



## SHORT COMMUNICATION

### EARLIEST AFRICAN RECORD OF THE *VARANUS* STEM-CLADE (SQUAMATA: VARANIDAE) FROM THE EARLY OLIGOCENE OF EGYPT

KRISTER T. SMITH,<sup>1,\*</sup> BHART-ANJAN S. BHULLAR,<sup>2,†</sup> and PATRICIA A. HOLROYD<sup>3</sup>; <sup>1</sup>Vertebrate Paleontology Lab, J. J. Pickle Research Campus, 10100 Burnet Rd. Bldg. 6, The University of Texas, Austin, U.S.A.; <sup>2</sup>Department of Geological Sciences, 1 University Station Stop C1100, The University of Texas, Austin, U.S.A.; <sup>3</sup>University of California Museum of Paleontology, 1101 Valley Life Sciences Building, University of California, Berkeley, U.S.A.

The resemblances between the Recent squamates of (north-ern) Africa and those of the European Paleogene—in particular those from the Phosphorites du Quercy—have been thought remarkable (Filhol, 1876 [1877]; de Stefano, 1903; Fejérváry, 1918). However, the biogeographical relations of these faunas are still uncertain, owing in part to our poor understanding of the detailed evolutionary relations of the taxa concerned. Moreover, almost all reported Paleogene African squamates are aquatic (e.g., Andrews, 1901; Arambourg, 1952; Hoffstetter, 1961; Rage, 1975, 1983; Wight, 1980). Terrestrial taxa are known only from an early Oligocene site in Oman (Thomas et al., 1991) and the early Paleogene of Morocco (Augé and Rage, 2006). The Moroccan taxa could have close relatives in the European Paleogene (see Rage, 2006), but the material affords only low taxonomic resolution (Augé and Rage, 2006).

One component of the modern African herpetofauna which is wanting in these Paleogene African assemblages is the clade of monitor lizards placed in the subgenera *Varanus* (*Psammosaurus*) and *V. (Polydaedalus)* (Böhme, 2003); this ‘African clade’ is considered the sister-group to the remainder of *Varanus* (Ast, 2001; Jennings and Pianka, 2004). African varanid fossils are presently restricted to one or two species from the early Miocene of Namibia (Rage, 2003), *V. rusingensis* and possibly a second species from the middle Miocene of Kenya (Clos, 1995), indeterminate species from the late Miocene of Uganda (Bailon and Rage, 1994), and Pleistocene specimens from Uganda and Eritrea referred to *V. niloticus* (Bailon and Rage, 1994; Delfino et al., 2004). Varanids also appear in certain Neogene faunal lists (e.g., Nakaya et al., 1984; Retallack, 1991:290, 296).

We report here on a squamate vertebra from the early Oligocene portion of the Jebel Qatrani Formation, Fayum Province, Egypt. The specimen, YPM 57012, was recovered from Yale Quarry I, a freshwater fluvial deposit in the upper sequence of the Jebel Qatrani Formation (Bown and Kraus, 1988) by Elwyn L. Simons. This quarry is best known for having produced an abundance of early anthropoid primates and other Paleogene mammals (e.g., Simons, 1995; Gagnon, 1997). Based on Kappelman et al.’s (1992) magnetostratigraphic data from the upper part of the Jebel Qatrani Formation, Quarry I is now interpreted as between 30.2 and 29.5 Myr in age, occurring within Chron 11n (Seiffert, 2006). YPM 57012 is the first record of a lizard from

those deposits. In this paper, we describe it, justify its status as the earliest African record of the *Varanus* stem-clade, and examine the implications of this record for models of Tertiary faunal evolution.

**Institutional Abbreviations**—**MSUVP**, Michigan State University, East Lansing, Michigan; **SDNHM**, San Diego Natural History Museum, San Diego, California; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UF**, Florida Museum of Natural History, Gainesville, Florida; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

#### SYSTEMATIC PALEONTOLOGY

Order SQUAMATA Oppel, 1811

Superfamily VARANOIDEA Camp, 1923 (sensu Estes et al., 1988)

