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SIZE ESTIMATES OF THE EXTINCT MARINE SNAKE *PTEROSPHENUS SCHUCHERTI* FROM EOCENE-AGED SEDIMENTS OF CENTRAL GEORGIA

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ABSTRACT

Fossil snakes are most often identified from isolated vertebrae, complicating estimations of total body lengths of extinct taxa. Here we estimate the range of total body length of the late Eocene North American palaeophiid marine snake *Pterosphenus schucherti* based on 29 recently collected fossil vertebrae from Wilkinson County, Georgia, USA. Previous research suggests that the palaeophiids are most closely related to modern boids. Total body length estimates here are based on family-specific regressions of centrum length versus known total body length in extant members of Boidae, Pythonidae, and Colubridae. The high correlation coefficients for the family specific regressions supports previous studies that used centrum length to estimate total body length in extinct snakes. Here, size estimates for *Pterosphenus schucherti* ranged from 2.5 to 4.8 m using boids, 3.4 to 13.0 m using pythonids, and 2.8 to 5.3 m using colubrids. This study demonstrates how the lumping of multiple extant clades greatly increases the range of variability for length estimations. For the TL estimates of fossil snakes, it appears that regressions generated from the lowest taxonomic level of the most closely related extant species should be used.

Keywords: Eocene snakes, *Pterosphenus schucherti*, size estimation, southeast North America

INTRODUCTION

Eocene-aged marine sediments in Central Georgia have produced a diversity of vertebrate fossils ranging from sharks to mammals (Case and Borodin 2000; Parmley and Cicimurri 2003, 2005; Rhinehart et al. 2019; Westgate 2001). *Palaeophis* and *Pterosphenus* are two genera of extinct Eocene marine snakes recovered from these deposits (Holman 1977; Parmley and Case 1988; Parmley and DeVore 2005; Parmley and Reed 2003; Westgate 2001). Palaeophiid snakes have been found across much of the Eocene southeastern Coastal Plain in North America as well as Old World Eocene localities (Parmley and Case 1988; Parmley and DeVore 2005; Rage 1984; Westgate and Ward 1981). These snakes are believed to be marine species based on their laterally compressed vertebrae as well as their direct association with other fossil marine taxa and marine sediments (McCartney et al. 2018; Rage et al. 2003). They likely lived in subtropical, nearshore, shallow waters present during the Eocene (Parmley and Cicimurri

2003; Parmley and DeVore 2005; Westgate 2001). Previous research has suggested that the Palaeophiid snakes are most likely related to modern boids (Hoffstetter 1955; Holman 1977), not extant sea snakes (Elapidae). Holman (1977: p. 142) suggested that they should "be considered as specialized marine offshoots of the Boidae."

Eocene-aged sediments in central Georgia are exposed just south of the modern Fall Line which separates the Coastal Plain Physiographic Province to the south from the Piedmont to the north (Huddlestun and Hetrick 1985, fig. 1). The late Eocene sediments of the Clinchfield Formation overlay kaolin bearing units in this region (Huddlestun and Hetrick 1985, fig. 4). Kaolin mining operations frequently expose fossil bearing Clinchfield sediments and several authors have documented the presence of vertebrate fossils from these sediments (Case and Borodin 2000; Parmley and Case 1988; Parmley and Cicimurri 2003, 2005; Parmley and DeVore 2005; Parmley and Reed 2003; Rhinehart et al. 2019; Westgate 2001). The most productive locality in the southeastern United States has been the Hardie Mine, Wilkinson County, Georgia (Parmley and Cicimurri 2003, fig. 1) which has yielded sharks and rays (Parmley and Cicimurri 2003), a chimaeroid fish (Parmley and Cicimurri 2005), the earliest North American colubrid snake (Parmley and Holman 2003), two genera of Palaeophiid snakes (Parmley and DeVore 2005), five genera of turtles (Parmley et al. 2006), an auk (Chandler and Parmley 2002), and four species of terrestrial mammals (Rhinehart et al. 2019). The focus of the current study was to estimate the total body length of *Pterosphenus schucherti* Lucas, 1899 using recently collected vertebrae from an active kaolin mine also located in Wilkinson Co. This new locality is approximately 24 kilometers southeast of the Hardie Mine and a comparison of the new Wilkinson County mine fossils with the nearby Hardie Mine fauna strongly suggests comparable ages: Late Eocene 36.0-34.2 ma (Parmley and Holman 2003).

