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37. T. P. Barnett, *J. Clim.* **1**, 225 (1988).
38. H. van Loon and J. Williams, *Mon. Weather Rev.* **105**, 636 (1977).
39. K. E. Trenberth, *NCAR Tech. Note NCAR/TN-373+STR* (NCAR, Boulder, CO, 1992).
40. T. N. Krishnamurti, H. S. Bedi, M. Subramanian, *J. Clim.* **2**, 321 (1989).
41. ———, *Meteorol. Atmos. Phys.* **42**, 19 (1990).
42. G. A. Meehl, G. W. Branstator, W. M. Washington, *J. Clim.* **6**, 42 (1993).

43. I thank G. Branstator and A. Mai for collaboration on the specified heating experiments. A portion of this study was supported by the Office of Health and Environmental Research, U.S. Department of Energy, as part of its Carbon Dioxide Research Program. The National Center for Atmospheric Research is sponsored by the National Science Foundation.

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A major question in Mesozoic biogeography is how the land-based dinosaurian radiation responded to fragmentation of Pangaea. A rich fossil record has been uncovered on northern continents that spans the Cretaceous, when continental isolation reached its peak. In contrast, dinosaur remains on southern continents are scarce. The discovery of dinosaurian skeletons from Lower Cretaceous beds in the southern Sahara shows that several lineages of tetanuran theropods and broad-toothed sauropods had a cosmopolitan distribution across Pangaea before the onset of continental fragmentation. The distinct dinosaurian faunas of Africa, South America, and Asiamerica arose during the Cretaceous by differential survival of once widespread lineages on land masses that were becoming increasingly isolated from one another.

Although increased continental isolation has been implicated as the driving force behind the differentiation of Cretaceous dinosaurian faunas (*1*), a coherent picture of dinosaurian biogeography during this period has not been possible because of the near absence of fossil evidence from key southern land masses such as Africa. With rare exceptions (*2*, *3*), available information on Cretaceous dinosaurs from Africa is based on preliminary paleontological surveys in the Sahara (*4*), isolated or fragmentary bones and teeth (*5*), and a small fossil collection from Egypt that was destroyed during World War II (*6*, *7*). We report here on the discovery of dinosaurs from Lower Cretaceous rocks in the southern Sahara Desert (Fig. 1) that impact on the understanding of late Mesozoic dinosaurian biogeography.

The fossils include the first relatively complete skeleton of a theropod dinosaur from the Cretaceous of Africa, *Afrovenator abakensis*, n. gen. n. sp. (*8*). The skull is low compared to that of other large-skulled predators such as *Allosaurus* (*9*). Maximum height at the orbit is less than one-third the skull length (Fig. 2A). Unlike *Allosaurus* and many other theropods, cranial crests and rugosities are poorly developed. The lacrimal crest, for example, has a low, rounded profile. As in many theropods, the lacrimal crest is hollowed by a pneumatic cavity. The maxilla has a slit-shaped promaxillary fenestra, a small, posteriorly positioned maxillary fenestra, and sockets for 14 blade-shaped teeth. The quadrate is tall with a dorsoventral length more than one-half the skull height at the orbit.

The skeleton is relatively gracile judging from the length and diameter of the long bones (Fig. 2C). Cervical vertebrae have deep pleurocoel cavities and articulate in an upward curve that elevates the skull above the dorsal column. The forelimb appears to be similar in length to that of *Allosaurus* but has different proportions within the limb. In *Afrovenator* the humerus is relatively longer, the carpus is flatter, the first metacarpal has stouter proportions, and the ungual on the third digit is particularly small (Fig. 2D and Table 1) (*10*). The pelvic girdle is similar in structure to that of *Allosaurus* (Fig. 2B). The ilium has a moderately developed supraacetabular crest and brevis fossa, the ischium has a trapezoidal obturator process and well-developed distal foot, and the pubis has a slender shaft and small distal foot. The hind limb has more elongate distal segments than in *Allosaurus* (Table 1). The femur is only slightly longer than the tibia and has a broad wing-shaped anterior trochanter. The astragalus preserves the base of a low plate-shaped ascending process (Fig. 2E), and the foot is slender and elongate (Fig. 2C).

Fig. 1. Paleogeographic map of land surfaces during the Early Cretaceous (Barremian-Hauterivian, 130 million years ago). Mollweide projection with latitude and longitude lines spaced at 30° intervals (longitude greater than 120° not shown) (*37*). +, dinosaur locality.