Family VARANIDAE Gray, 1827 (sensu Estes et al., 1988)  
Varanidae indeterminate

**Material**—YPM 57012, nearly complete posterior presacral vertebra (Fig. 1A–E).

**Locality and Horizon**—Yale Quarry I, early Oligocene Jebel Qatrani Formation, Fayum Province, Egypt.

**Description**—YPM 57012 is missing only the left pre- and postzygapophyses and the tip of the neural spine. To judge by the small size of the synapophysis (Fig. 1A, E), it represents a posterior presacral. Several oblique fractures cut through the bone, but the bone surface is well preserved. The vertebra is 8.4 mm in length along the base; widths of 12.8 mm and 9.2 mm at the pre- and postzygapophyses, respectively, were estimated by doubling the dimensions of the right side. The base of the centrum is generally flat but shows a weak depression just posterior to the cotyle (Fig. 1A); the bone surface is roughened in places. The centrum shows weak precondylar constriction, which is more distinct on the right side (Fig. 1A). The condyle is markedly oblique, facing posterodorsally, and the cotyle correspondingly faces anteroventrally (Fig. 1E). The condyle is oval in outline, long axis horizontal, when viewed posteriorly (Fig. 1C); it measures 6.1 mm in width and 3.0 mm in height. The neural canal is arched dorsally and flat ventrally (height = 2.5 mm, width = 4.2 mm anteriorly; Fig. 1D), but inside the neural arch, a prominent median ridge flanked by paired grooves is developed on the dorsal surface of the centrum.

The lateral and dorsal surfaces of the neural arch are distinguished by distinct and generally discontinuous striae (Fig. 1B, E). These striae extend posterodorsally on the lateral surface, and posteromedially on the dorsal surface. They appear deeper on the left side. Dorsally, the striae converge as they ascend the

\*Corresponding author/current address: Abteilung Messelforschung, Senckenberg Museum, Senckenberganlage 25, D60325 Frankfurt am Main, Germany; krister.smith@senckenberg.de

†Current address: Harvard University, Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA 02138.

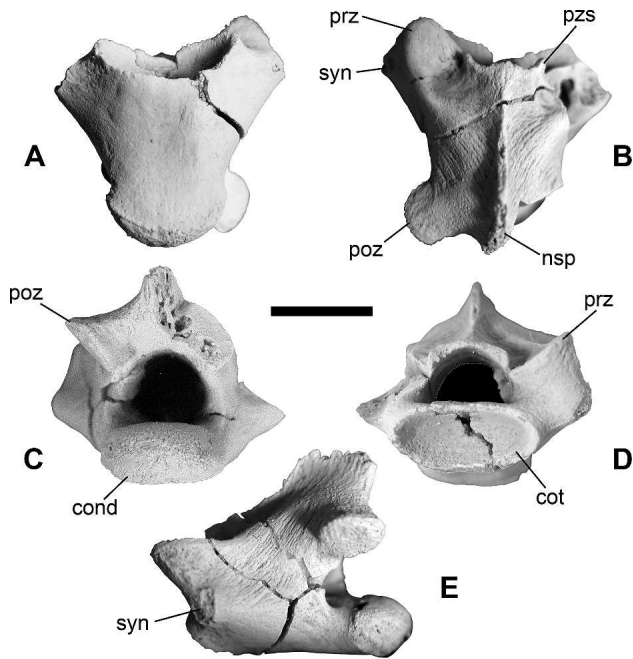


FIGURE 1. YPM 57012, posterior presacral vertebra of indeterminate varanid (stem-*Varanus*) in **A**, ventral, **B**, dorsal, **C**, posterior, **D**, anterior, and **E**, left lateral views. **Abbreviations:** **cond.**, condyle; **cot.**, cotyle; **nsp.**, neural spine; **poz.**, postzygapophysis; **prz.**, prezygapophysis; **pzs.**, pseudozygosphene; **syn.**, synapophysis. Scale bar is 5 mm.

neural spine. Dorsal to the postzygapophysis and on the anterior-most portion of the neural arch, the striae are less well developed and less clearly linear.

