29. The compilation is provided in the supplementary material (*38*).
30. C. D. Gebelein, in *Stromatolites*, M. R. Walter, Ed. (Elsevier, Amsterdam, 1976), pp. 499–515.
31. J. P. Grotzinger, J. F. Kasting, *J. Geol.* **101**, 235 (1993).
32. J. Bertrand-Sarfati, M. R. Walter, *Precambrian Res.* **15**, 353 (1981).
33. J. P. Grotzinger, D. H. Rothman, *Nature* **383**, 423 (1996).
34. A. H. Knoll, I. J. Fairchild, K. Swett, *Palaios* **8**, 512 (1993).
35. R. Riding, *J. Geol. Soc. London* **149**, 979 (1992).
36. B. Laval *et al.*, *Nature* **407**, 626 (2000).
37. D. L. Parkhurst, D. C. Thorstenson, L. N. Plummer, *U.S. Geol. Surv. Wat.-Res. Invest. Rep.* **80-96** (1990).
38. Supplementary data are available on *Science* Online at www.sciencemag.org/cgi/content/full/292/5522/1701/DC1.

39. We thank R. Riding and P. Westbroek for comments on an earlier draft and the Pyramid Lake Paiute Tribal Council and the Western Australian Department of Conservation and Land Management for sampling permits. Funded by the German Research Foundation and the Studienstiftung des deutschen Volkes (G.A.).

6 November 2000; accepted 10 April 2001

A Giant Sauropod Dinosaur from an Upper Cretaceous Mangrove Deposit in Egypt

**Joshua B. Smith,[1]* Matthew C. Lamanna,[1] Kenneth J. Lacovara,[2]
Peter Dodson,[1,3] Jennifer R. Smith,[1] Jason C. Poole,[4]
Robert Giegengack,[1] Yousry Attia[5]**

We describe a giant titanosaurid sauropod dinosaur discovered in coastal deposits in the Upper Cretaceous Bahariya Formation of Egypt, a unit that has produced three *Tyrannosaurus*-sized theropods and numerous other vertebrate taxa. *Paralititan stromeri* is the first tetrapod reported from Bahariya since 1935. Its 1.69-meter-long humerus is longer than that of any known Cretaceous sauropod. The autochthonous scavenged skeleton was preserved in mangrove deposits, raising the possibility that titanosaurids and their predators habitually entered such environments.

In the early 20th century, the Bavarian geologist Ernst Stromer described a diverse biota from the Upper Cretaceous [Cenomanian: 93.5 to 99.0 million years ago (Ma)] Bahariya Formation (*1*) of the Bahariya Oasis, Egypt (Fig. 1). The vertebrate discoveries included fish, turtles, plesiosaurs, squamates, crocodyliforms, and four dinosaurs: the theropods *Spinosaurus*, *Carcharodontosaurus*, and *Bahariasaurus*, and the sauropod *Aegyptosaurus* (*2*). Tragically, Stromer's collections were largely destroyed during an Allied bombing of Munich in 1944 (*3*). With exceptions from Morocco (*4–6*) and Algeria (*7*), evidence of Late Cretaceous African dinosaurs remains limited. An improved understanding of Late Cretaceous African terrestrial vertebrates is important for the paleoecology of this region and is needed to evaluate biogeographic hypotheses pertaining to Gondwanan fragmentation (*5*, *8–10*). Here we describe the partial skeleton of an extremely large sauropod dinosaur, the first tetrapod reported from Bahariya since 1935 (*11*). The specimen consists largely of vertebrae, pectoral girdle, and forelimb elements and is preserved in sediments indicative of intertidal deposits. A number of morphological differences distinguish the humerus of the specimen (Fig. 2A) from that of *Aegyptosaurus*, precluding referral to that genus (*12*). Because of these distinctions and its possession of several autapomorphies, we designate the new specimen as *Paralititan stromeri*, gen. et sp. nov. (*13*).

