

Palaeopheid Snakes from the Late Eocene Hardie Mine Local Fauna of Central Georgia

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Abstract - Palaeopheid snake fossils from the Late Eocene Hardie Mine local fauna (l.f.) of Wilkinson County, central Georgia, include *Pterosphenus schucherti* Lucas and *Palaeophis africanus* Andrews. This occurrence represents a new geographic record for *P. africanus* because this species was previously known only from the type locality in Nigeria. The Hardie Mine l.f. is the first North American Late Eocene fauna where *Pterosphenus* and *Palaeophis* co-occur in the same local stratigraphic context. The stratigraphic range of *Palaeophis* is extended from the Middle Eocene into the Late Eocene. The nearshore marine paleoenvironment of the Hardie Mine was inhabited by juvenile and adult palaeopheid snakes of both genera. Based on our specimens, *Pterosphenus* appears to have been more common than *Palaeophis*.

Introduction

Snakes of the family Palaeopheididae are a small but specialized group of extinct aquatic species whose origins date back to the Upper Cretaceous of Africa (Rage and Wouters 1979). In North America, this group is known by two genera from uppermost Paleocene (Erickson 1998) to Upper Eocene (Holman 2000) marine and marine-influenced sediments of the Atlantic and Gulf Coastal regions (also see Parmley and Case 1988). The taxon is represented almost exclusively by isolated vertebrae (Holman 2000), but a few ribs (Jim Knight, South Carolina State Museum, pers. comm.) and, questionably, a few teeth (Weems 1999) have also been reported. To date, no skull element of a North American palaeopheid snake has been reported. Despite the fact that palaeopheid snakes have been known to science for over 150 years (Owen 1841) and are relatively common fossils in some Paleogene marine Gulf Coast depositional environments of North America (Holman 2000), they are under studied and poorly known. For example, a new diminutive species, *Palaeophis casei* Holman, was described from the Lower Eocene (possibly uppermost Paleocene, see Holman 2001) of Mississippi as recently as 1982 (Holman 1982). Here we report the occurrence of the two known genera of palaeopheid snakes, *Palaeophis* Owen and *Pterosphenus* Lucas, from a Upper Eocene site in central Georgia previously designated as the Hardie Mine locality (Westgate 2001). Although Westgate (2001) noted the presence of *Pterosphenus* in the Hardie Mine vertebrate fauna, our report provides the first descriptive accounts of palaeopheid fossils from the site. These fossils

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add new information on the paleoecology, biogeography, and paleostratigraphic co-occurrence of the genera.

Locality

The Hardie Mine is an inactive, open-pit kaolin mine located in central Georgia, 3.9 km NNW of Gordon, Wilkinson County (32°54.335'N, 83°21.543'W). Upper Eocene (ca. 36–34.2 Ma; Parmley and Holman 2003) fossiliferous sediments of the Clinchfield Formation (basal unit of the Barnwell Group; Huddleston and Hetrick 1985) are exposed in the mine. On the north-facing wall of the mine, a 1–1.5-m-high stratum of *in situ* Clinchfield Formation sediments is exposed (Fig. 1). The sediments unconformably overlay nonfossiliferous kaolin clays and underlie local Twiggs Clay sediments, which are also nonfossiliferous (Fig. 1; also see Westgate 2001). Past mining operations in the pit have resulted in tons of fossiliferous Clinchfield sediments being deposited as surface spoil piles near the *in situ* sediments. These spoil piles are especially rich in shark, ray, and to a lesser degree, bony fish, reptile, and mammal fossils. It is important to note that because there is no evidence to suggest that mixing of intrusive fossils from older or younger horizons has occurred, the Clinchfield sediments of the Hardie Mine represent a discrete fossiliferous unit (local fauna).

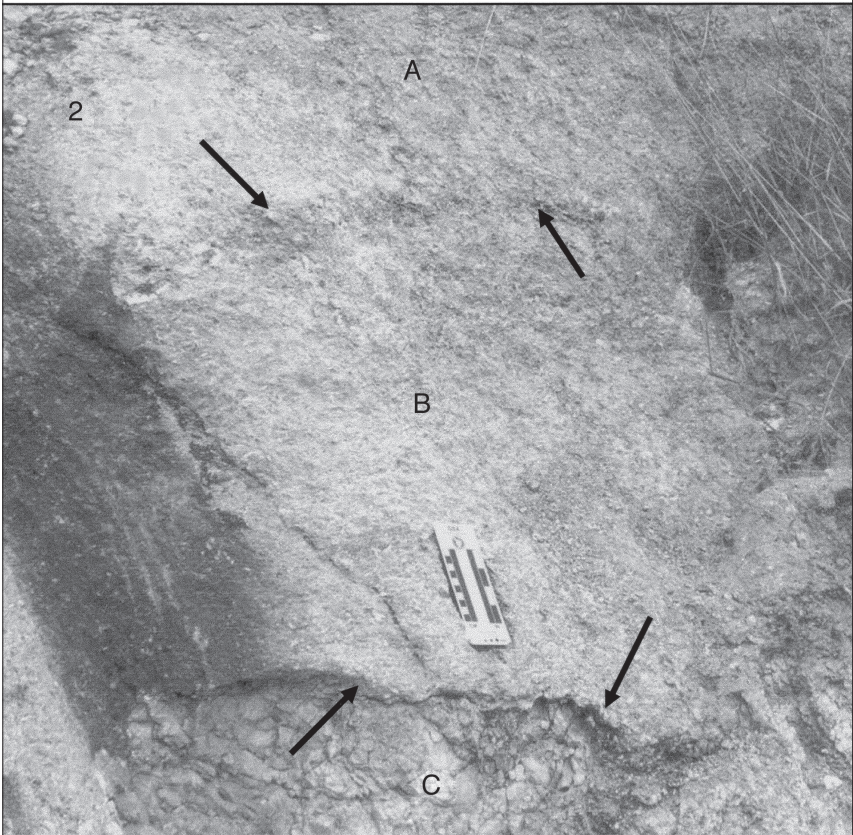
Although fossils have been collected from the Hardie Mine for many years, only recently have vertebrates from the site been reported in the literature (Westgate et al. 1994). Most recently, Westgate (2001) listed 26 taxa of vertebrates in the Hardie Mine local fauna (hereafter l.f.), which primarily included shark and ray species, in addition to bony fish, reptile, and a few mammalian species. Since the summer of 1997, parties from Georgia College and State University (GC&SU) have collected in the Hardie Mine. Intensive surface collecting of spoil piles and screen washing of *in situ* sediments has yielded fossils of several taxa that are new to Westgate's (2001) faunal list (Chandler and Parmley 2003, Parmley and Cicimurri 2003, Parmley and Holman 2003, unreported fossils in the GC&SU collections). This report focuses on palaeopheid snake fossils that were mainly collected from spoil piles on the site, but some specimens were recovered from *in situ* matrix.