The synapophysis is small and conical (Fig. 1A, E). Its surface is poorly preserved. It is connected by a thick, anterodorsally oriented ridge of bone with the prezygapophysis, which extends about 1 mm beyond the anterior margin of the cotyle. The zygapophyseal surfaces are oval (Fig. 1A, B), with long and short axis lengths of 3.5 and 2.9 mm, respectively. Immediately medial to the prezygapophysis, the neural arch is upturned into a small, vertical face (Fig. 1D), forming a pseudozygosphene (Hoffstetter, 1968 [1969]). In dorsal view, the anterior-most end of the neural arch is weakly concave with a rounded median projection (Fig. 1B). The neural spine was supported by the posterior two-thirds of the arch; it rises dorsally and slightly posteriorly to project slightly over the neural canal. Its hinder portion becomes progressively mediolaterally swollen. Since the anterior margin of the spine is incomplete, its shape in lateral aspect cannot be reconstructed with certainty. However, the homogeneous mediolateral thickness of the broken edge of the anterior portion suggests that, much like in modern *Varanus*, the neural spine may have been flat-topped, forming a crest. In contrast, in all other living anguimorphs examined (Appendix), the spine gradually tapers in thickness anteriorly.

#### DISCUSSION

Apart from *Varanus*, the only potential fossil African relation of YPM 57012 is *Pachyvaranus crassispondylus* Arambourg, 1952, a problematic but probably platynotan species from the terminal Cretaceous of Morocco (Molnar, 2004). This taxon, known only from vertebrae, is distinguished by pachyostosis that markedly restricts the neural canal and by certain histological features (de Buffrénil et al., 2007) and lacks zygosphenes-zygantral articulations and precondylar constriction (pers. obs. on MSUVP 1343). Moreover, its surface texture is dominated by

tiny pores rather than clear striae. Thus, *P. crassispondylus* has autapomorphies that YPM 57012 lacks and lacks apomorphies that YPM 57012 possesses (discussed in full below), and there is no reason at present to consider the two to be related.

In contrast, several morphological considerations suggest that the species represented by YPM 57012 is closely related to *Varanus* but outside the crown. Zygosphenes, present in certain squamate taxa (e.g., Teiidae, some Iguanidae), are absent in all living anguimorphs (except Serpentes, if it belongs with them). The Eocene-aged *Saniwa*, however, is distinguished by a small zygosphene (e.g., Camp, 1923; Dollo, 1923 [1925]; Hecht and Hoffstetter, 1962; Rieppel and Grande, 2007; “pseudozygosphène” of Hoffstetter, 1968 [1969]:1055). A pseudozygosphene is also present in the Late Cretaceous *Palaeosaniwa canadensis* (Gilmore, 1928; Estes, 1964), which may be related to Helodermatidae (Balsai, 2001), and many mosasauroids (Caldwell, 1999). If zygosphenes are derived in Anguimorpha (e.g., Lee, 1997), their presence in YPM 57012 could support its reference to *Saniwa*, given the additional data presented below.

Another feature of phylogenetic import is precondylar constriction. Marked constriction is an autapomorphy of *Varanus* (Rieppel, 1980; Pregill et al., 1986), where it is better developed than in any other varanoid, including fossil species referred to *Saniwa* (Gilmore, 1928; Clos, 1995). Although the centrum in YPM 57012 is more constricted anterior to the condyle than in *Heloderma* or *Lanthanotus*, it has a higher ratio of centrum width at the constriction to condyle width (0.87) than living *Varanus* (see Clos, 1995). In this respect, it is similar to *Saniwa ensidens* (Clos, 1995) and *S. orsmalensis* (Hoffstetter, 1968 [1969]:fig. 2; Augé, 1990:fig. 1), which further suggests it lies outside crown *Varanus*.

A third feature of interest is the ridge of bone that extends posteromedially from the lateral edge of the prezygapophysis and ascends the neural arch. It is sharply developed in YPM 57012, as it is in many species of *Varanus* (e.g., *V. exanthematicus*; Fig. 2C, D) and *Saniwa ensidens* (Gilmore, 1928:pl. 5), but is poorly developed in all ontogenetic stages of *Heloderma* (Fig. 2A, B), especially early ones.