Jurassic and Cretaceous theropods belong to one of two clades, Ceratosauria and Tetanurae (*11*), which diverged during the Late Triassic (Fig. 3). The skeletal remains of *Afrovenator* clearly indicate that it belongs within the tetanuran radiation (Fig. 3A) (*12*). Tetanuran synapomorphies in the skull include an opening in the antorbital fossa (maxillary fenestra), a pneumatic excavation in the jugal, and the position of the posteriormost maxillary tooth (anterior to the orbit) (Fig. 2A). Tetanuran synapomorphies in the postcranial skeleton include specialized wrist bones that constrain motion of the hand to a transverse plane (semilunate carpal with an articular troch-

Table 1. Length measurements (millimeters) and ratios in *Afrovenator* and *Allosaurus* (*10*). All unguals are measured perpendicular to the articular end. Parentheses indicate estimation.

Measurement	*Afrovenator*	*Allosaurus*
	Forelimb	
Humerus (h)	(400)	310
Metacarpal I (I)	62	73
Metacarpal II (II)	135	123
Digit I—phalanx 1 (I-1)	112	136
Digit I, ungual	80	102
Digit II, ungual	76	92
Digit III—phalanx 3	53	53
Digit III, ungual	40	54
I/h	0.16	0.24
II/h	0.34	0.40
I/II	0.46	0.59
I/I-1	0.55	0.54
	Hind limb	
Femur (f)	760	850
Tibia (t)	(687)	690
Metatarsal I (I)	103	85
Metatarsal IV (IV)	321	275
Digit II—phalanx 1	122	120
Digit II (or III) ungual	76	(72)
Digit IV—phalanx 1	90	75
Digit IV—phalanx 2	106	50
Digit IV—phalanx 3	87	30
t/f	0.90	0.81
IV/t	0.47	0.40
I/IV	0.32	0.31

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lea for a disc-shaped radiale) (Fig. 2D). The hand is similar to that in other tetanurans, which show a reduction in the size of digit III as compared to digits I and II (Fig. 2D). In the hind limb the femur has a blade-shaped anterior trochanter (Fig. 2C), and the astragalus has a plate-shaped ascending process (Fig. 2E).

The phylogenetic relationships between *Afrovenator* and other basal tetanurans were evaluated by cladistic analysis of skeletal characters (Fig. 3A). That analysis supports the monophyly of three principal tetanuran subgroups: Torvosauroidea, Allosauroidea, and Coelurosauria. Torvosauroids include *Afrovenator*, the Laurasian genera *Torvosaurus*, *Eustreptospondylus*, and *Chilantaisaurus* (*13*), and tentatively the spinosaurids *Spinosaurus* and *Baryonyx* (6, *14*). Although there is some homoplasy among basal tetanurans, several cranial features support torvosauroid monophyly, including the long anterior ramus of the maxilla and the transversely broad ventral process of the postorbital (*12*). *Afrovenator* appears to represent a basal lineage within Torvosauroidea because it lacks the sickle-shaped ungual on the first digit of the hand that characterizes more advanced torvosauroids (Fig. 3A) (*12*). Allosauroids are united by a suite of cranial features that are unique to the group (*12*), which includes *Allosaurus* and *Acrocanthosaurus* from North America (9, *15*), *Monolophosaurus*, *Sinraptor*, and *Yangchuanosaurus* from Asia (*16*), and *Cryolophosaurus* from Antarctica (*17*). Coelurosauria has been recognized as a monophyletic group that includes *Ornitholestes* from the Upper Jurassic of North America (*18*) and all more derived theropods including birds (*11*, *19*). Allosauroids and coelurosaurs, united here as Neotetanurae, share a more recent common ancestry than either does with torvosauroids (*12*).

Sauropod remains are particularly abundant in the Lower Cretaceous rocks that yielded *Afrovenator* and represent a new species (*20*). Cranial remains include fragmentary jaw bones that preserve teeth with broad crowns similar to those in *Camarasaurus* (Fig. 4). The postcranium also resembles *Camarasaurus*. The sternal plates are oval, the distal caudal vertebrae are short anteroposteriorly, the inner two digits of the hand terminate in large unguals, and the pubic blades are broad (Fig. 5A). Unlike *Camarasaurus*, however, the tooth crowns are denticulate, the neck is considerably longer, and the neural spines of presacral vertebrae are single rather than bifurcate. Although the relation between the new sauropod and Upper Jurassic *Camarasaurus*, *Haplocanthosaurus*, or *Brachiosaurus* remains unclear, there is no affinity between the new sauropod and diplodocids or titanosaurids, which account for nearly all Cretaceous sauropod remains (*21*).