Two preserved caudal sacral centra of *Paralititan* lack pleurocoels. The centrum of the first caudal vertebra (Fig. 2B) is wider than high and procoelous, and has a convex distal articular condyle. The centrum is not biconvex, as in the titanosaurids *Alamosaurus* (*14*), *Neuquensaurus* (*14*), and *Pellegrinisaurus* (*15*). Its ventral surface has weakly developed longitudinal ridges laterally bordering a sagittal concavity. A postspinal lamina is present between spinopostzygapophyseal laminae on the distal surface of the neural spine. A second proximal caudal (Fig. 2C) is strongly procoelous and has a well-developed distal condyle.

The scapula is concave medially. A prominent dorsomedial rugosity borders the medial concavity as in the titanosaurids *Aeolosaurus*, *Lirainosaurus*, *Neuquensaurus*, and *Saltasaurus* (*14*, *16*). Distal to the glenoid, a well-developed tabular process projects from the caudoventral margin of the scapula. The development of this structure in *Paralititan* is equaled only in a scapulocoracoid referred to the brachiosaurid *Brachiosaurus altithorax* (*17*).

The humerus is strongly expanded proximally and distally. Because of the modest de-

Table 1. Phylogenetic data matrix. The macronarian *Camarasaurus* is postulated as an outgroup of titanosauriformes (*45*, *46*). Character codings are as follows: 0, hypothesized plesiomorphic states; 1 and 2, hypothesized derived states; ?, missing or uncertain data (*19*).

Taxa	Characters											
	5	10	15	20	25	30	35	40	45	50	55	
					Outgroup							
Camarasaurus	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0
					Ingroup							
Brachiosaurus brancai	11001	01000	00000	00000	00000	001?1	00000	001?0	00001	01010	01000	0
Andesaurus	??111	11000	1100?	?0?00	00??0	001??	?????	?????	?????	??111	?????	?
Epachthosaurus	??111	??010	11011	?0?01	1?011	1110?	1????	???1?	???11	111?1	?101?	0
Opisthocoelicaudia	???12	11101	?1111	1?002	01110	10111	11011	01111	11111	11101	11011	0
Alamosaurus	?????	?????	?????	??101	10011	11101	11?11	101?1	1111?	?1??1	1????	?
Malawisaurus	11?12	1???1	1100?	?0101	10011	00111	1???0	?????	?????	????1	?????	1
Paralititan	?????	?????	?????	??011	1101?	?????	??1??	?111?	???1?	?????	?????	?
Saltasaurus	??112	11111	11001	11111	11101	11101	1?111	11111	1???1	11?11	?1111	1

---

[1]Department of Earth and Environmental Science, University of Pennsylvania, 240 South 33rd Street, Philadelphia, PA 19104–6316, USA. [2]Engineering Geology, Drexel University, 3141 Chestnut Street, Philadelphia, PA 19104, USA. [3]Department of Animal Biology, School of Veterinary Medicine, University of Pennsylvania, 3800 Spruce Street, Philadelphia, PA 19104–6045, USA. [4]Academy of Natural Sciences, 1900 Ben Franklin Parkway, Philadelphia, PA 19103, USA. [5]Egyptian Geological Museum, Egyptian Geological Survey and Mining Authority, Athar El Nabi, Maadi, Cairo, Egypt.

*To whom correspondence should be addressed. E-mail: smithjb@sas.upenn.edu

velopment of a proximolateral process, the proximal end is sinusoidal in cranial view, as in *Saltasaurus* and *Opisthocoelicaudia* (*18*). A well-defined muscular depression occupies the proximal region of the cranial surface. The deltopectoral crest is extremely developed and medially deflected, extending more than 53% of the length of the element. The rectangular radial condyle is well developed distally. A shallow fossa, bounded by medial and lateral ridges, occupies most of the proximocaudal surface of the humerus. The lateral ridge develops into a tuberosity approximately 350 mm from the proximal margin, as in *Lirainosaurus* and *Saltasaurus* (*16*), whereas the medial ridge, unknown in titanosaurids, is most developed 560 mm from the proximal end. Elongate supracondylar ridges that extend over one-third of the length of the humerus define an extensive olecranon fossa. The distal surface of the preserved metacarpal is rectangular and flattened, suggesting phalangeal reduction or absence on this digit.