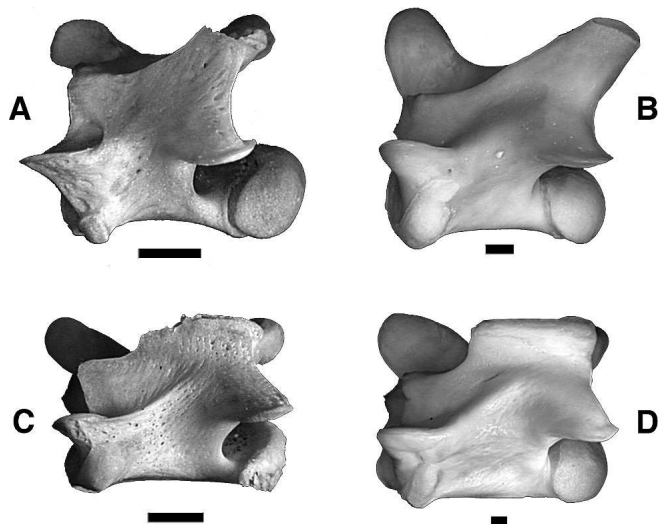


FIGURE 2. Anterior presacral vertebrae of living varanoids in oblique left lateral views. **A**, *Heloderma horridum* (UCMP 131264), SVL = 135 mm; **B**, *H. horridum* (SDNHM 59460), SVL = ?, frontal length 1.8× previous individual; **C**, *Varanus exanthematicus* (TMM M9015), SVL = 110 mm; **D**, *V. exanthematicus* (TMM M8956), SVL = 395 mm. The bone surface shows a porous texture in the juveniles of both species, but in *V. exanthematicus* the pores are more numerous and accompanied by distinct grooves on the lateral surface of the neural arch; these grooves are much reduced but still visible in the adult. Scale bars are 1 mm.

Finally, the surface texture of YPM 57012 is noteworthy. Bone surface texture varies significantly during ontogeny in many amniotes (e.g., Sanz et al., 1997; Tumarkin-Deratzian et al., 2006), and the rough texture of YPM 57012 might simply indicate skeletal immaturity. We therefore sought to compare vertebral surface texture in varanoid outgroups (Appendix). A broad post-natal ontogenetic survey of *Heloderma* spp. revealed that vertebral striae are absent at all ontogenetic stages, from very young individuals (Fig. 2A) to mid-sized animals (Fig. 2B) and large adults. However, in neonates the exterior surface of the neural arch is pierced by a number of pores (Fig. 2A), which are best developed just posterior to the prezygapophysis and on the lateral surface of the neural spine. Small grooves may extend along the bone surface from the pores, imparting a weak grain to the texture. Striae were not developed in the single (adult) specimen available to us of the varanid *Lanthanotus borneensis*.

In contrast, striae are variably but commonly present on the neural arch in vertebrae of *Varanus*. We examined the vertebrae of many species spread throughout the geographic range and phylogenetic breadth of the clade (Appendix). Striae were observed in *V. albigularis* with snout-vent length (SVL) as great as 504 mm, *V. bengalensis*, *V. dumerilii*, *V. exanthematicus* (Fig. 2C, D), juvenile *V. griseus*, large *V. doriensis* (weak development of striae), *V. indicus* (weak), *V. melinus* (weak), large *V. niloticus*, and *V. salvator* (weak but distinct). Striae were nearly absent in *V. prasinus* and *V. mertensi* and absent in *V. beccari*, *V. gilleni*, a juvenile (SVL = 175 mm) *V. jobiensis*, *V. panoptes*, *V. storri* and *V. tristis*. When striae are present, they are sometimes well developed on posterior trunk vertebrae and caudals but poorly developed on anterior trunk vertebrae and cervicals (e.g., *V. bengalensis*). An ontogenetic series of *Varanus exanthematicus* showed that both striation and porosity are pronounced in young individuals (Fig. 2C). In adults, porosity is highly reduced or absent, whereas more or less prominent striae are still expressed (Fig. 2D). *Varanus exanthematicus* has a hatchling SVL of ~70 mm, and most adults in nature have SVL < 500 mm (Bennett, 2004). In *Heloderma horridum*, hatchlings with a SVL of ~120 mm were reported by Ramírez-Bautista (1994, cited by Beck, 2005), and the largest wild-caught adult had a SVL of 483 mm (Beck, 2005). The juvenile of *H. horridum* (Fig. 2A) is therefore relatively smaller than the juvenile of *V. exanthematicus* (Fig. 2C), and likewise the larger *H. horridum* (Fig. 2B), yet both specimens of *H. horridum* display less porosity and neither shows striae. Thus, although there is some variation, it appears that vertebrae of *Varanus* exhibit greater porosity and striation of the bone surface at all stages of their ontogeny than those of *Lanthanotus borneensis* (for which more data are desirable) and *Heloderma*. Additionally, we examined representatives of other major squamate clades (Iguanidae, Gekkonidae, Cordyliformes, Teioidea, Lacertidae, Scincidae, Anguillidae, Xenosauridae), including both juvenile and adult forms (when available) of large species. Almost all of these lacked striae too, except larger teiids (especially *Tupinambis*), and in these the striae become more prominent with increased size, in contrast to the pattern in *Varanus*.