In modern snakes, vertebral count has been shown to correlate with snout-vent body length, but the relationship is less applicable for giant fossil taxa (Head and Polly 2007). However, in fossil snakes, disarticulated isolated vertebrae are normally the material recovered. Most studies exploring the body length of fossil species have used estimates derived from regressions of vertebral dimensions against known body lengths of modern taxa. For example, in an attempt to estimate body length of the giant Paleocene boid, *Titanoboa*, postzygapophyseal width was regressed against snout-vent length and total body length (TL) in 21 extant boids (Head et al. 2009). To estimate the size of the Pleistocene rattlesnake *Crotalus giganteus*, the average centrum length of three mid-body vertebrae from each of 37 extant *Crotalus adamanteus* were regressed against TL (Christman 1975). For five species of North American palaeophiid snakes, TLs were estimated using a centrum length versus body length regression based on a combined group of 16 extant boids and pythonids (Parmley and Reed 2003). More recently, to estimate total body length of *Palaeophis colossaeus* from the Eocene of Mali, West Africa, the prezygapophyses width and the transverse cotyle width of the largest vertebrae from extant snakes in six families (Boidae, Colubridae, Elapidae, Pythonidae, Tropidophiidae, and Typhlopidae) were used (McCartney et al. 2018). In the current study, using vertebral measurements of extant boids, pythonids, and colubrids to create family specific regressions, we estimated the TL of *Pt. schucherti* using recently collected vertebrae from the Eocene of Georgia.

Taxonomic and Paleohabitat Note. *Pterosphenus* is the derived sister taxon to the more primitive genus *Palaeophis*; both genera were aquatic snakes of the subfamily

Palaeophiinae. The genera are known from the Eocene of the Old World and New World, and both were extinct by the end of the Eocene (Parmley and DeVore 2005). These snakes inhabited paleocoastal marine influenced habitats and modifications to an aquatic life is reflected in their vertebral morphology (e.g., Holman 2000; Holman et al. 1990).

Although 17 species of palaeophiid snakes have been described from the Old and New World Eocene, this diversity is very likely inflated by: 1) a relative lack of fossil specimens for many of the described species; 2) inadequate detailed studies of many taxa; and 3) strong intravertebral morphological similarities in many Old World taxa. This report focuses on the single species of *Pterosphenus* in North America, *Pt. schucherti*. Fortunately, this species is relatively common and represented by many Middle to Late Eocene fossil vertebrae. Moreover, this species' vertebral morphology is better documented than any of the other palaeophiids.