Phylogenetic analysis of titanosauriform sauropods (*19*) places *Paralititan* within Titanosauridae (Fig. 3 and Table 1). Characters supporting its inclusion within the clade include strongly procoelous proximal caudal centra with well-developed postspinal laminae, a proximolateral process on the humerus, and reduced manual phalanges. The position of *Paralititan* within Titanosauridae permits an estimation of its body size (Fig. 2D). The humerus is 1.69 m in length, ~14% longer than the next longest known humerus from a Cretaceous sauropod (*20*). The South American titanosaurid *Argentinosaurus* is regarded as the most massive terrestrial animal known and may have approached 90 metric tons (*21*) and 30 m in length (*22*). The humerus of *Argentinosaurus* is unknown, but we estimate its length at 1.81 m (7.5% longer than that of *Paralititan*), using more complete titanosauriforms (*23*). Therefore, *Paralititan* is probably not as large as *Argentinosaurus* but represents one of the heaviest terrestrial vertebrates yet discovered.

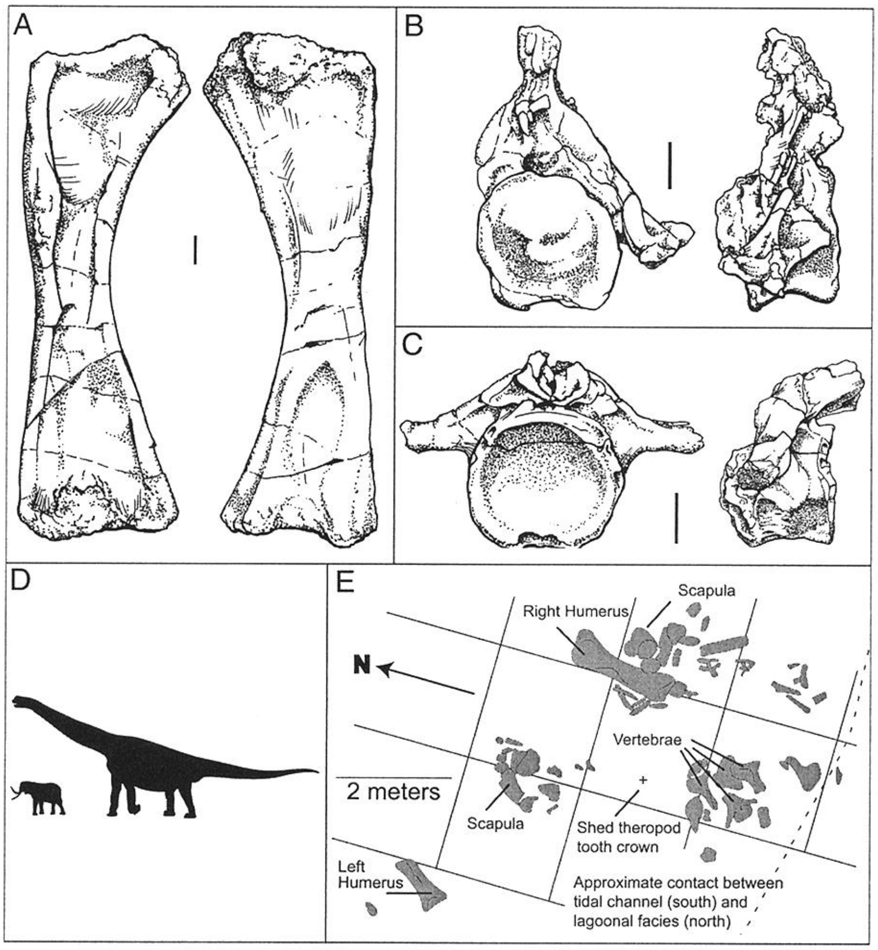

Fig. 2. Anatomy, taphonomy, and estimated size of *Paralititan*. (**A**) Right humerus in cranial and caudal views. (**B**) First caudal vertebra in distal and right lateral views. (**C**) Proximal caudal vertebra in proximal and right lateral view. Scale bars in (A) through (C) equal 10 cm. (**D**) Size comparisons between *Paralititan* and an African elephant. (**E**) Quarry map of BDP 2000-18.