Among fossil varanoids, vertebral striae have been observed in *Saniwa ensidens* (Rieppel and Grande, 2007). Although they have not been reported for other species, striae are also seen in vertebrae referred to *S. crassus* (Gilmore, 1928:pl. 10-7) and '*Megalania*' *prisca* (Fejérváry, 1918:figs. 33, 34) and in a large (2-cm-long) vertebra referred to *V. niloticus* (Delfino et al., 2004:fig. 5A, C). This latter observation is consistent with the development of striae in even large individuals of *V. niloticus* and *V. albigularis*.

It is possible that striae are caused by modifications to *m. interarcuales* and *m. interarticulares*, muscles which insert on the lateral portion of the neural arch in squamates (Herrel and De Vree, 1999; Tsuihiji, 2005). However, striae in *Varanus* appear to

become less prominent with size (age), in contrast to the development of rugose muscle scars in other amniotes (e.g., Brinkman, 1988), casting doubt on this hypothesis.

In summary, the possession by YPM 57012 of distinct precondylar constriction and well-developed porosity and striation of the neural arch are both apomorphies suggesting relationship with crown *Varanus*. However, the relatively small degree of precondylar constriction and the presence of a pseudozygosphene indicate that the species is outside crown *Varanus* and could possibly be referred to *Saniwa*. Vertebral striae appear to have arisen on the *Varanus* stem and are retained as plesiomorphy in many crown *Varanus*, especially the African forms.

*Varanus* has been considered to have an Asiatic origin (e.g., Hoffstetter, 1968 [1969]; see also Fejérváry, 1918). Jennings and Pianka (2004) suggested that the African radiation of *Varanus* did not begin until the Miocene, although early and middle Miocene species of *Varanus* already show the bulbous teeth characteristic of *V. (Polydaedalus)* and so clearly lie within the crown of the 'African clade' (Clos, 1995; Rage, 2003). As discussed above, the early Oligocene species represented by YPM 57012 is probably outside crown *Varanus*. Thus, assuming an Asian origin of crown *Varanus*, YPM 57012 suggests a separate Tertiary dispersal into Africa by the *Varanus* stem. The European pattern of replacement of stem-*Varanus* (*Saniwa*) in the early Paleogene (Dollo, 1923 [1925]; Hoffstetter, 1943; Augé, 2005) by (possible) crown-clade *Varanus* in the Neogene (e.g., Roger, 1898; Hoffstetter, 1943; Rage and Bailon, 2005) might have been replicated in Africa. Interestingly, Rage (2003) distinguished his two early Miocene varanid vertebral morphotypes by the degree of precondylar constriction (one was strongly constricted, the other weakly so). If two different lineages were in fact present, it is possible that both stem and crown *Varanus* co-existed in Africa at that time.

Fejérváry (1918:370–371) explained the similarity between European Paleogene squamates and modern (northern) African ones by the persistence in Africa of subtropical climes, arguing specifically that European forms must have "passed over to Africa" where they found conditions amenable to their "survival" in the face of late Neogene climatic deterioration. YPM 57012 is consistent, at present, with this notion, but given the currently sparse record it is difficult to pinpoint the timing of possible Eocene or Oligocene dispersal events. Yet, the occurrence of stem *Varanus* in the early Oligocene of Africa complements the pattern of limited Paleogene Asian–African faunal exchange that is indicated by other Fayum mammals (e.g., Holroyd and Maas, 1994; Ducrocq, 1997; Egi et al., 2005; Gheerbrant and Rage, 2006). The phylogenetic relationships of these taxa suggest some middle to late Eocene faunal exchange between Eurasia and Africa, perhaps via an Iranian route (Gheerbrant and Rage, 2006). If we have correctly identified it, YPM 57012, like testudinid turtles (Holroyd and Parham, 2003), would represent a reptilian example of such interchange.

**Acknowledgments**—We thank W. G. Joyce, M. A. Turner, and D. Brinkman (YPM) for assistance in curation. We are grateful to T. Tsuihiji, J. Lindgren and others for helpful discussions. C. J. Bell pointed out relevant literature on African varanids and made helpful comments. M. Caldwell, R. Holmes, and three anonymous reviewers read and improved the manuscript. This is UCMP contribution number 1958.