The skeletal remains of *Afrovenator* and the new sauropod were buried in shallow, mud-filled channel deposits on a floodplain located approximately 5° north of the paleoequator (Figs. 1 and 5) (*22*). Nearly all of the skeletal remains show evidence of fluvial transport (Fig. 5). The channel sequences pass upward into paleosols and occasional thin lacustrine limestone. The absence of caliche deposits and marked periodic growth in fossilized wood suggests that a relatively uniform climatic regime may have prevailed (*22*). Associated nondinosaurian vertebrates include the coelacanth *Mawsonia*, the dipnoan *Ceratodus*, the semionotid *Lepidotes*, a pleurodiran turtle, and crocodyliforms. The nondinosaurian vertebrates from the Tiourarén beds and other Lower Cretaceous sites in Niger (*23*) are similar to those from Lower Cretaceous (Aptian-Albian) rocks in Brazil (*24*). The fauna from the Tiourarén beds

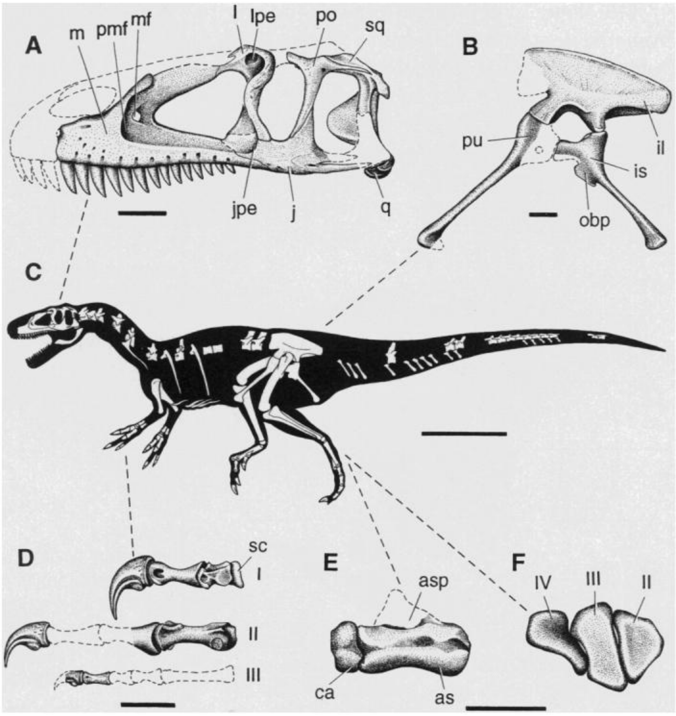

Fig. 2. Skeletal anatomy of *Afrovenator abakensis*. (**A**) Skull reconstruction in left lateral view; (**B**) pelvic reconstruction in left lateral view; (**C**) skeletal reconstruction (length is approximately 9 m); (**D**) partial left manus in lateral view; (**E**) right astragalus and calcaneum in anterior view (ascending process based on articular depression on distal tibia); (**F**) left metatarsus in proximal view (anterior toward top). Scale bar in (A), (B), and (D) to (F) is 10 cm. Scale bar in (C) is 1 m. I–IV, manual or pedal digits I–IV; as, astragalus; asp, ascending process; ca, calcaneum; il, ilium; is, ischium; j, jugal; jpe, jugal pneumatic excavation; l, lacrimal; lpe, lacrimal pneumatic excavation; m, maxilla; mf, maxillary fenestra; obp, obturator process; pmf, promaxillary fenestra; po, postorbital; pu, pubis; q, quadrate; sc, semilunate carpal; sq, squamosal.

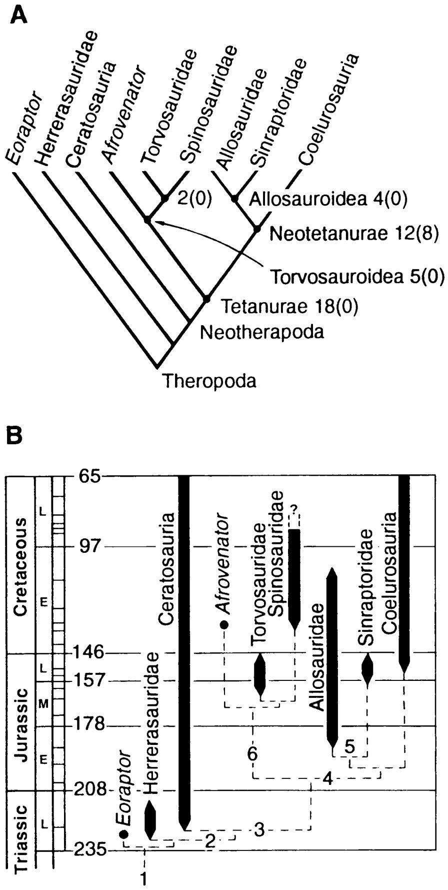

Fig. 3. Phylogenetic and temporal relationships among basal neotheropods. (**A**) Cladogram based on phylogenetic analysis of 44 characters (*12*) in seven terminal taxa (*38*), with Herrerasauridae and *Eoraptor* as successive outgroups (*39*). Numbers at nodes indicate total number of synapomorphies under delayed transformation (*40*). Parenthetical numbers indicate the portion of total synapomorphies for a given node that may occupy a more basal node (due to missing data or homoplasy). The cladogram is strongly supported by the data (consistency index, 0.85; rescaled consistency index, 0.76; retention index, 0.89). (**B**) Phylogram based on the cladogram and recorded temporal ranges, which are calibrated on a recent time scale (*41*). 1, Theropoda; 2, Neotheropoda; 3, Tetanurae; 4, Neotetanurae; 5, Allosauroidea; 6, Torvosauroidea.