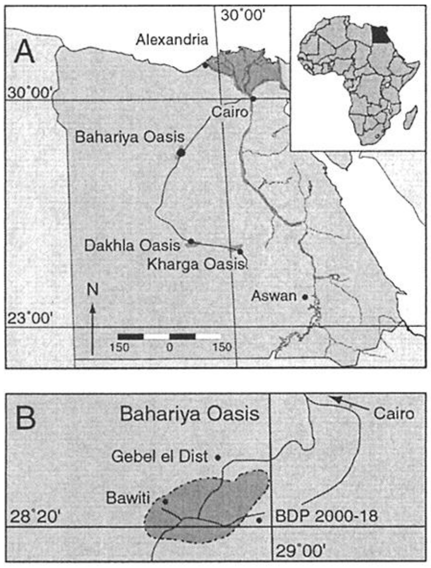

Fig. 1. (**A**) The Bahariya Oasis, ~300 km southwest of Cairo, Egypt. (**B**) Location of BDP 2000-18.

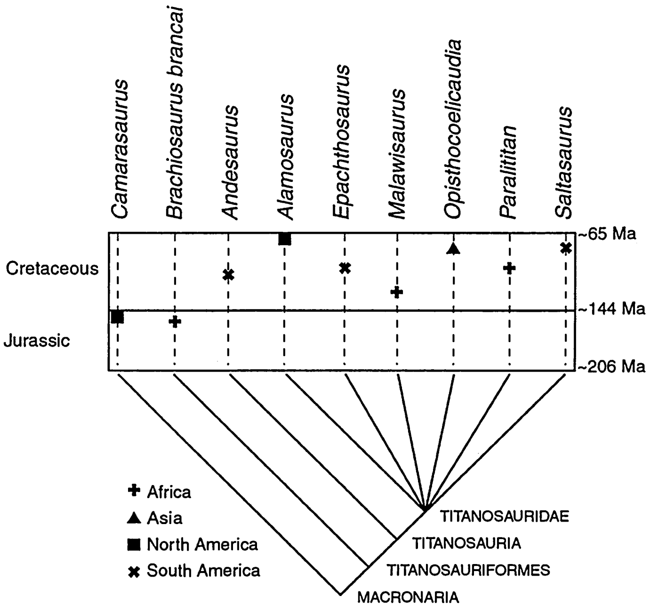

Fig. 3. Summary of phylogenetic, temporal, and geographic relationships among titanosauriform sauropods. The cladogram depicts the strict consensus of 12 most parsimonious trees (length, 72 steps; consistency index, 0.806; retention index, 0.759) resulting from a parsimony analysis of eight titanosauriforms and 56 anatomical characters (*19*).

Paralititan is preserved in low-energy paralic sediments, representing vegetated tidal flats and tidal channels. These units alternate vertically and are laterally variable. The tidal flat facies is a brown friable shale, rich in rhizoliths and plant remains, often containing leaf compressions and stems of the mangrove (*24*) tree fern *Weichselia reticulata* (*25*, *26*). In some places the facies is found, conformably, above glauconitic nearshore marine sands, a stratigraphic relationship that supports a mangrove interpretation. The relationship appears to be conformable, as evidenced by a lack of ravinement surfaces between occasional rhizoliths that extend from lagoonal muds into marine sands. This succession of environments is known to occur along modern low-energy coasts, where mangroves prograde out onto the active shore face (*27*, *28*). The seaward migration of mangroves into the open marine realm requires both a low-energy littoral zone and wave-resistant salt-tolerant plants, such as *Weichselia*.