Systematic Paleontology

The fossils reported here are in the vertebrate paleontological collections of Georgia College and State University (GCVF). Figure 2 shows many of

Figure 1 (opposite page). Stratigraphic context of the Hardie Mine fossil-bearing Clinchfield Formation sediments: (1) northfacing wall of the mine with arrow indicating stratigraphic level of exposed Clinchfield sediments; (2) *in situ* Clinchfield sediments (B) unconformably bounded above by nonfossiliferous Twiggs Clay sediments (A), and below by nonfossiliferous kaolin (C); arrows indicate unconformities.

the vertebral structures and characteristics discussed herein, and measurements of vertebrae identified at least to genus are given in Table 1.



Class Reptilia Laurenti
Order Squamata Opper
Suborder Alethinophidia Nopcsa

Family Palaeopheidae Lydekker

The phylogenetic placement of Palaeopheidae is still an unsettled issue. The palaeopheids have no known living descendants, but they have

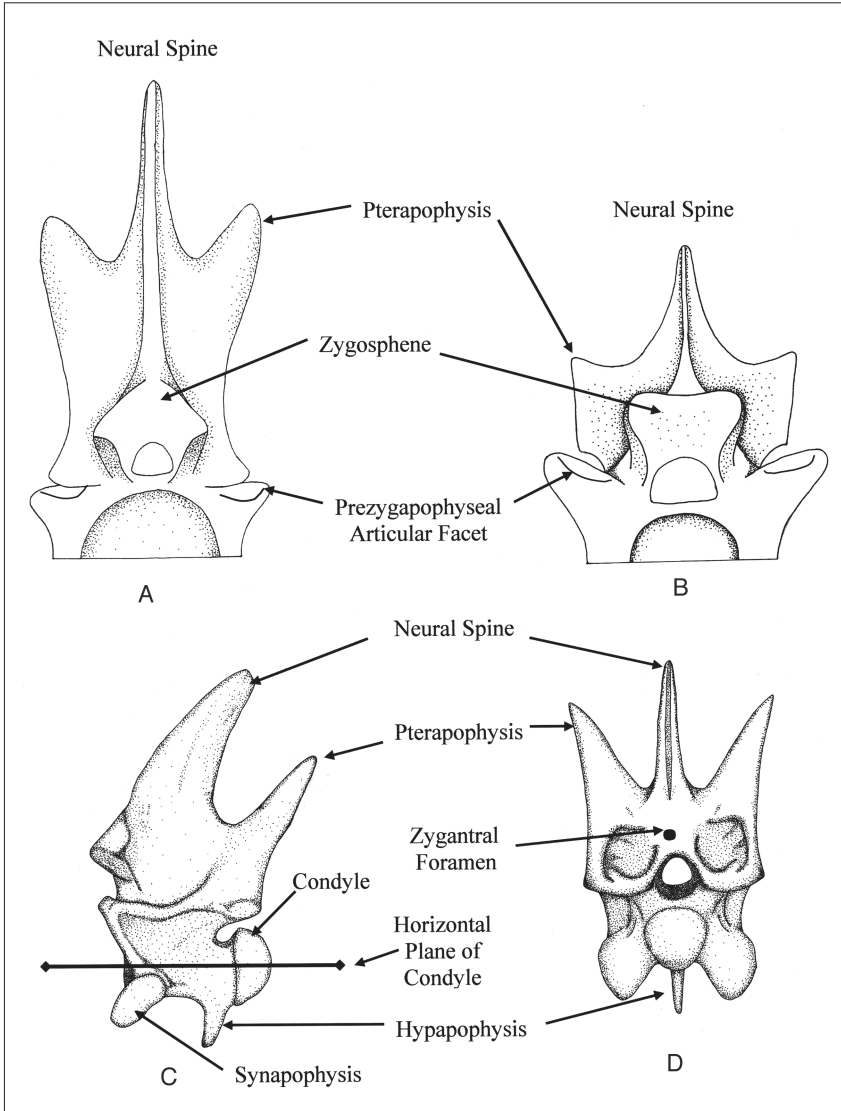


Figure 2. Stylized palaeopheid vertebrae: *Pterosphenus* (A), and *Palaeophis* (B) in anterior views (modified from Parmley and Case 1988); generalized palaeopheid vertebra in lateral (C) and posterior (D) views.

been allied with Booidea on the basis of shared vertebral characters (Holman 2000, Parmley and Case 1988, Rage 1984). Rage (1984) noted that palaeopheids had booid-type vertebrae modified for aquatic habits, but he (1988) questioned their affinities with the booids. McDowell (1987) placed Palaeopheididae within the Acrochordoidea on the basis of shared vertebral characters with Acrochordidae. These systematic and phylogenetic problems are beyond the scope of this paper, thus for simplicity we refer the palaeopheid snakes to Alethinophidia (also see similar discussion in Rage and Werner 1999).

Table 1. Vertebral types and measurements in millimeters of the Hardie Mine palaeopheid vertebrae. Abbreviations are: CAT = cervical to anterior trunk; MPT = middle to posterior trunk; PC = precloacal; cl = centrum length; naw = neural arch width; pr-poz = length through prezygapophysis and postzygapophysis; zw = zygosphene width.

