NOTE

FIRST REPORT OF SNAKES (SERPENTES) FROM THE LATE MIDDLE EOCENE PONDAUNG FORMATION, MYANMAR

JASON J. HEAD[1, 2], PATRICIA A. HOLROYD[3], J. HOWARD HUTCHISON[3], and RUSSELL L. CIOCHON[4], [1]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20012–7012, USA, head.jason@nmnh.si.edu; [2]School of Biological Sciences, Queen Mary, University of London, London, E1 4NS, United Kingdom; [3]Museum of Paleontology, University of California, Berkeley, CA 94720, USA; [4]Department of Anthropology, University of Iowa, Iowa City, IA 52242, USA

The reptile fauna of the Eocene Pondaung Formation of central Myanmar (Fig. 1) has received little attention compared to its well-known mammalian fauna (e.g., Colbert, 1938; Tsubamoto et al., 2000). In prior reports, Buffetaut (1978) described indeterminate crocodylians and dyrosaurids. Hutchison et al. (in press) described carettochelyid, trionychid, testudinoid, and pelomedusoid turtles from the formation. They additionally noted the presence of agamid lizards, a pristichampsine crocodilian, and snakes. The snakes are described here.

The occurrence of snakes in the Pondaung Formation is significant because the fossil history of Paleogene South Asian snakes has historically been under studied relative to the North American and European records (e.g., Rage, 1984; Szyndlar, 1984; Holman, 2000), despite hypotheses predicting the region as the origin of extant clades (e.g., Underwood and Stimson, 1990; Rage et al., 1992). The South Asian record consists primarily of marine palaeophiid taxa as well as terrestrial/terrigenous specimens referred to Boidae (Boinae + Erycinae, Table 1). The only derived snakes from the South Asian Paleogene are six colubrid vertebrae from the late Eocene Krabi Basin of Thailand (Rage et al., 1992) and a single vertebra referred to Colubroidea (possibly Colubridae) from the early Eocene of India (Rage et al., 2003). The absence of coeval colubroids elsewhere (Rage, 1988), combined with the occurrence of the Krabi Basin record, led Rage et al. (1992) to conclude that Asia represents the center of origin for Colubridae, the most speciose and diverse extant snake clade.

The Pondaung snake record consists of two specimens derived from terrestrial sediments occurring in the upper 100+ meters of the otherwise marine Pondaung Formation as it crops out to the west and northwest of Mogaung village, Myaing Township, central Myanmar (Fig. 1). The snake localities are interpreted as swale-fills and/or paleosols deposited in an ancient floodplain (Soe et al., 2002; see also Ciochon and Gunnell, 2002, and Gunnell et al., 2002 for more detailed discussions of the lithology and stratigraphy of these localities). Traditionally, the age of the Pondaung fauna was considered to be late Eocene (e.g., Pilgrim, 1928; Bender, 1983); however, Holroyd and Ciochon (1994) concluded that the Pondaung fauna is latest middle Eocene (Bartonian) in age and broadly contemporaneous with Asian faunas assigned to the Sharamurunian Land Mammal Age, a finding confirmed by fission-track dates of 37.2 ± 1.3 Ma (Tsubamoto et al., 2002). These findings indicate that the Pondaung fauna is slightly older than the Krabi Basin record, which has been dated between 33.54 and 34.65 Ma in age based on paleomagnetic correlations (Benammi et al., 2001).

Here we describe the Pondaung snakes and discuss their relative implications for paleoecology, divergence timings, and biogeographic histories. We refrain from erecting new taxa for the Pondaung specimens because the record is limited to just the two elements and neither is complete. Additional material will be necessary to determine whether or not the Pondaung record represents new, distinct taxa, or individual or intracolumnar variants of previously known South Asian snakes.

Institution Abbreviations—**AMNH**, American Museum of Natural History; **UCMP**, University of California Museum of Paleontology; **USNM**, United States National Museum.

SYSTEMATIC PALEONTOLOGY

OPHIDIA Brongniart, 1800
ALETHINOPHIDIA Nopcsa, 1923
PALAEOPHIIDAE Lydekker, 1888
Cf. *PTEROSPHENUS* Lucas, 1899

Referred Material—UCMP 147018, isolated precloacal vertebral centrum.