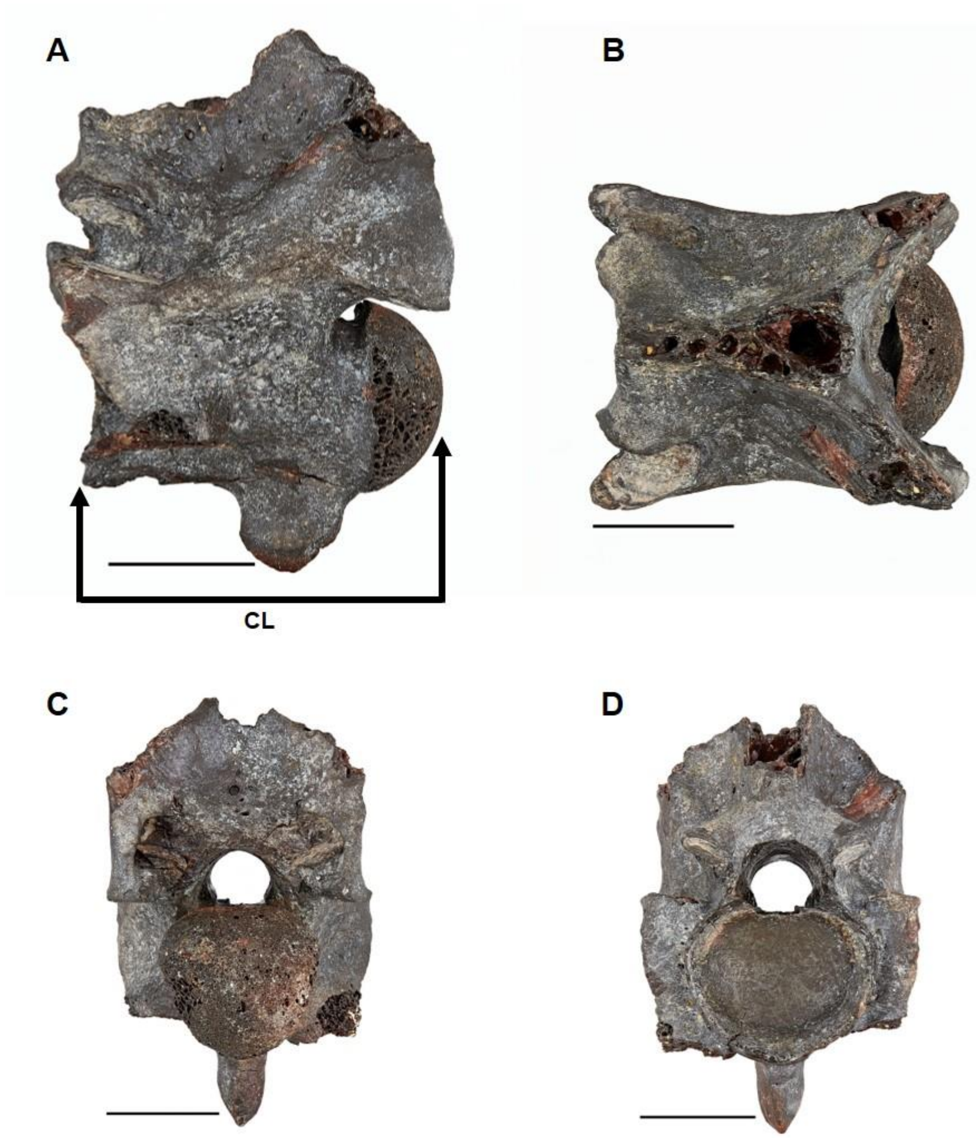

Figure 1. Vertebra of the Late Eocene aquatic snake *Pterosphenus schucherti* (GCVP 19863) from Clinchfield Formation sediments in Wilkinson County, Georgia: A) lateral, B) dorsal, C) posterior, and D) anterior views. Anterior to the left in A and B. CL = centrum length. Scale = 10 mm.

MATERIALS & METHODS

Fifty isolated *Pt. schucherti* fossil vertebrae (Figure 1) were recovered through surface collection of Clinchfield Formation sediments in an active kaolin mine in Wilkinson County, Georgia. All fossils were cleaned, stabilized, and cataloged in the Georgia College Vertebrate Paleontology Collection (GCVP). Of these, centrum length was recorded for 29 measurable fossils of adult snakes. Following Christman (1975), centrum length (CL) was recorded as the straight-line distance from the most posterior edge of the vertebral condyle to the anterior edge of the cotyle (Figure 1A). The same measurement was taken on trunk vertebrae of 31 modern snakes of known total body length (TL; measured before skeletonization) from three different families: Boidae (n=7), Pythonidae (n=15), and Colubridae (n=9) (Table 1). All extant specimens are housed in the Georgia College Herpetology Collection (GCH). It has been

Table I. Total body length (TL) and average centrum length (ACL) for modern boids (n=7), pythonids (n=15), and colubrids (n=9). Each ACL is the average of 40 trunk vertebrae per individual. Standard deviation (SD) and coefficient of variation (CV) were calculated for each ACL.