Taxon	Specimen number	Vertebral type	cl	naw	pr-poz	zw
<i>Palaeophis africanus</i>						
	GCVP 4916	CAT	12.72	10.51	13.02	—
	GCVP 4915	MPT	17.52	13.41	—	9.39
<i>Palaeophis</i> sp. indet.						
	GCVP 5407	CAT	10.32	7.85	10.56	4.38
	GCVP 4919	CAT	10.04	7.63	—	5.99
	GCVP 4917	MPT	13.69	10.35	—	7.21
	GCVP 4918	MPT	13.21	9.13	—	6.18
	GCVP 4920	PC	7.46	6.42	—	3.49
<i>Pterosphenus schucherti</i>						
	GCVP 4898	CAT	26.30	19.22	—	15.84
	GCVP 4923	CAT	22.12	20.08	21.57	13.58
	GCVP 4899	CAT	21.04	15.37	—	10.79
	GCVP 4902	CAT	18.60	15.91	19.05	11.49
	GCVP 4941	CAT	18.90	18.20	19.54	12.25
	GCVP 4927	CAT	16.83	15.64	—	12.25
	GCVP 4944	CAT	14.09	13.78	14.94	9.23
	GCVP 4903	MPT	11.65	13.18	13.48	—
	GCVP 4924	MPT	9.88	8.87	9.91	5.62
	GCVP 4900	MPT	9.09	10.20	11.28	6.89
	GCVP 4901	MPT	8.82	8.35	—	5.14
<i>Pterosphenus</i> sp. indet.						
	GCVP 4911	CAT	19.53	16.47	—	10.58
	GCVP 4904	CAT	18.65	17.84	—	13.30
	GCVP 4912	CAT	18.59	13.75	—	—
	GCVP 4905	CAT	17.86	18.00	18.80	—
	GCVP 4914	CAT	15.30	13.89	—	—
	GCVP 4913	CAT	15.22	15.07	—	—
	GCVP 4908	CAT	11.32	7.08	—	—
	GCVP 4906	MPT	16.90	14.18	—	11.01
	GCVP 4907	MPT	14.54	13.92	—	8.33
	GCVP 5408	?	13.80	10.92	—	6.58
	GCVP 5409	?	16.86	16.27	—	9.92

Subfamily Palaeopheinae Lydekker

Palaeopheidae is comprised of two subfamilies: Palaeopheinae Lydekker and Archaeopheinae Janensch, of which only Palaeopheinae is known from North America. Palaeopheinae vertebrae are unique among snakes in the following features: they are tall and laterally compressed to some degree; possess distinct pterapophyses (posterior extensions of the neural arch); a single, often large foramen opens medially and usually dorsal to the zygantral cavities; roof of the zygantrum is reduced (Rage 1983a); axes of the condyles are positioned along a horizontal plane (Rage 1983b, a character state seen in very few snakes); synapophyses positioned ventro-laterally for rib attachment; one or two laterally compressed and ventrally directed hypapophyses on all but caudal vertebrae (Parmley and Case 1988); and lacking or having weakly developed subcentral ridges. Of these characters, pterapophyses and double hypapophyses appear to be synapomorphies uniting Palaeopheinae because they do not occur in other snakes. The presence of medial zygantral foramina is likely not a synapomorphy for Palaeopheinae because they can also occur in the Xenopeltidae genus *Xenopeltis* Reinhardt. It is interesting to note that the Achrochordidae lack medial zygantral foramina, and xenopeltids are thought by some to be closer to boids than are achrochordids (e.g., Dowling 1975, Dowling and Duellman 1978, Underwood 1976). This suggests the possibility of a Boidae-Palaeopheidae-Xenopeltidae phyletic relationship (also see discussion in Rage 1984, Rage et al. 2003), but unfortunately fossils of xenopeltid snakes have yet to be discovered.

Genera *Palaeophis* and *Pterosphenus*

Vertebral characteristics of the North American palaeopheid genera *Pterosphenus* and *Palaeophis* have been discussed in some detail (e.g., Gilmore 1938, Holman 2000, Holman et al. 1991, Parmley and Case 1988, Parmley and Reed 2003, Rage 1984, Rage and Werner 1999, Rage et al. 2003). In general, *Pterosphenus* vertebrae are morphologically similar to those of *Palaeophis*, but are more derived. This reflects relatively simple modifications in *Pterosphenus* vertebrae from the geologically older and more pleisiomorphic *Palaeophis* vertebral type. Diagnosis of the genera *Palaeophis* and *Pterosphenus* used here (given below) follow (in part) Holman (2000), Parmley and Case (1988), Rage (1984), and Rage et al. (2003), but characters determined diagnostic during the course of this study were also utilized.

Palaeophis diagnosis: vertebrae low and moderately to weakly laterally compressed; neural spine originates on (or near) the posterior to mid-region of zygosphenal roof; pterapophyses short; zygosphenes flat to slightly convex dorsally and remains distinct from the neural spine; prezygapophyses expanded with articular facets often strongly angled upward; synapophyses (paradiapophyses of some workers) set high.

Pterosphenus diagnosis: vertebrae high and moderately to strongly laterally compressed; neural spine originates on the anterior border of the

zygosphenal roof; pterapophyses tall; zygosphenes strongly convex dorsally and merges (or nearly so) with anterior base of neural spine; prezygapophyses reduced with articular facets often weakly angled upward; synapophyses set low.

Vertebral types

Listed below are three types of palaeopheid vertebrae believed to be represented among the fossils in our sample (also see discussion in Parmley and Case 1988).

Cervical to anterior trunk (CAT). These vertebrae have anterior and posterior hypapophyses that are laterally compressed, ventrally directed, and often connected by a keel. The anterior hypapophysis is considerably smaller than the posterior one.

Middle to posterior trunk (MPT). These vertebrae have a single posterior hypapophysis that is short, laterally compressed and ventrally directed, often extending anteriorly as a keel along the centrum to near the rim of the cotyle.

Precloacal (PC). These vertebrae are generally shorter than the aforementioned types, with a single posterior hypapophysis that may be semi-round (not compressed), short, strongly hooked in a posterior direction, and there is no keel.

Fossil Accounts

Palaeophis africanus Andrews (Fig. 3)

Material. Two vertebrae: one CAT vertebra (GCVP 4916); one MPT vertebra (GCVP 4915).