Locality and Age—UCMP V96001, late middle Eocene.

Description—The specimen is a procoelous centrum lacking complete neural processes, synapophyses, and a hypapophysis. In anterior view (Fig. 2A.1), the cotyle is vertically elongate. The majority of the cotylar margin is broken, but a small portion on the left ventrolateral side of the cotyle preserves a sharp margin. Shallow triangular pockets formed by the confluence of the ventrolateral margins of the cotyle, dorsal margins of the synapophyses, and lateral margins of the centrum body are present, as in *Pterosphenus schweinfurthi* (UCMP 41252). The lateral margins of the element are concave in anterior view, from the broken bases of the synapophyses to the bases of the neural arch.

In dorsal view (Fig. 2A.2), the preserved portions of the neural arch are robust, wide processes forming the lateral walls of the neural canal. The transverse section of the arches demonstrates smaller internal pneumaticities than described for *Pterosphenus schucherti* (Hutchison, 1985). Medially, small, paired communicative foramina are present on the floor of the neural canal. These foramina connect to a large central lacuna in the centrum of other snakes (Hoffstetter and Gasc, 1969), and the condition in UCMP 147018 is smaller than observed in many other taxa.

In ventral view (Fig. 2A.3), the synapophyseal bases are elongate, anteroposteriorly oriented, and closely appressed with only a narrow space between them. Just posterior to the synapophyses is the base for a small hypapophysis. The shape and orientation of the base indicate that the hypapophysis was rounded to slightly ovoid in cross section, and extended more ventrally than posteroventrally. The hypapophyseal base is separate from the anterior margin of the condyle, as opposed to contacting the margin as in most other hypapophysial taxa (Smith, 1943). The condyle is separated from the rest of the centrum by a gradual constriction that begins at the level of the hypapophyseal base and the posterior margins of the neural arch bases.

In lateral view (Fig. 2A.4), a broad, shallow pocket is present toward the neural arch bases. Several small foramina are present within the pocket. This condition differs from the single, large lateral foramen seen in most alethinophidians. The condyle is vertically oriented, unlike that in most other snakes, in which the articular surface is posteroventrally oriented. The lateral margins of the cotyle are too poorly preserved to determine if it was vertical or angled.

In posterior view (Fig. 2A.5), the condyle is ovoid, with a wider dorsal than ventral region. Dorsally, the bases of the neural arch diverge from the centrum at a steep angle. Ventral to the neural arches, the lateral margins of the centrum are strongly concave, extending to the bases of the synapophyses. The preserved margins of the hypapophysis are ventromedially angled, suggesting that the process was not elongate.
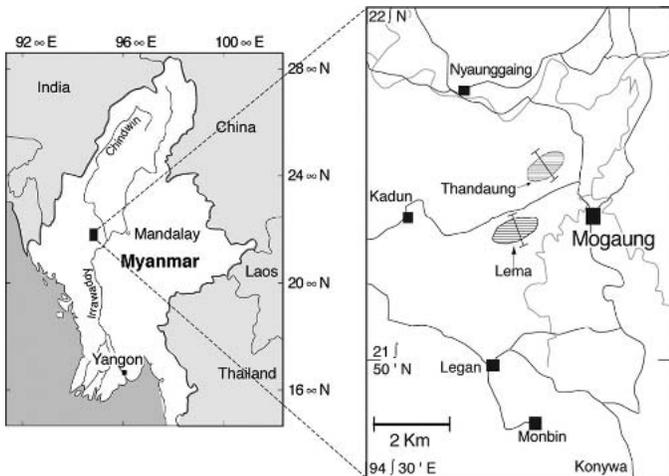
FIGURE 1. Map showing Pondaung Formation fossil localities modified from Gunnell et al. (2002). UCMP locality V78102 corresponds to Thandaung kyitchaung, and UCMP locality V96001 (as well as AMNH locality A22) corresponds to Lema kyitchaung. See Hutchison et al. (in press) for a discussion of locality concordances.

CAENOPHIDIA Hoffstetter, 1939
COLUBROIDEA Oppel, 1811
Gen. et sp. indet.