GCH #	Species	TL (mm)	ACL (mm)	SD	CV
	Boidae				
901	*Boa constrictor*	2300	12.46	0.25	0.020
2736	*Boa constrictor*	2500	13.35	0.26	0.019
2737	*Boa constrictor*	1340	7.44	0.18	0.024
2738	*Boa constrictor*	1690	9.10	0.14	0.015
2739	*Boa constrictor*	2800	14.45	0.22	0.015
2740	*Boa constrictor*	1960	11.46	0.15	0.013
2741	*Boa constrictor*	1790	9.66	0.15	0.016
	Pythonidae				
2627	*Liasis boeleni*	2150	9.89	0.21	0.021
2628	*Liasis boeleni*	2665	11.91	0.24	0.020
2629	*Liasis boeleni*	2075	9.55	0.26	0.027
2634	*Liasis macklonti*	2205	8.78	0.15	0.017
2636	*Morelia amethstina*	2150	8.51	0.17	0.020
2644	*Python curtus*	1400	11.11	0.11	0.009
2645	*Python curtus*	1778	13.52	0.22	0.016
2646	*Python curtus*	1600	12.07	0.24	0.020
2648	*Python curtus*	1700	12.38	0.25	0.020
2651	*Python curtus*	1310	10.03	0.19	0.019
2652	*Python curtus*	1447	13.25	0.28	0.021
945	*Python molurus*	2450	11.99	0.18	0.015
2654	*Python molurus*	3100	16.12	0.32	0.020
2655	*Python molurus*	2700	13.13	0.28	0.021
935	*Python regius*	1840	11.41	0.21	0.018
	Colubridae				
1010	*Pantherophis obsoletus*	1524	6.98	0.14	0.020
1011	*Pantherophis obsoletus*	1600	7.01	0.22	0.031
1014	*Pantherophis obsoletus*	1625	7.85	0.21	0.027
1018	*Pantherophis obsoletus*	1375	6.00	0.11	0.018
1019	*Pantherophis obsoletus*	1824	8.53	0.23	0.027
1883	*Pantherophis obsoletus*	1360	6.16	0.19	0.031
1886	*Pantherophis obsoletus*	1400	5.41	0.13	0.024
1891	*Pantherophis obsoletus*	1665	7.91	0.24	0.030
1892	*Pantherophis obsoletus*	1685	7.89	0.19	0.024

demonstrated that due to intracolumnar variation, it is challenging to differentiate anterior trunk vertebrate from mid- or posterior trunk vertebrate (LaDuke et al. 2010). To account for this intracolumnar variation, 40 trunk vertebrae from each extant individual were measured using digital calipers and an average centrum length (ACL) was calculated. The ACLs were plotted against known TLs, linear regressions were performed, and lines of best fit were plotted for each family. For each fossil vertebra, TL size estimates were generated using the regression equations for each family.

RESULTS

The TL and ACL for modern taxa are displayed in Table 1. The relatively small standard deviation for each individual in each family suggests comparable intracolumnar variation amongst the extant taxa. The scatter plot of ACL versus TL, the regression lines, and regression equations are displayed in Figure 2. The boid regression displays the strongest correlation ($R^2 = 0.9766$) followed by the colubrids ($R^2 = 0.5562$) and pythonids ($R^2 = 0.0959$). The estimated TL for *Pt. schucherti* range from 2.5 to 4.8 m using the boid regression, 3.4 to 13.0 m using the pythonid regression, and 2.8 to 5.3 m using the colubrid regression (Table 2). For the smallest fossil vertebra measured (CL = 13.19; GCVP 19878), the pythonids are 1.36 times larger compared to boids, while colubrid based estimates are 1.14 times larger compared to boids. For the largest fossil vertebra measured (CL 24.75; GCVP 19863), the pythonid based estimates are 2.70 times larger than boids, and colubrid based estimates are 1.10 times larger than boids.