#### LITERATURE CITED

- Andrews, C. W. 1901. Preliminary notes on some recently discovered extinct vertebrates from Egypt. Part. II. Geological Magazine 8: 436–444.
- Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc–Algérie–Tunisie). Notes et Mémoires du Service Géologique du Maroc 92:1–372.

- Ast, J. C. 2001. Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). *Cladistics* 17:211–226.
- Augé, M. 1990. La faune de lézards et d'Amphisbenes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocene inférieur). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 60:161–173.
- Augé, M. 2005. Évolution des lézards du Paléogène en Europe. *Mémoires du Muséum National d'Histoire Naturelle* 192:1–369.
- Augé, M. and J.-C. Rage. 2006. Herpetofaunas from the upper Paleocene and lower Eocene of Morocco. *Annales de Paléontologie* 92: 235–253.
- Bailon, S. and J.-C. Rage. 1994. Squamates Néogènes et Pléistocènes du Rift Occidental, Ouganda; pp. 129–135 in B. Senut and M. Pickford (eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Volume II: Palaeobiology (CIFEG Occasional Publication 29)*. Centre International pour la Formation et les Échanges Géologiques, Orléans, France.
- Balsai, M. J. 2001. The phylogenetic position of *Palaeosaniwa* and the early evolution of the platynotan (varanoid) anguimorphs. Ph.D. dissertation, University of Pennsylvania, Philadelphia, Pennsylvania, 340 pp.
- Beck, D. D. 2005. *Biology of Gila Monsters and Beaded Lizards*. University of California Press, Berkeley, California, 211 pp.
- Bennett, D. 2004. *Varanus exanthematicus*; pp. 95–103 in E. R. Pianka, D. R. King, and R. A. King (eds.), *Varanoid Lizards of the World*. Indiana University Press, Bloomington, Indiana.
- Böhme, W. 2003. Checklist of the living monitor lizards of the world (family Varanidae). *Zoologische Verhandlungen* 341:1–43.
- Bown, T. M. and M. J. Kraus. 1988. Geology and paleoenvironment of the Oligocene Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. United States Geological Survey Professional Paper 1452, U. S. Government Printing Office, Washington, D.C., 59 pp.
- Brinkman, D. B. 1988. Size-independent criteria for estimating relative age in *Ophiacodon* and *Dimetrodon* (Reptilia, Pelycosauria) from the Admiral and Lower Belle Plains Formations of west-central Texas. *Journal of Vertebrate Paleontology* 8:172–180.
- de Buffrénil, V., N. Bardet, X. Pereda-Suberbiola, and B. Bouya. 2008. Specialization of bone structure in *Pachyvaranus crassispondylus* Arambourg, 1952, an aquatic squamate from the Late Cretaceous of the southern Tethyan margin. *Lethaia* 41:59–69.
- Caldwell, M. W. 1999. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society* 125:115–147.
- Camp, C. L. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History* 48:289–481.
- Clos, L. M. 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *Journal of Vertebrate Paleontology* 15:254–267.
- Delfino, M., A. Segid, D. Yosief, J. Shoshani, L. Rook, and Y. Libsekal. 2004. Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, northern Danakil Depression). *Rivista Italiana di Paleontologia e Stratigrafia* 110 (Suppl.):51–60.
- Dollo, L. 1923 [1925]. *Saniwa orsmaelensis*. Varanide nouveau du Landénien supérieur d'Orsmael (Brabant). *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 33:76–82.
- Ducrocq, S. 1997. The anthracotheriid genus *Bothriogenys* (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: phylogenetical and paleobiogeographical relationships. *Stuttgarter Beiträge zur Naturkunde, B (Geologie und Paläontologie)* 250:1–44.
- Egi, N., P. A. Holroyd, T. Tsubamoto, A. N. Soe, M. Takai, and R. L. Ciochon. 2005. Proviverrine hyaenodontids (Creodonta: Mammalia) from the Eocene of Myanmar and a phylogenetic analysis of the proviverrines from the Para-Tethys area. *Journal of Systematic Palaeontology* 3:337–358.
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. University of California Publications in Geological Sciences 49:1–187.