Remarks. The vertebrae are easily assigned to the genus *Palaeophis* on the basis of being only moderately compressed, with short neural spines that originate at or near the posterior to mid-region of the zygosphenal roofs, low pterapophyses, flat to slightly convex zygosphenes that are distinct from the neural spines, and in having expanded prezygapophyses (Holman 2000, Parmley and Case 1988, Rage et al. 2003). One of the Hardie Mine fossils (GCVP 4916; Fig. 3) is remarkably similar to the type vertebra of *P. africanus* figured by Andrews (1924, fig. 1). An additional vertebra (GCVP 4915) is more abraded and damaged on one side, but its discernable features correspond in many respects with *P. africanus*.

Andrews (1924) erected this nominal taxon on the basis of three Middle Eocene vertebrae from near Lagos, Nigeria. His description of the type material is brief, but fortunately the most complete vertebra is well illustrated. From his text and illustrations, a clear descriptive diagnosis of *P. africanus* is available. Rage (1984) described *P. africanus* as follows: "This species seems to be morphologically intermediate between the primitive and advanced species. It retains primitive characters (zygosphenes thick, prezygapophyses rather well developed), but some features foreshadow the advanced species (vertebrae not very massive and slightly compressed, neural canal rather broad). *Palaeophis africanus* exhibits well defined, sharp

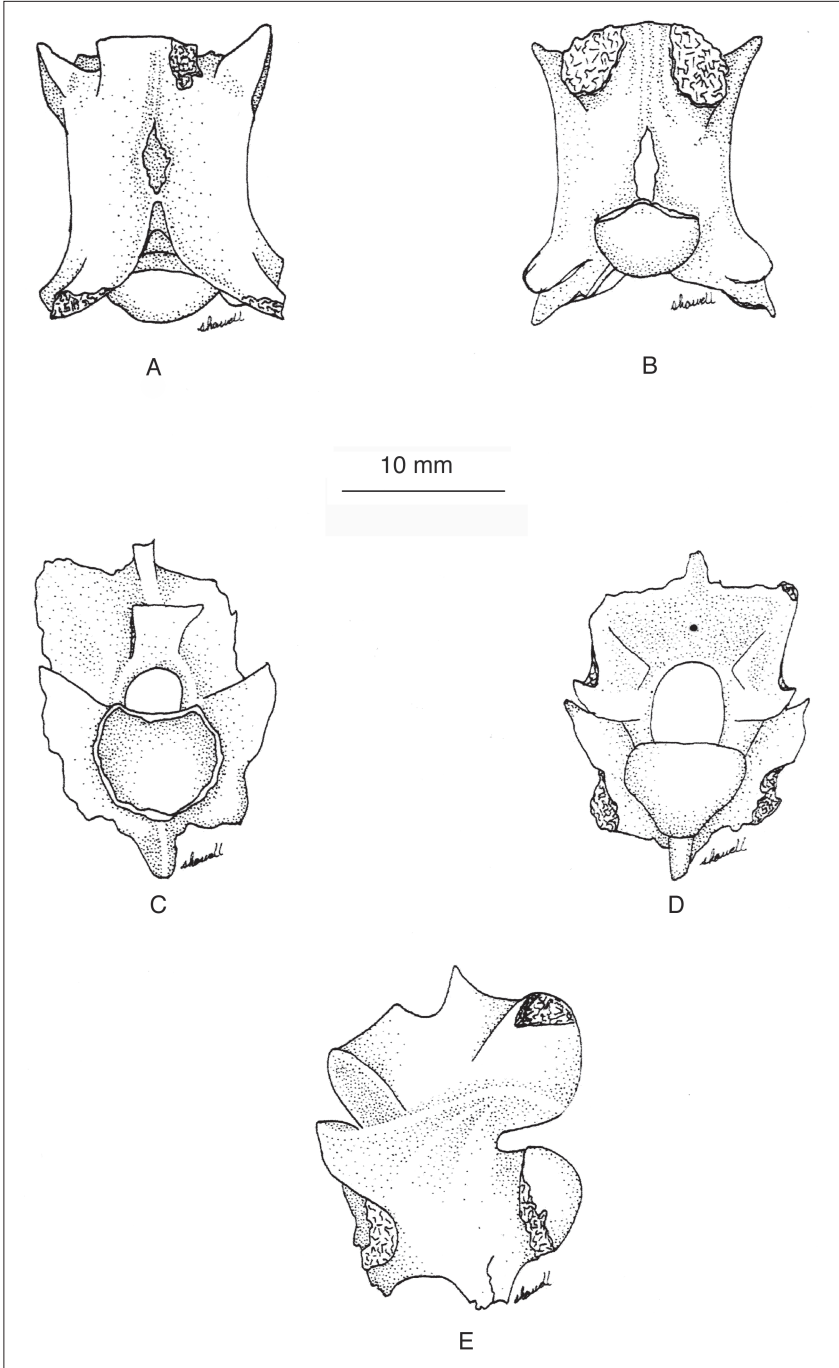


Figure 3. *Palaeophis africanus* vertebra: cervical or anterior trunk (GCVP 4916) in dorsal (A), ventral (B), anterior (C), posterior (D), and left lateral (E) views.

inter-zygapophyseal ridges.” The Hardie Mine vertebrae exhibit not only these features, but also sharp, well-defined inter-zygapophyseal ridges.

Excluding species of questionable validity (see remarks in Rage et al. 2003), four species of *Palaeophis* are currently known from North America (Holman 2000, Rage 1984) and an additional eight species (including *P. africanus*) are known from other parts of the world, including three recently described species from Eocene sites in former USSR lands, for a total of 12 species (Averianov 1997, Rage 1984). *Palaeophis africanus* and the Hardie Mine fossils (GCVF 4915 and GCVF 4916) differ from these taxa in having better developed interzygapophyseal ridges and in other characters that are discussed below.

***Palaeophis casei* Holman - North America**

Palaeophis africanus vertebrae clearly differ from those of this diminutive species on the basis of their larger size, longer and higher neural spines, and absence of grooved neural arches, a character state apparently unique to *P. casei* (Parmley and Case 1988).