Referred Material—UCMP 147114, isolated precloacal vertebra.
Locality and Age—UCMP V78090, late middle Eocene.
Description—The specimen is from the precloacal region of the skeleton. It is nearly complete, lacking only the majority of the neural spine, right prezygapophysis, and right synapophysis. In anterior view (Fig. 2B.1), the cotyle is circular, with well-developed lateral margins. Prominent cotylar ventrolateral processes (LaDuke, 1991) are present at the base of the cotyle, giving the ventral margin a squared appearance. The process forms the medial margin of a semicircular anterior opening of the paralymphatic channel with the synapophysis forming the lateral margin. Deep paracotylar fossae are present on both sides of the cotyle; however, the presence of paracotylar foramina within the fossae was not observed. The prezygapophyseal articular facets are horizontally oriented.

In dorsal view (Fig. 2B.2), the element is robust, with shallowly concave interzygapophyseal ridges extending between the pre- and postzygapophyses. The prezygapophyseal articular facet is approximately circular. The zygosphene is well developed with a strongly crenulate anterior margin (tectum). The posterior margins of the neural arch are

sharply concave, meeting at the sagittal midline of the element where they form a wide posterior median notch. The base of the neural spine is triangular in outline, originating at the posterior median notch of the neural arch and thinning anteriorly, where it extends onto the zygosphene.

In ventral view (Fig. 2B.3), the centrum is triangular. A prominent haemal keel originates at the ventral margin of the cotyle and defines the medial margins of the paralymphatic channels. The keel is medially constricted approximately halfway along its length, and flares posteriorly, where it is capped by a small hypapophysis. The condyle is round and is differentiated from the centrum body by a strongly constricted anterior neck. The posterior margin of the hypapophysis is a bluntly pointed process. Lateral to the hypapophysis, two deep subcentral paralymphatic fossae (LaDuke, 1991) excavate the ventral surface of the centrum. They are continuous anteriorly with the channels formed by the synapophyses and cotylar ventrolateral processes. The surface of the element is too poorly preserved to determine the presence or absence of subcentral foramina.

In lateral view (Fig. 2B.4), the zygosphenal articular facets are ovoid and anterodorsally angled. The preserved margins of the neural spine are angled toward the midline of the element, suggesting a relatively lower, shorter neural spine than seen in many extant colubrids. The neural arch is elevated, with an approximately vertical posterior margin. The paralymphatic channels and fossae are wide in lateral view, and are defined by the confluence of the posterior margin of the synapophyses and the hypapophysis with the centrum. The ventral margin of the hypapophysis is broadly convex with an obtuse posterior tip. Just dorsal to the posterior margin of the hypapophysis, the condyle is strongly angled posteroventrally, as is the cotyle. Dorsal to the synapophyses, the prezygapophysis preserves a wide, ovoid base of a large accessory process.

In posterior view (Fig. 2B.5), the posterior median notch is wide, with smooth external margins. The zygantrum is prominent, with well-developed articular facets. The lateral margins of the postzygapophyses are rounded, with no indications of epizygapophyseal spines. Lateral to the condyle, the dia- and parapophyseal articular facets of the synapophyses are distinct, well-developed, ovoid surfaces.

DISCUSSION

Systematic Assignments

Assignment of UCMP 147018 to Palaeophiidae is problematic because there are few morphological characters that unambiguously unite included taxa (e.g., Rage, 1984; Holman, 2000). Historically, the clade has been subdivided into *Palaeophis* and *Pterosphenus* (Lucas, 1899; Hoffstetter, 1958; Holman, 2000), which are generally recognized on the presence of vertically oriented pterapophyses on the dorsal margin of the postzygapophyses, and differentiation of the condyle by a gradual anterior constriction. UCMP 147018 is included within Palaeophiidae on the basis of the condyle differentiation.