The *Paralititan* quarry spans both tidal channel and vegetated tidal flat facies (Fig. 2E). In situ plant roots, throughout the bone layer, indicate limited water depth, and fine-grained sediments suggest low current velocities. The closely associated elements could not have been transported to this location as clasts. In addition, the shallow, vegetated tidal flat would prevent a large sauropod carcass from floating to this location. Evidence therefore indicates that this individual walked to this location, over tidal flats and along tidal channels, before its death. Furthermore, the specimen shows indications of being scavenged by a carnivorous dinosaur (*29*). Therefore at least two species of Bahariya dinosaur traversed paralic environments.

It is interesting that this extremely productive biota, containing some of the largest known terrestrial vertebrates (*30*), occurs during a time with extremely low thermal gradients from pole to pole and high global sea levels (*31*, *32*). Mid-Cretaceous ocean-atmosphere systems are of particular interest in paleoclimate research, representing extreme "hothouse" conditions for post-Pangaean Earth history. The apparently high productivity of this Cenomanian environment may reflect a biotic response to some aspect of this condition.

References and Notes

1. W. Dominik, *Berl. Geowiss. Abh. Reihe A* **62**, 1 (1985).
2. E. Stromer, *Abh. Bayer. Akad. Wiss. Math. Nat. Abt. N. F.* **33**, 1 (1936).
3. Material from only 2 of Stromer's 15 Bahariya tetrapods survived.
4. R. Lavocat, *Comptes rendus 19e Congrés géologique international (Alg.) 1952, Academie des Sciences de Paris* **15**, 65 (1954).
5. P. C. Sereno *et al.*, *Science* **272**, 986 (1996).
6. D. A. Russell, *Bull. Mus. Natl. Hist. Nat. Paris 4th Ser.* **18**, 349 (1996).
7. P. Taquet, D. A. Russell, *C. R. Acad. Sci. Paris* **327**, 347 (1998).
8. S. D. Sampson *et al.*, *Science* **280**, 1048 (1998).
9. S. D. Sampson, M. T. Carrano, C. A. Forster, *Nature* **409**, 504 (2001).
10. D. W. Krause, G. V. R. Prasad, W. v. Koenigswald, A. Sahni, F. E. Grine, *Nature* **390**, 504 (1997).
11. Other new Bahariya vertebrates include remains of chondrichthyans, osteichthyans, turtles, plesiosaurs, squamates, crocodyliforms, and dinosaurs. Theropod remains represent *Spinosaurus*, cf. *Carcharodontosaurus*, and two indeterminate forms. Sauropod remains include an indeterminate partial skeleton and a possible rebbachisaurid scapula.
12. Although the holotype of *Aegyptosaurus* (1912VIII61) was destroyed, and comparison with *Paralititan* is thus difficult, several characters distinguish them. Specimen 1912VIII61 was substantially smaller (humerus length 59% that of *Paralititan*), may have had pleurocoelous proximal caudals (*33*), possessed a weakly medially convex scapula with no dorsomedial prominence, had a humerus with a weak proximomedial expansion and more medially positioned deltopectoral crest restricted to the proximal third of the element, and lacked the autapomorphies of *Paralititan*. Stromer (*33*) tentatively referred several isolated elements to *Aegyptosaurus*, including an indeterminate vertebra (1912VIII66), two possible caudal cervicals (1912VIII67), and an isolated procoelous caudal (1912VIII65). Because two Bahariya Formation titanosaurids are now recognized, this material referred to *Aegyptosaurus* must be considered Titanosauria incertae sedis.