***Palaeophis virginianus* Lynn - North America**

Palaeophis africanus vertebrae differ from those of *P. virginianus* in being smaller, more laterally compressed, and having more vaulted neural arches (cf. Holman 2000).

***Palaeophis grandis* (Marsh) - North America**

Mainly because this palaeopheid species was based on a single, poorly preserved vertebra from the Middle Eocene of New Jersey (Marsh 1869), Rage (1984) considered the validity of *Palaeophis grandis* questionable, suggesting that it may actually be synonymous with *P. typhaeus* Owen from the Eocene of Europe. Although *P. typhaeus* does have a similar vertebral morphology to *P. grandis*, it is a comparatively smaller species than *P. grandis*. In their reviews of palaeopheid snakes, Rage (1984) and Parmley and Case (1988) were unaware of a *P. grandis* vertebra described and figured by Blake (1941) from the Eocene of Maryland. Holman (2000) noted that Blake’s vertebra was considerably more complete than Marsh’s type specimen, and that it had a high neural arch and compressed cotyle. These differences appear to be diagnostic enough to maintain *P. grandis* as a valid taxon, at least until detailed comparisons with *P. typhaeus* are made. Nonetheless, *P. africanus* differ from those of *P. grandis* in having lower, less vaulted neural arches, depressed rather than compressed cotyles (cf. Holman 2000), stronger and better developed interzygapophyseal ridges, and possibly in having flatter zygosphenes (viewed anteriorly). Zygosphene morphology may be too variable to be of diagnostic value, and additional vertebrae of both taxa are needed to determine this.

***Palaeophis littoralis* Cope - North America**

This species was originally described by Cope (1868) on the basis of three poorly preserved vertebrae from the Middle Eocene of New Jersey.

Miller (1955) reported a single *P. littoralis* vertebra from the Eocene of New Jersey, which he stated was in better condition than Cope's type specimen (actually a syntype). Since then, additional, more complete *P. littoralis* vertebrae have been reported from the Lower and Middle Eocene of North America (see Holman 2000 for a review), and Parmley and Case (1988) presented a revised description of the taxon in their report on vertebrae from the Lower Eocene (see Holman 2001) of Mississippi. Nonetheless, the validity of the species has been questioned by Rage (1984), who suggested that *P. littoralis* may be a junior synonym of *P. toliapicus* Owen, a taxon known from the Lower Eocene of England. Weems (1999) recently assigned nearly 200 vertebrae from the Lower Eocene Fisher/Sullivan site of Virginia to *P. toliapicus* on the basis of shared characters with this species, but how the vertebrae compared with *P. littoralis* was not discussed. To our knowledge, no detailed comparisons of *P. littoralis* and *P. toliapicus* vertebrae have been made. However, based on arguments presented by Parmley and Case (1988) and additional discussion in Holman (Holman 2000), we retain *P. littoralis* as a valid species. *Palaeophis africanus* vertebrae are clearly similar to those of *P. littoralis* in size and overall morphology, and both taxa were medium-sized palaeopheids having short pterapophyses and vaulted neural arches. However, *P. africanus* vertebrae differ from those of *P. littoralis* in being more laterally compressed, with lower neural arches and better developed interzygapophyseal ridges. As previously noted, sharp interzygapophyseal ridges are unique to *P. africanus* (Andrews 1924, Rage 1984), and Parmley and Case (1988) noted that these distinct ridges appear to be absent in *P. littoralis*.

***Palaeophis ferganicus* Averianov; *P. nessovi* Averianov; *P. udovichenkoi* Averianov - Kirghizia, Kachar, and Ukraine, respectively**

Because they are presently known only by type material (Averianov 1997), much of which appears to be somewhat abraded, it is difficult to ascertain the relationships between these recently described species and other previously described, better known species. Vertebrae of *Palaeophis ferganicus* and *P. nessovi* are similar to each other and appear to morphologically fit into the *P. littoralis*, *P. toliapicus*, and *P. africanus* "complex" (on the basis of similar vertebral sizes, shapes, neural arch heights, and pterapophyseal lengths). Nonetheless, *P. africanus* vertebrae differ from those of *P. ferganicus* and *P. nessovi* in having a lighter, more gracile build with better developed interzygapophyseal ridges. Vertebrae of *P. undovichenkoi* are unique and appear to be considerably more derived than those of *P. ferganicus* and *P. nessovi*. For instance, they are more laterally compressed, with comparatively thinner zygosphenes and neural spines, and more posteriorly directed pterapophyses. These characters, and the lack of well developed interzygapophyseal ridges, clearly separate *P. undovichenkoi* vertebrae from those of *P. africanus* and the Hardie Mine fossils.

***Palaeophis colossaeus* Rage and *P. maghrebianus* Arambourg - Mali and Morocco, respectively**

The vertebrae of *P. africanus* clearly differ from these taxa in being smaller, more delicate, more laterally compressed, and possessing better-developed interzygapophyseal ridges.

***Palaeophis toliapicus* Owen - North America, England, Belgium, France, and Denmark**

Owen's (1841) original description of *P. toliapicus* is confusing and provides little diagnostic information. The type material consists of two matrix nodules from the Lower Eocene London Clay containing several vertebrae (Rage 1984) that are badly in need of re-study and re-description. Additional *P. toliapicus* material includes two fairly well-preserved vertebrae from the Eocene of France and Denmark (Rage 1983b), and a remarkably well-preserved vertebra from the lower Eocene of Denmark tentatively referred to this taxon (Hoch 1975). *Palaeophis africanus* clearly resembles *P. toliapicus* in overall vertebral size and shape (also see discussion under *P. littoralis* account), but with a lower neural spine and sharper, better-developed interzygapophyseal ridges than the latter species.

***Palaeophis typhaeus* Owen - England, Belgium, and Ital**

Palaeophis typhaeus is a poorly understood species occurring in Middle Eocene strata of Europe (Rage 1984). Rage (1984) described the species as having a shorter vertebral form than *P. toliapicus*, but with high pterapophyses. Nonetheless, *P. africanus* vertebrae appear to be longer, with lower neural spines, lower neural arches, lower pterapophyses, and sharper, more pronounced interzygapophyseal ridges than those of *P. typhaeus*.