Comparison to *Pterosphenus* is based on the presence of a dorsoventrally elongate centrum, ventrolaterally positioned paracotylar fossae,

TABLE 1. Paleogene snake record of Southeastern-Central Asia. *Calamagras turkestanicus* (Erycinae) is the only named species that is not included in Palaeophiidae

| Taxon	Country	Formation/locality and Age	Reference
Vialovophis zhylan	Kazakhstan	Chimkent Region (late Paleocene)	Averianov (1997)
Nessovophis zhylga	Kazakhstan	Chimkent Region (early Eocene)	Averianov (1997)
Archaeophis turkmenicus	Turkmenistan	Danata Formation (early Eocene)	Tatarinov (1963, 1988)
Pterosphenus biswasi, P. kutchensis, "Madtsoiidae"/Boidae indet., Palaeophiidae indet., Colubroidea indet.	India	Naredi Formation (early Eocene)	Bajpai and Thewissen (2002), Rage et al. (2003)
Calamagras turkestanicus, Palaeophis ferganicus	Kirghizia	Alay beds (early Eocene)	Averianov (1997), Danilov and Averianov, (1999)
cf. *Palaeophis ferganicus*	Tajikistan	Bukhara Formation (early Eocene)	Averianov (1997)
Pterosphenus sp.	Pakistan	Domanda Formation (middle Eocene)	Gingerich et al. (1979)
Boinae and Erycinae indet.	Pakistan	Kuldana Formation (early middle Eocene)	(Rage, 1987)
Nessovophis tamdy, Pterosphenus muruntau, cf. "Boidae"	Uzbekistan	Bukhara Viloyat (early late Eocene)	Averianov (1997)
Palaeophis sp.	Kazakhstan	Shorym Formation (early late Eocene)	Averianov (1997)
Palaeophis udovichenkoi	Ukraine	Bodrak horizon (late Eocene)	Averianov (1997)
Palaeophis nessovi	Kazakhstan	Tavda Formation (late Eocene)	Averianov (1997)
"Boidae" and Colubridae	Thailand	Krabi Basin (late Eocene)	Rage et al. (1992), Ducrocq et al. (1992)
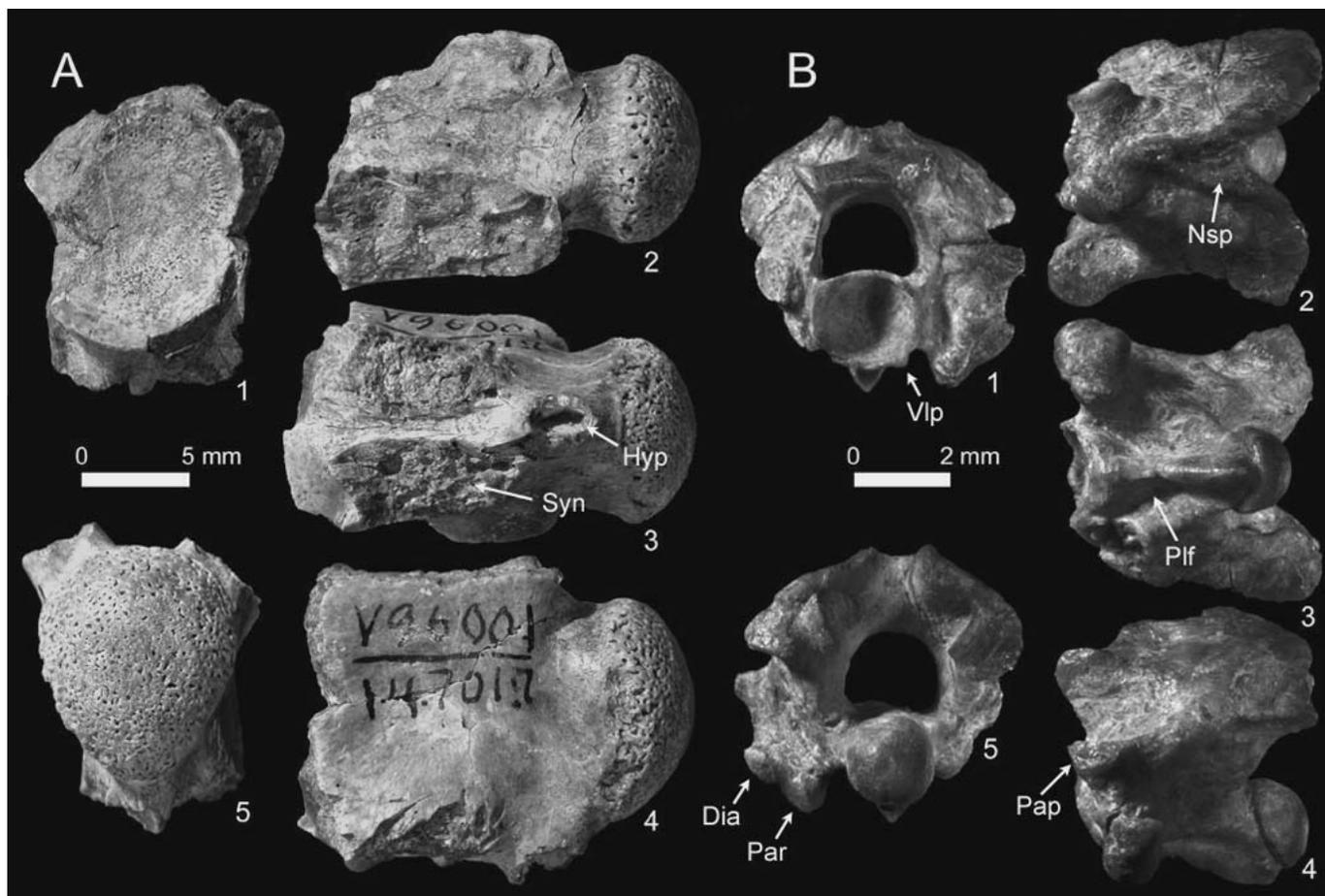
FIGURE 2.   **A**, cf. *Pterosphenus* sp., precloacal vertebral centrum. **B**, Colubroidea indeterminate, precloacal vertebra. Both specimens are shown in anterior (**1**), dorsal (**2**), ventral (**3**), left lateral (**4**), and posterior (**5**) views. **Abbreviations**: **Dia**, diapophyseal articular facet of synapophysis; **Hyp**, base of hypapophysis; **Nsp**, base of neural spine; **Pap**, base of prezygapophyseal accessory process; **Par**, parapophyseal articular facet of synapophysis; **Plf**, subcentral paralymphatic fossa; **Syn**, base of synapophysis; **Vlp**, cotylar ventrolateral process.