13. **Etymology**: *Paralititan stromeri* (pa·ral′i·ti′·tan strom′·er·i): paralos (Greek), near the sea (paralic refers to tidal environments); Titan (Greek), an offspring of Uranus and Gaea, symbolic of brute strength and large size (effectively, "tidal giant"); *stromeri*, in honor of Ernst Stromer. **Holotype**: CGM 81119 (Egyptian Geological Museum, Cairo). **Locality**: BDP 2000-18, near Gebel Fagga (28°20′10.7″N latitude, 28°59′04.7″E longitude). **Material**: Two fused caudal sacral vertebrae (probably 5 and 6), first caudal vertebra; proximal caudal vertebra; dorsal and sacral ribs; incomplete scapulae; complete right and incomplete left humeri; distal metacarpal; and several additional elements. **Diagnosis**: Very large titanosaurid characterized by proximal caudal centra wider than tall; prominent tabular process on caudoventral margin of scapula distal to the proximal expansion; and humerus with medial ridge on the proximocaudal face and rectangular radial condyle. *Paralititan* shares the following characters with other titanosaurids: lack of pleurocoels on caudal sacrals; proximal caudal vertebrae with strongly concave proximal articular surface, well-developed distal articular condyle, ventral excavation, and postspinal lamina; humerus with proximolateral process and strong supracondylar ridges; and reduction or absence of manual phalanges. **Referred material**: Stromer (*33*) described a very large cranial dorsal vertebra (1912VIII64). Specimen 1912VIII64 was opisthocoelous, pleurocoelous, and caudally wider than tall, as in *Epachthosaurus* and *Pellegrinisaurus* (*15*), and may pertain to *Paralititan*.
14. L. Salgado, R. A. Coria, J. O. Calvo, *Ameghiniana* **34**, 3 (1997).
15. L. Salgado, *Ameghiniana* **33**, 355 (1996).
16. J. L. Sanz, J. E. Powell, J. Le Loeuff, R. Martinez, X. Pereda-Suberbiola, in *Geology and Palaeontology of the Upper Cretaceous Vertebrate-Bearing Beds of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula)*, H. Astibia, J. C. Corral, X. Murelaga, X. Orue-Etxebarria, X. Pereda-Suberbiola, Eds. (Estudios del Museo de Ciencias Naturales de Alava, Alava, Portugal, 1999), pp. 235–255.
17. B. D. Curtice, K. L. Stadtman, L. J. Curtice, in *The Continental Jurassic*, M. Morales, Ed. (Museum of Northern Arizona, Flagstaff, AZ, 1996), pp. 87–95.
18. P. Upchurch, *Zool. J. Linn. Soc.* **124**, 43 (1998).
19. The character list is available as Appendix 1 of the supplementary information (*34*).
20. Humerus lengths of large Cretaceous sauropods are as follows: *Jobaria*, 1360 mm (*35*); *Chubutisaurus*, 1450 mm (*36*); *Aegyptosaurus*, 1000 mm (*33*); *Argyrosaurus*, 1435 mm (estimate) (*37*); *Titanosaurus? colberti*, 1480 mm (*38*).
21. G. S. Paul, in *Dinofest International*, D. L. Wolberg, E. Stump, G. D. Rosenberg, Eds. (Academy of Natural Sciences, Philadelphia, PA, 1997), pp. 129–154.
22. C.-M. Jianu, D. B. Weishampel, *Geol. Mijnbouw* **78**, 335 (1999).
23. See Web fig. 1 (*34*).
24. Mangroves are vegetated paralic environments, defined by Thanikaimoni (*39*) as intertidal tropical forests. Mangroves first developed in the Carboniferous (360 to 286 Ma), when salt-tolerant gymnosperms and pteridophytes adapted to the habitat (*40*, *41*). Modern mangroves include members of 27 plant genera (*42*) and first developed along the Late Cretaceous Tethys Seaway (*43*).