***Palaeophis* sp. indet.**

Material. Five vertebrae: two CAT vertebrae (GCVP 4919, 5407); two MPT vertebrae (GCVP 4917, 4918); one PC vertebra (GCVP 4920).

Remarks. These vertebrae are too fragmentary for specific identification, but they are like *Palaeophis* in all trenchant characters, including neural spines that originate posteriorly on the zygosphenal roofs, flat, rectangular-shaped zygosphenes, and strongly angled prezygapophyseal articular facets.

One vertebra (GCVP 4920) represents a juvenile snake (Table 1) because it is small, with thin vertebral processes and a relatively large neural canal (Parmley and Case 1988). Based on Recent juvenile boids having similar-sized vertebrae, the fossil represents a snake in the 1.0- to 1.2-meter total-length range. Overall, the vertebra is consistent with *Palaeophis* in its morphology, but it is peculiar in having a single short and robust posterior hypapophysis that projects (hooks) posteriorly (rather than ventrally) in its orientation to the centrum. In lateral view, the hypapophysis does not extend past the centrum. Moreover, it is more triangular-shaped in cross section than it is laterally compressed. There is no evidence of a median keel extending posteriorly from the base of the hypapophysis, and no subcentral

ridges are present. If we are correct in our interpretation of positional placement of palaeopheid vertebrae along the vertebral column, the vertebra may have occupied a precloacal position. A postcloacal (caudal) position is ruled out because, as Parmley and Case (1988) were able to show, palaeopheid vertebrae from this region bear paired ventrolateral processes (pleura- and hemapophyses). Nonetheless, one vertebra does not provide enough evidence to say with certainty that this type of hypapophysis morphology is characteristic of all precloacal vertebrae in *Palaeophis*.

***Pterosphenus schucherti* Lucas (Fig. 4)**

Material. Eleven vertebrae: seven CAT vertebrae (GCVP 4898, 4902, 4927, 4923, 4899, 4941, 4944); four MPT vertebrae (GCVP 4900, 4901, 4903, 4924).

Remarks. Compared with *Palaeophis*, *Pterosphenus* (= *Pt.*) was a relatively short-lived genus. Parmley and Case (1988) reported *Pterosphenus* from the Lower Eocene Yazoo Clay of Louisiana, but this was in error because the deposits that yielded the fossil are actually Middle Eocene in age (McPherson and Manning 1986). In North America, the genus did not appear until late in the Middle Eocene (Rage 1984, Westgate 1989), and apparently went extinct early in the Upper Eocene (Holman 2000). Westgate (2001) reported *Pt. schucherti* from the Hardie Mine l.f., and included in the GC&SU collection of Hardie Mine palaeopheid fossils are an additional eleven vertebrae referable to *Pt. schucherti*. These specimens are large in size (in part; Table 1), generally compressed with high overall vertebral shape, high neural spines (inferred for damaged specimens) that originate on the anterior edges of the zygosphenes, convex zygosphenes that merge with the neural spines (or nearly so), high pterapophyses, and moderately to weakly expanded prezygapophyses. Six species of *Pterosphenus* are known from the Eocene (Averianov 1997, Holman 2000, Rage 1984, Rage et al. 2003): *Pt. schucherti* from North America; *Pt. schweinfurthi* (Andrews) from Egypt and Libya; *Pt. sheppardi* Hoffstetter from Ecuador; *Pt. kutchensis* Rage and *Pt. biswasi* Rage from northwestern India; and *Pt. muruntau* Averianov from Uzbekistan. Vertebral characteristics that can be used to identify isolated *Pterosphenus* vertebrae to species are not significant and are inadequately studied. Excluding the species recently erected by Averianov (1997) and Rage et al. (2003), the single most important diagnostic character used to separate the species has been differences in pterapophyseal length. Rage (1984) summarized the various species as follows: *Pt. schucherti* has tall pterapophyses (also see Lucas 1899), *Pt. schweinfurthi* has comparatively shorter pterapophyses, and *Pt. sheppardi* has even shorter pterapophyses than *Pt. schweinfurthi*, and (possibly) thinner zygantral roofs. Although *Pterosphenus sheppardi* has significantly lower pterapophyses than the other two species, pterapophyseal height of *Pt. schucherti* and *Pt. schweinfurthi* is not significantly different, suggesting that *Pt. schweinfurthi* may be a junior synonym of *Pt. schucherti* (also see discussion in Rage et al. 2003). However, in the absence of definitive