- Estes, R., K. de Queiroz, and J. A. Gauthier. 1988. Phylogenetic relationships within Squamata; pp. 119–281 in R. Estes and G. K. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Stanford, California.
- de Fejérváry, G. J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. *Annales Historico-Naturales Musei Nationalis Hungarici* 16:341–467.
- Filhol, H. 1876 [1877]. Sur les Reptiles fossiles des phosphorites du Quercy. *Bulletin de la Société Philomathique de Paris (Série 6)* 11:27–28.
- Gagnon, M. 1997. Ecological diversity and community ecology in the Fayum sequence (Egypt). *Journal of Human Evolution* 32:133–160.
- Gheerbrant, E. and J.-C. Rage. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* 241:224–246.
- Gilmore, C. W. 1928. Fossil lizards of North America. *Memoirs of the National Academy of Sciences* 22:1–201.
- Gray, J. E. 1827. A synopsis of the genera of saurian reptiles, in which some new genera are indicated and others reviewed by actual examination. *The Philosophical Magazine, or Annals of Chemistry, Mathematics, Astronomy, Natural History, and General Science* 2: 54–58.
- Hecht, M. K. and R. Hoffstetter. 1962. Note préliminaire sur les Amphibiens et les Squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 38:1–30.
- Herrel, A. and F. De Vree. 1999. The cervical musculature in helodermatid lizards. *Belgian Journal of Zoology* 129:175–186.
- Hoffstetter, R. 1943. Varanidae et Necrosauridae fossiles. *Bulletin du Muséum Nationale d'Histoire Naturelle, Série 2* 15:134–141.
- Hoffstetter, R. 1961. Nouvelles récoltes de serpents fossiles dans l'Éocène Supérieur du désert Libyque. *Bulletin du Muséum National Histoire Naturelle, Paris* 33:326–331.
- Hoffstetter, R. 1968 [1969]. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bulletin du Muséum National d'Histoire Naturelle (Série 2)* 40:1051–1064.
- Holroyd, P. A. and M. C. Maas. 1994. Paleogeography, paleobiogeography, and anthropoid origins; pp. 297–334 in J. G. Fleagle and R. F. Kay (eds.), *Anthropoid Origins*. Plenum Press, New York.
- Holroyd, P. A. and J. F. Parham. 2003. The antiquity of African tortoises. *Journal of Vertebrate Paleontology* 23:688–690.
- Jennings, W. B. and E. R. Pianka. 2004. Tempo and timing of the Australian *Varanus* radiation; pp. 77–87 in E. R. Pianka, D. R. King, and R. A. King (eds.), *Varanoid Lizards of the World*. Indiana University Press, Bloomington, Indiana.
- Kappelman, J., E. L. Simons, and C. C. Swisher III. 1992. New age-determinations for the Eocene-Oligocene boundary sediments in the Fayum Depression, northern Egypt. *Journal of Geology* 100: 647–667.
- Lee, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London, Series B* 352:53–91.
- Molnar, R. 2004. The long and honorable history of monitors and their kin; pp. 10–67 in E. R. Pianka, D. R. King, and R. A. King (eds.), *Varanoid Lizards of the World*. Indiana University Press, Bloomington, Indiana.
- Nakaya, H., M. Pickford, Y. Nakano, and H. Ishida. 1984. The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs, Supplementary Issue* 2:87–131.
- Oppel, M. 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, Munich, 86 pp.
- Pregill, G. K., J. A. Gauthier, and H. W. Greene. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Transactions of the San Diego Society of Natural History* 21:167–202.
- Rage, J.-C. 1975. Un serpent du Paléocène du Niger. Etude préliminaire sur l'origine des Caenophidiens (Reptilia, Serpentes). *Comptes Rendus des Séances de l'Académie des Sciences, Paris II* 281: 515–518.
- Rage, J.-C. 1983. *Palaeophis colossaeus* nov. sp., le plus grand Serpent connu de l'Éocène du Mali et le problème du genre chez les Palaeopheinae. *Comptes Rendus des Séances de l'Académie des Sciences, Paris II* 296:1741–1744.
- Rage, J.-C. 2003. Squamate reptiles from the early Miocene of Arrisdrift (Namibia); pp. 43–50 in M. Pickford and B. Senut (eds.), *Geology and Palaeobiology of the Central and Southern Namib, Vol. 2: Palaeontology of the Orange River Valley, Namibia (Memoir of the Geological Survey of Namibia 19)*. Ministry of Mines and Energy, Windhoek.
- Rage, J.-C. 2006. The lower vertebrates from the Eocene and Oligocene