closely appressed synapophyses, and a ventrally oriented hypapophysis that does not extend posteriorly to contact the condyle. The specimen lacks the "anterior hypapophysis" (McDowell, 1979) of *Pterosphenus*; however, the process appears to be an intracolumnar variant in *Pterosphenus* (*P. schucherti*, USNM 4047), and may reflect the posterior enlargement of the paralymphatic system where present. UCMP 147018 shares extreme lateral compression, including anteroposterior orientation of the synapophyseal bases and close positioning of the synapophyses, with *Pterosphenus kutchensis* (Rage, et al., 2003), but is too incomplete to make a definitive assignment to that species.

Because the specimen is so fragmentary, we considered the possibility that it represents a non-snake squamate, a turtle, or a crocodyloid. However, the combined presence of synapophyses and a distinct hypapophysis does not occur in crocodilians or turtles, and only occurs in the cervical vertebral column of non-snake squamates. The condition in UCMP 147018 is unique to snakes in that the synapophyses are located on the ventral margin of the centrum, unlike the condition in other squamates where the synapophyses diverge from the lateral margin of the centrum and are continuous with the ventral margin of the prezygapophysis.

Assignment of UCMP 147114 to Colubroidea is based on the occurrence of the following derived characters: well-developed cotylar ventrolateral processes, discrete haemal keel, circular cotyle and condyle, and prominent prezygapophyseal accessory process. Several of these characters are present as intracolumnar variants in non-colubroid snakes; however, the combination of all the aforementioned characters only occurs in colubroid taxa. Within Colubroidea, UCMP 147114 appears to be distinct from Colubridae by the absence of a uniformly thin and elongate neural spine and deeply concave interzygapophyseal ridges. Additionally, the Pondaung specimen is similar to elapid snakes in that

it is more robust and anteroposteriorly short than many colubrids. However, these characteristics are subject to considerable intracolumnar variation (e.g., Hoffstetter and Gayrard, 1965; Thireau, 1967a, b; Hoffstetter and Gasc, 1969).