25. *Paradoxopteris stromeri* has been synonymized with *Weichselia reticulata* (*44*).
26. Shinaq and Bandel (*45*) identified an Early Cretaceous *Weichselia* mangrove in Jordan.
27. R. A. Davis, A. C. Hine, E. A. Shinn, in *Quaternary Coasts of the United States: Marine and Lacustrine Systems*, J. F. Wehmiller, C. H. Fletcher III, Eds. (Society for Sedimentary Geology (SEPM), Tulsa, OK, 1992), pp. 193–212.
28. Additional evidence of low-energy environments includes fine-grained sediments, low-velocity bedforms, the absence of ravinement surfaces, in situ bivalves, and horizontal burrows. All nonfossil clasts in the Bahariya system are medium sand size or smaller.
29. A cf. *Carcharodontosaurus* tooth (crown height = 65 mm), recovered from BDP 2000-18, is larger than clasts that could have been transported to this location.
30. *Paralititan* coexisted with three *Tyrannosaurus*-sized carnivores (*Carcharodontosaurus*, *Bahariasaurus*, and *Spinosaurus*) and with other large vertebrates (such as the 3.5-m coelacanth *Mawsonia* and the 10-m crocodyliform *Stomatosuchus*).
31. B. U. Haq, J. Hadenbol, P. R. Vail, *Science* **235**, 1156 (1987).
32. M. L. Fassell, T. J. Bralower, in *Evolution of the Cretaceous Ocean Climate System*, E. Barrera, C. C. Johnson, Eds. (Geological Society of America, Boulder, CO, 1999), vol. 332, pp. 121–142.
33. E. Stromer, *Abh. Bayer. Akad. Wiss. Math. Nat. Abt. N. F.* **10**, 1 (1932).
34. Supplementary Web material is available on *Science* Online at www.sciencemag.org/cgi/content/full/292/5522/1704/DC1
35. P. C. Sereno *et al.*, *Science* **286**, 1342 (1999).
36. L. Salgado, *Ameghiniana* **30**, 265 (1993).
37. R. Lydekker, *Ann. Mus. La Plata Sect. Paleontol.* **2**, 1 (1893).
38. S. L. Jain, S. Bandyopadhyay, *J. Vert. Paleontol.* **17**, 114 (1997).
39. G. Thanikaimoni, in *Mangrove Palynology* (Travaux de la Section scientifique et technique, UNDP/UNESCO Regional Project on Training and Research on Mangrove Ecosystems, French Institute, Pondicherry, India, 1987) pp. 1–100.
40. A. A. Cridland, *Palaeontology* **7**, 186 (1964).
41. A. Raymond, T. L. Phillips, in *Biology and Ecology of Mangroves*, H. Teas, Ed., vol. 8 of *Tasks for Vegetative Science* (Junk, the Hague, 1983), pp. 19–30.
42. N. C. Duke, in *Tropical Mangrove Ecosystems*, A. I. Robertson, D. M. Alongi, Eds. (American Geophysical Union, Washington, DC, 1992), pp. 63–100.
43. A. M. Ellison, E. J. Farnsworth, R. E. Merkt, *Global Ecol. Biogeogr.* **8**, 95 (1999).
44. E. Boureau, A. F. de Lapparent, *C. R. Somm. Seances Soc. Geol. Fr.* **7-8**, 107 (1951).
45. R. Shinaq, K. Bandel, *Freib. Forschungsh. C* **474**, 39 (1998).
46. J. A. Wilson, P. C. Sereno, *Soc. Vertebr. Paleontol. Mem.* **5**, 1 (1998).
47. Supported by Cosmos Studios, MPH Entertainment, the University of Pennsylvania, the Andrew K. Mellon Foundation, E. de Hellebranth, and the Delaware Valley Paleontological Society. We thank K. Soleiman and the Egyptian Geological Survey and Mining Authority, Drexel University, T. Holtz, H. Sues, J. Harris, K. Curry-Rogers, J. Lacovara, and R. Martínez. We also thank A. Tumarkin, Y. Abdelrazik, M. Said Abdel-Ghani, P. Kane-Vanni, and J. Caton for assistance in the field.

9 March 2001; accepted 30 April 2001