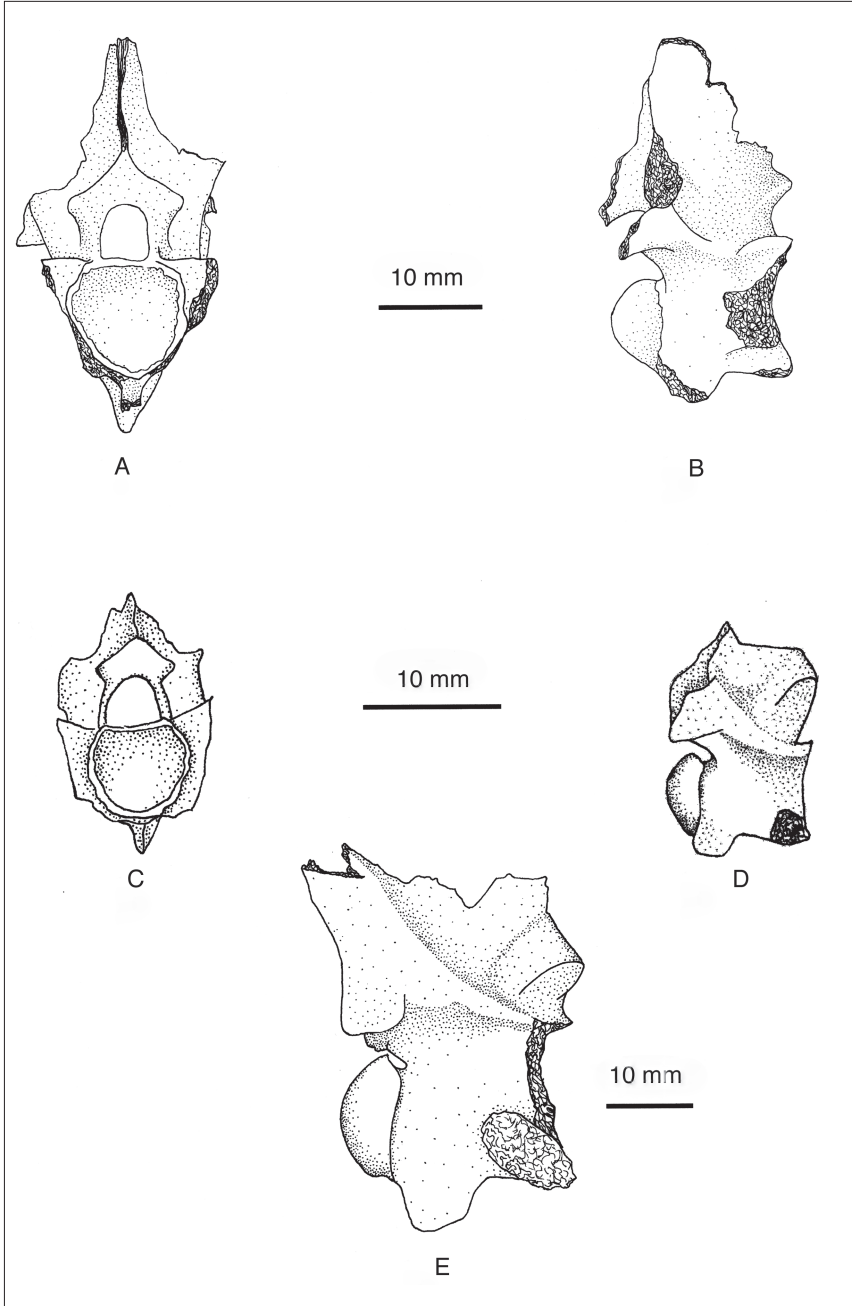


Figure 4. *Pterosphenus schucherti* vertebrae: cervical or anterior trunk vertebra (GCVP 4902) of an adult in anterior (A) and right lateral (B) views; middle or posterior trunk (GCVP 4924) of a juvenile in anterior (C), and right lateral (D) views; and cervical or anterior trunk (GCVP 4923) of large adult in right lateral (E) view.

evidence to the contrary, *Pt. schweinfurthi* is here maintained as a valid species. *Pterosphenus muruntau* is somewhat problematic because the type material is poorly preserved, but this species has even shorter pterapophyses than *Pt. sheppardi* (Averianov 1997). Although the Hardie Mine fossils are somewhat damaged, they differ from the previously discussed species and are assignable to *P. schucherti* on the basis of having longer (taller) and slightly more dorsally angled pterapophyses, and higher neural spines than those of the aforementioned species. Due to the fragmentary condition of several of the fossils, heights of these processes were estimated by comparisons with more complete vertebrae of similar size. *Pterosphenus kutchensis* is known from many vertebrae, and the degree of pterapophyseal development in this species is more similar to *Pt. schucherti* and *Pt. schweinfurthi* than to the other species of *Pterosphenus*. Nonetheless, vertebrae of this species clearly differ from those of *Pt. schucherti* and the Hardie Mine fossils in being smaller, more laterally compressed, and in having longer paradiapophyses that are derived from a common base (or nearly so; see discussion and figure 2 in Rage et al. 2003). The paradiapophyses of *Pt. schucherti* and the Hardie Mine fossils are short and separated. The differentiation of *Pt. schucherti* and *Pt. biswasi* is more problematic because vertebrae of adult individuals of both species are similar in size and pterapophyseal height. Rage et al. (2003) stated that *Pt. biswasi* vertebrae are distinguished from those of *Pt. schucherti* in having zygosphenes with shallower (less concave) anterior borders, and in having the zygosphenal planes positioned slightly higher. The Hardie Mine *Pt. schucherti* vertebrae differ from those of *Pt. biswasi* in having the anterior borders of their zygosphenes more concave, but some of the fossils have their zygapophyseal planes positioned as high as Rage et al. (2003) described and figured for *Pt. biswasi*. This suggests that zygosphenal plane height in these species is influenced by intracolumnar and possibly intercolumnar variation, and thus is probably of little diagnostic value.

Judging from vertebrae of living boids of known total lengths (see Parmley and Reed 2003), at least three distinct age classes of *Pt. schucherti* are represented in the Hardie Mine l.f.: adult, younger adult to subadult, and juvenile. The largest fossils (Table 1, GCVP 4898, 4923; Fig. 4E,) represent large snakes with total lengths in the ca. 4 to 5 meter range. Three of the fossils (Table 1, GCVP 4900, 4901, 4924; Fig. 4C,D) represent juvenile snakes in the ca. 1.9- to 2.1-meter total-length range.

***Pterosphenus* sp. indet.**

Material. Fourteen vertebrae: seven CAT vertebrae (GCVP 4904, 4905, 4908, 4911, 4912, 4913, 4914); two MPT vertebrae (GCVP 4906, 4907); five vertebrae missing hypapophyses (GCVP 4909; 4910; 4925; 5408; 5409).

Remarks. These vertebrae are too fragmentary for specific identification. Nonetheless, they possess important diagnostic characteristics of *Pterosphenus* like arched, triangular-shaped zygosphenes, and/or reduced prezygapophyses with flat to slightly dorsolaterally angled articular facets.

Palaeopheidae gen. indet.

Material. Twenty-one partial vertebrae (GCVP 4942, 4943).

Remarks. The vertebrae are fragmentary and lack any identifiable generic features. One specimen, GCVP 4943, is a pathological specimen consisting of two vertebral centra fused together.