- of the Phosphorites du Quercy (France): an overview. *Strata* (Série 1) 13:161–173.
- Rage, J.-C. and S. Bailon. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas* 27:413–441.
- Retallack, G. J. 1991. Miocene Paleosols and Ape Habitats of Pakistan and Kenya. Oxford University Press, Oxford, U.K., 346 pp.
- Rieppel, O. 1980. The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). *Amphibia-Reptilia* 1:95–112.
- Rieppel, O. and L. Grande. 2007. The anatomy of the fossil varanid lizard *Saniwa ensidens* Leidy, 1870, based on a newly discovered complete skeleton. *Journal of Paleontology* 81:643–665.
- Roger, O. 1898. Wirbelthierreste aus dem Dinotheriensande, II. Theil. Bericht des naturwissenschaftlichen Vereins für Schwaben und Neuburg (a.V.) in Augsburg 33:385–396.
- Sanz, J. L., L. M. Chiappe, B. P. Pérez-Moreno, J. J. Moratalla, F. Hernández-Carrasquilla, A. D. Buscalioni, F. Ortega, F. J. Poyato-Ariza, D. Rasskin-Gutman, and X. Martínez-Delclòs. 1997. A nestling bird from the Lower Cretaceous of Spain: Implications for avian skull and neck evolution. *Science* 276:1543–1546.
- Seiffert, E. R. 2006. Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman. *Proceedings of the National Academy of Science* 103:5000–5005.
- Simons, E. L. 1995. Egyptian Oligocene Primates: a review. *Yearbook of Physical Anthropology* 38:199–238.
- de Stefano, G. 1903. I sauri del Quercy appartenenti alla collezione Rossignol. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 42:382–418.
- Thomas, H., J. Roger, S. Sen, J. Dejax, M. Schuler, Z. al-Sulaimani, C. Bourdillon de Grissac, G. Breton, F. de Broin, G. Camoin, H. Capetta, R.-P. Carriol, C. Cavalier, C. Chaix, J.-Y. Crochet, G. Fajanel, M. Gayet, E. Gheerbrant, A. Lauriat-Rage, D. Noël, M. Pickford, A.-F. Poignant, J.-C. Rage, J. Roman, J.-M. Rouchy, S. Secrétan, B. Sigé, P. Tassy and S. Wenz. 1991. Essai de reconstitution des milieux de sédimentation et de vie des primates anthropoïdes de l'Oligocène de Taqah (Dhofar, Sultanat d'Oman). *Bulletin de la Société Géologique de France* 162:713–724.
- Tsuihiji, T. 2005. Homologies of the transversospinalis muscles in the anterior presacral region of Sauria (crown Diapsida). *Journal of Morphology* 263:151–178.
- Tumarkin-Deratzian, A. R., D. R. Vann and P. Dodson. 2006. Bone surface texture as an ontogenetic indicator in long bones of the Canada goose *Branta canadensis* (Anseriformes: Anatidae). *Zoological Journal of the Linnean Society* 148:133–168.
- Wight, A. W. R. 1980. Palaeogene vertebrate fauna and regressive sediments of Dur at Talhah, southern Sirt Basin, Libya. *Symposium on the Geology of Libya* 2:309–325

Submitted June 13, 2007; accepted February 6, 2008.

#### APPENDIX. Modern varanoid specimens examined for this paper.

Helodermatidae: *Heloderma horridum* (SDMNH 59460, UCMP 131264, YPM R10618), *H. suspectum* (UF 52565, YPM R11201, 14352).  
 Varanidae: *Lanthanotus borneensis* (YPM R12673), *Varanus albigularis* (YPM R13981, 13717), *V. beccari* (YPM R13267), *V. bengalensis* (YPM R11028, R11089), *V. dumerilii* (YPM R11203, R12148), *V. exanthematicus* (TMM M8956, 9015), *V. griseus* (YPM R10370), *V. doriensis* (YPM R13989), *V. jobiensis* (R11074, R13659), *V. indicus* (YPM R10381), *V. mertensi* (YPM R11658), *V. melinus* (YPM R11202), *V. niloticus* (YPM R10878), *V. prasinus* (YPM R10328), *V. panoptes* (YPM R10394), *V. rudicollis* (YPM R12235), *V. salvator* (YPM R10131, R11064, R12723), *V. storri* (YPM R11042), *V. tristis* (YPM R11175).