Ecology, Divergence Timings, and Biogeography

The presence of a possible member of the *Pterosphenus* lineage from terrestrial-estuarine sediments represents either reworked materials from the lower marine Pondaung sediments, or active habitation in fluvolacustrine environments. There are no additional indicators of marine reworking into terrestrial sediments, however, and other palaeophiid taxa are known from estuarine to freshwater environments: *Palaeophis* is known from sediments that include terrigenous components, and is inferred to have inhabited estuarine to riverine environments (e.g., Holman and Case, 1988). Westgate and Gee (1990) suggested that *Pterosphenus* inhabited fluvial, palustrine, and pelagic environments, whereas Holman (2000) proposed that *Pterosphenus* was obligately pelagic, based on the observations of Hutchison (1985). If the Pondaung specimen is a sister taxon to *Pterosphenus*, then its occurrence in the terrestrial facies of the Pondaung Formation supports hypotheses of hyposaline habitats for the lineage.

The occurrence of a colubroid in the Pondaung Formation further corroborates hypotheses of an early Paleogene divergence of Colubroidea in Asia (Rage et. al., 1992). Conversely, Rage and Werner (1999) described a diverse fossil snake assemblage from the Cenomanian Wadi Milk Formation of Sudan that includes specimens assigned to indeterminate colubroids. The presence of colubroids in the Wadi Milk Formation is surprising, as it extends the predicted divergence timing of Colubroidea to prior to the early Late Cretaceous, and requires an approxi-

mately 40 million year unrecovered history between the Wadi Milk fauna and the Paleogene records discussed here. The Cenomanian materials are additionally problematic in the absence of preservation for vertebral characters that are important for establishing phylogenetic interrelationships (e.g., synapophyseal and prezygapophyseal morphologies). Additionally, colubroid characteristics, such as the presence of well-developed paracotylar ventrolateral processes, appear to be absent. Because of these problems, we consider the presence of colubroids at the Early/Late Cretaceous boundary a fascinating but tentative hypothesis at this time.

Rage et al. (2003) reported a possible colubrid from the early Eocene of Kutch, based on an isolated precloacal vertebra. Although this specimen possesses a derived character of colubrids (elongate neural spine that extends onto zygosphene), it also possesses parazygosphenal foramina and multiple paracotylar foramina. The presence of both characters is derived within *Acrochordus*, and it is possible that the Kutch specimen represents an apomorphic acrochordid as opposed to a colubrid.

An early Paleogene divergence of Colubroidea in southern Asia is consistent with the fossil record, immunological divergence times, and geographic distributions of extant clades (Cadle, 1987; Rage et al., 1992; Cundall et al., 1993). The aforementioned morphological differences between UCMP 147114 and Colubridae differentiate the Pondaung and Krabi Basin records, implying higher-order divergences within the clade had occurred by at least the late Eocene. The recent discovery of a colubrid from the marine latest Eocene of North America (Parmley and Holman, 2003) is further corroboration, and indicates that Colubroidea had achieved transcontinental distributions some 14 million years prior to dominating snake faunas in both ecological diversity and species richness beginning in the Miocene (e.g., Parmley and Holman, 1995; Ivanov, 2000).

LITERATURE CITED

Averianov, A. O. 1997. Paleogene sea snakes from the eastern part of Tethys. Russian Journal of Herpetology 4:128–142.

Bajpai, S., and J. G. M. Thewissen. 2002. Vertebrate fauna from Panandhro lignite field (lower Eocene), District Kachchh, western India. Current Science (Bangalore) 82:507–509.

Bender, F. 1983. The Geology of Burma. Beiträge zur Regionalen Geologie der Erde, Band 16.

Benammi, M., Y. Chaimanee, J.-J. Jaeger, V. Suteethorn, and S. Ducrocq. 2001. Eocene Krabi basin (southern Thailand): paleontology and magnetostratigraphy. Geological Society of America Bulletin 113:265–273.

Brongniart, A. 1800. Essai d'une classification naturelle des reptiles. 1ère partie. Establissement des Orders. Bulletin des Sciences, par la Societé Philomatique, Paris 11(2):81–82.

Buffetaut, E. 1978. A dyrosaurid (Crocodilia, Mesosuchia) from the upper Eocene of Burma. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 5:273–281.

Cadle, J. E. 1987. Geographic distribution: problems in phylogeny and zoogeography; pp. 77–105 in R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology. McGraw-Hill Publishing, New York.

Ciochon, R. L., and G. F. Gunnell. 2002. Chronology of primate discoveries in Myanmar: influences on the anthropoid origins debate. Yearbook of Physical Anthropology 45:2–35.