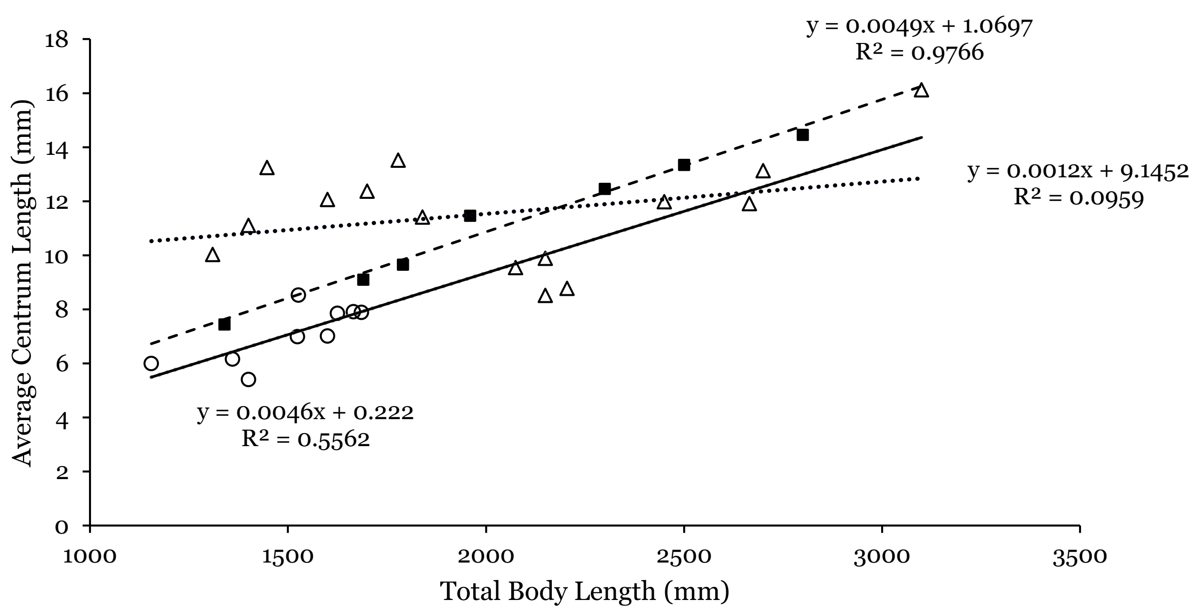

Figure 2. Plot of centrum length to body length with best fit lines for modern boids (solid squares and dashed line), pythons (open triangles and dotted line), and colubrids (open circles and solid line). Linear regression equations provided for each.

Table II. Centrum lengths (CL) of Late Eocene aquatic snake *Pt. schucherti* from Clinchfield Formation sediments in Wilkinson County, Georgia. Estimated total body lengths (TL) calculated using regression equations from extant taxa. CL measurements and TL estimates in mm.

GCVP #	Genus	CL	Est. TL w/ boids	Est. TL w/ pythonids	Est. TL w/ colubrids
19861	*Pt. schucherti*	17.76	3406.18	7179.00	3803.61
19862	*Pt. schucherti*	23.74	4626.59	12162.33	5103.61
19863	*Pt. schucherti*	24.75	4832.71	13004.00	5323.17
19864	*Pt. schucherti*	17.64	3381.69	7079.00	3777.52
19865	*Pt. schucherti*	22.11	4293.94	10804.00	4749.26
19866	*Pt. schucherti*	21.58	4185.78	10362.33	4634.04
19867	*Pt. schucherti*	18.27	3510.27	7604.00	3914.48
19868	*Pt. schucherti*	20.35	3934.76	9337.33	4366.65
19869	*Pt. schucherti*	18.84	3626.59	8079.00	4038.39
19870	*Pt. schucherti*	17.48	3349.04	6945.67	3742.74
19871	*Pt. schucherti*	20.32	3928.63	9312.33	4360.13
19872	*Pt. schucherti*	17.69	3391.90	7120.67	3778.39
19873	*Pt. schucherti*	16.04	3055.16	5745.67	3429.70
19874	*Pt. schucherti*	17.70	3393.94	7129.00	3790.57
19875	*Pt. schucherti*	18.65	3587.82	7920.67	3997.09
19876	*Pt. schucherti*	21.72	4214.35	10479.00	4664.48
19878	*Pt. schucherti*	13.19	2473.53	3370.67	2810.13
19879	*Pt. schucherti*	21.30	4128.63	10129.00	4573.17
19880	*Pt. schucherti*	23.33	4542.92	11820.67	5014.48
19881	*Pt. schucherti*	17.38	3328.63	6862.33	3721.00
19882	*Pt. schucherti*	21.81	4232.71	10554.00	4684.04
19883	*Pt. schucherti*	20.11	3885.78	9137.33	4314.48
19884	*Pt. schucherti*	20.45	3955.16	9420.67	4388.39
19885	c.f. *Pt. schucherti*	21.81	4232.71	10554.00	4684.04
19886	c.f. *Pt. schucherti*	19.46	3753.12	8595.67	4173.17
19887	c.f. *Pt. schucherti*	16.18	3083.73	5862.33	3460.13
19888	c.f. *Pt. schucherti*	19.80	3822.51	8879.00	4247.09
19889	c.f. *Pt. schucherti*	15.85	3016.39	5587.33	3388.39
19890	c.f. *Pt. schucherti*	20.25	3914.35	9254.00	4344.91

