 mm for minimum centrum length; 190.5 mm for anterior centrum width; and 165 mm for anterior centrum height.

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