Colbert, E. 1938. Fossil mammals from Burma in the American Museum of Natural History. Bulletin of the American Museum of Natural History 74:255–436.

Cundall, D., V. Wallach, and D. A. Rossman. 1993. The systematic relationships of the snake genus *Anomochilus*. Zoological Journal of the Linnean Society 109(3):275–299.

Danilov, I. G., and A. O. Averianov. 1999. A new species of *Calamagras* Cope, 1873 (Serpentes, Boidae, Erycinae) from the early Eocene of Kirghizia. Geodiversitas 21(1):85–91.

Ducrocq, S., E. Buffetaut, H. Buffetaut-Tong, R. Helmcke-Ingavat, J.-J. Jaeger, Y. Jongkanjanasoontorn, and V. Suteethorn. 1992. A lower Tertiary vertebrate fauna from Krabi (South Thailand). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 84:101–122.

Gingerich, P. D., D. E. Russell, D. Sigogneau-Russell, J.-L. Hartenberger, S. M. Ibrahim Shah, M. Hassan, K. D. Rose, and R. H. Ardrey. 1979. Reconnaissance survey and vertebrate paleontology of some Paleocene and Eocene formations in Pakistan. Contributions from the Museum of Paleontology, University of Michigan 25:105–116.

Gunnell, G. F., R. L. Ciochon, P. D. Gingerich, and P. A. Holroyd. 2002. New assessment of *Pondaungia* and *Amphipithecus* (Primates) from the late middle Eocene of Myanmar, with a comment on "Amphipithecidae." Contributions from the Museum of Paleontology, University of Michigan 30:337–372.

Hoffstetter, R. 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des ophidians. Archives du Muséum d'Histoire Naturelle de Lyon 15:1–78.

Hoffstetter, R. 1958. Un serpent marin du genre *Pterosphenus* (*Pt. Sheppardi* nov. sp.) dans L'Éocène supérieur de L'Équateur (Amérique de Sud). Bulletin de la Société Géologique de France 6:45–50.

Hoffstetter, R., and J.-P. Gasc. 1969. Vertebrae and ribs of modern reptiles; pp. 201–310 in C. Gans (ed.), Biology of the Reptilia, Volume 1: Morphology. Academic Press, London.

Hoffstetter, R., and Y. Gayrard. 1965. Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). Bulletin du Muséum National d'Histoire Naturelle 36:677–696.

Holman, J. A. 2000. The fossil snakes of North America. Indiana University Press, Indianapolis.

Holman, J. A., and G. R. Case. 1988. Reptiles from the Eocene Tallahatta Formation of Alabama. Journal of Vertebrate Paleontology 8:323–333.

Holroyd, P. A., and R. L. Ciochon. 1994. Relative ages of Eocene primate-bearing deposits of Asia; pp. 123–141 in Fleagle, J. G., and R. F. Kay (eds.), Anthropoid Origins. Plenum Press, New York.

Hutchison, J. H. 1985. *Pterosphenus* cf. *schucherti* Lucas (Serpentes, Palaeophidae) from the late Eocene of Peninsular Florida. Journal of Vertebrate Paleontology 18:412–419.

Hutchison, J. H., P. A. Holroyd, and R. L. Ciochon. In Press. A preliminary report on Southeast Asia's oldest Cenozoic turtle fauna from the late middle Eocene Pondaung Formation, Myanmar. Asiatic Herpetological Review.

Ivanov, M. 2000. Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône, France), with comments on the colonisation of Western Europe by colubroids. Geodiversitas 22:559–588.

LaDuke, T. C. 1991. The fossil snakes of Pit 91, Rancho La Brea, California. Natural History Museum of Los Angeles County Contributions in Science 424:1–28.

Lucas, F. A. 1899. A new snake from the Eocene of Alabama. United States National Museum Proceedings 21:637–638.

Lydekker, R. 1888. Notes on Tertiary Lacertilia and Ophidia. Geological Magazine 5:110–113.

McDowell, S. B. 1979. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part III: Boinae and Acrochordoidea (Reptilia, Serpentes). Journal of Herpetology 13:1–92.