DISCUSSION

Using CL from a combination of extant boids and pythonids for reference, Parmley and Reed (2003) estimated a TL range of 2.3 to 5.1 m for *Pt. schucherti* specimens from the Eocene of North America. This TL range is similar to our 2.5 to 4.8 m range using only boids. The slightly wider range makes sense due to their sample containing slightly smaller (11.2 mm) and slightly larger (28.9 mm) vertebrae. Compared to Parmley and Reed (2003), our estimates are approximately 2.0 times larger using the pythonids and 1.1 times larger using the colubrid regression. If we substitute the largest vertebra from the Parmley and Reed (2003) study into our equations, the estimated maximum TL for *Pt. schucherti* would be 5.7 m using boids, 16.5 m using pythonids, and 6.2 m using colubrids, an increase in estimated TL of approximately 20%. McCartney et al. (2018) used vertebral widths of extant species in multiple families and calculated a TL range of 8.1 to 12.3 m for *Palaeophis colossaeus,* a closely related species from Africa. The maximum TL is close to that suggested by our pythonid regression. If we substitute the cotylar width (McCartney et al. 2018, fig. 1) of our largest specimen (16.05 mm, GCVP 19863) into the regression equation provided by McCartney et al. (2018), the TL estimate is 8.8 m. This estimate is 1.83 times larger than our boid estimate, 0.67 times smaller than our pythonid estimate, and 1.67 times larger than our colubrid estimate. Based on our estimates, *Pt. schucherti* was considerably larger than modern sea snakes. The largest extant sea snake, *Hydrophis spiralis* (Elapidae) has a TL of 1.62 m in males and 1.83 m in females.

Based on the correlation coefficients for the regressions of our extant species, the boid regression appears to be the most reliable for estimates of TL (Table 1). The extant snakes used to create the boid and colubrid regressions were, in each case, from a single species. The extant snakes used for the pythonid regression were from multiple genera which is a possible cause for the large degree of variance observed in the pythonid regression. The lack of extant boid vertebrae in the size range of those recorded for *Pt. schucherti* is problematic when estimating the length of this taxon. However, the high correlation coefficient ($R^2 = 0.9766$) for the boid regression as well as the conclusion that palaeophiid snakes are most morphologically similar to modern-day boids (Hofstetter 1955; Holman 1977) supports the use of these estimates. The colubrid regression was not as strong ($R^2 = 0.5562$) and the extant colubrids' centrum lengths (and overall vertebral morphology) are much smaller than *Pt. schucherti*, leading us to question the validity of these estimates. The pythonid regression produced a low correlation coefficient value ($R^2 = 0.0959$), indicating minimal correlation between CL and TL in this taxon. The low correlation in pythonids is likely due to the use of several different genera of extant pythonids to create the regression. Subsequently, we have little confidence in the TL estimates derived from the pythonid regression. Our study uses family-specific and genus-specific regressions as opposed to previous studies that lumped specimens from extant families together. For the TL estimates of fossil snakes, it appears that regressions generated from the lowest taxonomic level of the most closely related extant species should be used.

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