Discussion

In North America, *Palaeophis* and *Pterosphenus* have on two occasions been reported to co-occur in the same stratigraphic context. However, Knight (2000) recently noted that these reports are in error. Miller (1955) reported a single vertebra each of *Palaeophis littoralis* and *Pterosphenus* cf. *P. schucherti* from the Eocene of New Jersey. The interval from within the Eocene that these vertebrae originated is not clear, but it is likely they are from Middle Eocene strata (Holman 2000). Despite the poor quality of the vertebra referred to *Pterosphenus*, it has a flat zygosphene characteristic of *Palaeophis*. Recent study of the actual specimen (Academy of Natural Sciences, Philadelphia, Fossil Vertebrae Collection 8996) by Jim Knight of the South Carolina State Museum (pers. comm. 2000) has confirmed that the specimen actually represents a species of *Palaeophis*, not *Pterosphenus*. Holman (1977) reported one *Palaeophis virginianus* and two *Pterosphenus schucherti* vertebrae from an Upper Middle Eocene site in Twiggs County, central Georgia. Recent examination of the vertebra referred to *P. virginianus* (University of Georgia Vertebrate Paleontology No. 53) by one of us (D. Parmley) revealed that it actually represents *Pterosphenus*. The fossil is badly worn and damaged, but it has two major characteristics of *Pterosphenus*: a convex zygosphene, and the one remaining pre-zygapophyseal articular facet is reduced and only slightly tilted upward. Although *Pterosphenus* and *Palaeophis* are known from the Middle Eocene time period (Holman 2000), the Hardie Mine l.f. represents the only Upper Eocene fauna in North America where both genera occur in the same local stratigraphic context. Moreover, the presence of *Palaeophis* in the Hardie Mine fauna extends the temporal range of the genus from the Middle Eocene (Holman 2000) into the Upper Eocene. Given the sympatric occurrence of *Palaeophis* and *Pterosphenus* in the Hardie Mine l.f., recent suggestions that (at least in North America) *Pt. schucherti* may be a good Upper Eocene index fossil (Knight 2000), and that the presence of *Palaeophis* rules out an Upper Eocene age (Holman 2000, 2001) are not correct. Admittedly, *Palaeophis* appears to have been rare in the Upper Eocene and its geographic distribution may have been limited.

Paleoecology and paleohabitat of the Hardie Mine snakes

Although it is clear that palaeopheid snakes lived in marine or marginal marine waters, there has been much discussion on the type of aquatic environment they preferred. For example, Westgate and Ward (1981) noted that most records of *Pt. schucherti* were from strata representing estuarine

or low salinity habitats. The species is also known from a Middle Eocene mangrove estuary deposit (Westgate 2001). In contrast, Hutchinson (1985) reported *Pterospheenus* cf. *Pt. schucherti* from a carbonate platform locality in Florida that was probably at least 300 km from shore. This suggests that the species may have ventured into open marine water, which Hutchinson described as a “full-marine environment.” Hoffstetter (1958) described *Pt. sheppardi* on the basis of vertebrae and ribs recovered from an Eocene shale deposit in Ecuador that was believed to have formed approximately 80 km from the nearest brackish water environment. McPherson and Manning (1986) suggested “an inner to middle shelf (20–100 meters depth)” habitat for *Pt. schucherti* collected from Upper Eocene sites in Louisiana. Holman and Case (1992) suggested that *P. casei*, *P. virginianus*, and *P. littoralis* from the Lower Eocene of Mississippi lived in a riverine (presumably tidally influenced) or estuarine habitat. The Hardie Mine snakes were preserved in a nearshore marine facies (Westgate 2001). The occurrence in the Hardie Mine l.f. of non-marine vertebrates such as gar fish (*Lepisosteus* sp.), at least two species of crocodylians, softshelled (trionychid) turtle, an emydid-like turtle, a small terrestrial colubrid snake, and at least three different land mammals (Parmley and Holman 2003, Westgate 2001, unpublished fossils in the GCVP collections) offer strong evidence that the paleoshoreline was very close by (also see discussion in Westgate 2001). Primarily on the basis of molluscan and byozoan components preserved in the Hardie Mine Clinchfield sediments, Garner et al. (2000) speculated that the Hardie Mine area was a “marginal marine environment composed of low lying and marshy areas.” Some of the aforementioned taxa support the interpretation for this type of habitat (or an estuarine habitat) for the Hardie Mine palaeopheid snakes. For example, gar are generally freshwater fishes today, but some species commonly inhabit marine marshes and estuaries of the Gulf Coast (D. Parmley, pers. observ.; Hoese and Moore 1977). Several freshwater species of crocodylians are known to thrive in tidal swamps and estuaries (Neil 1971), and some species of trionichid turtles will inhabit marginal marine habitats (Pritchard 1979), including marshes (D. Parmley, pers. observ.). Alternatively, the diversity of the Hardie Mine shark fauna (14 genera and at least 15 species; Parmley and Cicimurri 2003) suggests that low salinity coastal marshes or estuary habitats were not the only depositional environments available to the palaeopheids. Whereas many living shark species are capable of entering river-mouth or estuary habitats (e.g. Schwartz 2000), especially as juveniles, most others do not. The Hardie Mine shark fauna is a mixture of primarily nearshore forms (with an offshore component; see Parmley and Cicimurri 2003) that would be atypical of an estuary or river-mouth coastal selachian fauna (cf. Westgate 1999). Given this, it seems reasonable to suggest that open marine, nearshore shallow water habitats (similar to shallow inlet bays found today along the Gulf of Mexico coastline) were available to the Hardie Mine palaeopheids.

The number and size diversity of the fossil vertebrae offer some insight into the population structure of the Hardie Mine palaeopheid community. If the number of vertebrae recovered for each genus is any indication of relative abundance, then *Pterosphenus* (39 vertebrae; 25 reported here, 14 by Westgate 2001) was more abundant than was *Palaeophis* (7 vertebrae; Table 1). Large, medium, and small vertebrae of both species are present (Table 1), which we interpret to indicate adult, younger adult or subadult, and juvenile snakes, respectively. This is certainly true for the smallest vertebrae, as they exhibit characteristics that are typical of juvenile snakes (see previous systematic accounts). These vertebrae indicate that the shallow nearshore environment of the Hardie Mine area was being utilized by all age classes of palaeopheid snakes. It may be that the palaeopheids utilized the nearshore habitat to breed and give birth (Hutchinson 1985), and to hunt for food. If palaeopheids were piscivorous, the abundance and diversity (size and taxa) of fish fossils recovered from the Hardie Mine (GCVP unreported collections) suggests a prey-rich environment was available to the snakes.

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