Nopsca, F. 1923. *Eidolosaurus* und *Pachyophis*, Zwei neue Neocom-Reptilien. Palaeontographica 55:97–154.

Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben. Joseph Lindauer Verlag, München.

Parmley, D., and J. A. Holman. 1995. Hemphillian (late Miocene) snakes from Nebraska, with comments on Arikareean through Blancan snakes of midcontinental North America. Journal of Vertebrate Paleontology 15:79–95.

Parmley, D., and J. A. Holman. 2003. *Nebraskophis* Holman from the late Eocene of Georgia (USA), the oldest known North American colubrid snake. Acta Zoologica Cracoviensia 46(1):1–8.

Pilgrim, G. E. 1928. The Artiodactyla of the Eocene of Burma. Memoirs of the Geological Survey of India, New Series 8:1–39.

Rage, J.-C. 1984. Encyclopedia of Paleoherpetology, part 11, Serpentes. Gustav Fischer Verlag, Stuttgart.

Rage, J.-C. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Squamata. Contributions from the Museum of Paleontology, University of Michigan 27:187–193.

Rage, J.-C. 1988. The oldest known colubrid snakes. The state of the art. Acta Zoologica Cracoviensia 31:457–474.

Rage, J.-C., and C. Werner. 1999. Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. Palaeontologia Africana 35:85–110.

Rage, J.-C., E. Buffetaut, H. Buffetaut-Tong, Y. Chaimanee, S. Ducrocq, J.-J. Jaeger, and V. Suteethorn. 1992. A colubrid snake in the late Eocene of Thailand: the oldest known Colubridae (Reptilia, Serpentes). Comptes Rendus de l'Académie des Sciences, Série 2 (314): 1085–1089.

Rage, J.-C., S. Bajpai, J. G. M. Thewissen, and B. N. Tiwari. 2003. Early Eocene snakes from Kutch, western India, with a review of the Palaeophiidae. Geodiversitas 25:695–716.

Soe, A. N., Myitta, S. T. Tun, A. K. Aung, T. Thein, B. Marandat, S. Ducrocq, and J.-J. Jaeger. 2002. Sedimentary facies of the late middle Eocene Pondaung Formation (central Myanmar) and the paleoenvironments of its anthropoid primates. Comptes Rendus Palevol 1:53–160.

Smith, M. A. 1943. Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region. Reptilia and Amphibia. Volume III, Serpentes. Taylor and Francis, London.

Szyndlar, Z. 1984. Fossil snakes from Poland. Acta Zoologica Cracoviensia 28:1–156.

Tatarinov, L. P. 1963. [First discovery of ancient sea snakes in the USSR.] Paleontologicheskii Zhurnal, 2:109–115 [Russian].

Tatarinov, L. P. 1988. [Structure of the skull of the sea snake "Archaeophis" turkmenicus from the lower Eocene of Turkmenia.] Paleontologicheskii Zhurnal 1:75–82 [Russian].

Thireau, M. 1967a. Contribution à l'étude de la morphologie caudale et de l'anatomie vertébrale et costale des genres Atheris, Actractaspis, et Causus (Viperidés de l'Ouest africain). Bulletin du Muséum National d'Histoire Naturelle, Paris 2:454–470.

Thireau, M. 1967b. Analyse descriptive et biométrique de la colonne vertébrale du serpent marin Enhydrina schistosa Daudin (Hydrophiinés). Caractères vertébraux des hydrophiidés. Bulletin du Muséum National d'Histoire Naturelle, Paris 2:1044–1056.

Tsubamoto, T., N. Egi, M. Takai, N. Shigehara, T. Thein, A. N. Soe, and S. T. Tun. 2000. A preliminary report on the Eocene mammals of the Pondaung fauna, Myanmar. Asian Paleoprimatology 1:29–101.

Tsubamoto, T., M. Takai, N. Shigehara, N. Egi, S. T. Tun, A. K. Aung, M. Maung, T. Dunhara, and H. Suzuki. 2002. Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. Journal of Human Evolution 42:361–369.

Underwood, G., and A. F. Stimson. 1990. A classification of pythons (Serpentes, Pythoninae). Journal of Zoology (London) 221:565–603.

Westgate, J. W., and C. T. Gee. 1990. Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. Palaeogeography, Palaeoclimatology, Palaeoecology 78: 163–177.