may be somewhat older (Hauterivian or Barremian, 125 to 135 million years ago) because they lie stratigraphically below the Gadoufaoua fauna from eastern Niger, which is regarded as Aptian or Albian in age (*25*).

Although biogeographers have long recognized distinct Laurasian and Gondwanan biotas, this difference has not always been apparent (*26*), especially among dinosaurian faunas (*27*). Recent discoveries of ceratosaurian (abelisaurid) theropods and titanosaurid sauropods in several Cretaceous horizons in Argentina (*28*), nevertheless, have led to the view that these taxa are components of a distinct Gondwanan fauna (*29*).

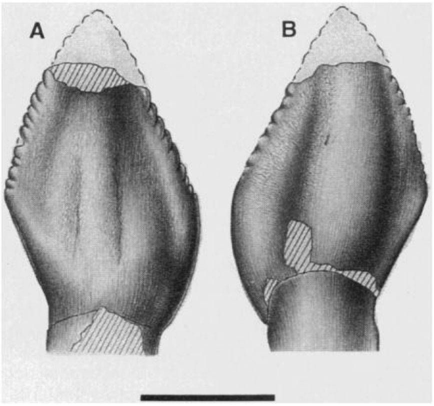

Fig. 4. Maxillary or dentary tooth from the new broad-toothed sauropod in (**A**) medial and (**B**) lateral views. Scale bar, 1 cm.

Except for South America, however, the dinosaurian fossil record for southern continents during the Cretaceous is poor. Ceratosaurian (abelisaurid) theropod finds outside South America are limited to a few cranial fragments from India (*30*). Unquestionable titanosaurid remains have been reported recently from the Lower Cretaceous of Africa (*3*), but titanosaurid remains including well-preserved skeletons (*31, 32*) are also known from several Cretaceous localities in Laurasia. Titanosaurids clearly were not restricted to Gondwana during the Cretaceous.

The new African dinosaurs help resolve biogeographic events during the early phase of the break-up of Pangaea. The presence of *Afrovenator* and a broad-toothed sauropod on Africa does not support the existence of a distinct Gondwanan fauna during the Cretaceous. *Afrovenator* does not share a close relation with ceratosaurian (abelisaurid) theropods but rather is more closely related to tetanurans, which are known from both northern and southern continents. Likewise, the sauropod lies outside the titanosaurid radiation and is more closely related to broad-toothed forms that are known from both northern and southern continents. The African fossils, along with earlier finds from Argentina, Antarctica, and Australia (*17, 33*), indicate that several lineages of tetanuran theropods and broad-toothed sauropods had achieved a cosmopolitan distribution before the break-up of Pangaea. Among theropods, the recent discovery of the Lower Jurassic tetanuran *Cryolophosaurus* (*17*) indicates that torvosauroid, allosauroid, and coelurosaur lineages already had diverged by the Early Jurassic (Fig. 3B) (*34*).

By the Late Jurassic, a persistent (although possibly intermittent) land connection from the north through Europe (Gibraltar) to Gondwana permitted enough exchange to maintain relatively uniform dinosaurian faunas (*35*). This land connection seems to have been severed during the Early Cretaceous at about the same time as the southern continents themselves were becoming biogeographically isolated. As a consequence, there is no recognizable phylogenetic unity among dinosaur groups that persisted on Gondwanan continents during the Cretaceous. Rather, these cosmopolitan dinosaur groups experienced different fates on each southern continent as isolation increased during the Cretaceous. The distribution of *Afrovenator* and other large-bodied Cretaceous theropods support that biogeographic scenario. In Asiamerica, allosauroids and then coelurosaurs became the dominant carnivores during the Cretaceous, whereas torvosauroids apparently went extinct. In South America, abelisaurids became the dominant theropods, whereas tetanurans were rare. And in Africa, torvosauroids such as *Afrovenator* and the enigmatic spinosaurids (*6, 36*) survived as the dominant large carnivores during the Cretaceous, whereas abelisaurids, allosauroids and nonavian coelurosaurs have yet to be definitely recorded. The distinct dinosaurian faunas on Asiamerica, South America, and Africa arose during the Cretaceous from differential survival of once widespread lineages with origins dating back to the Early Jurassic.

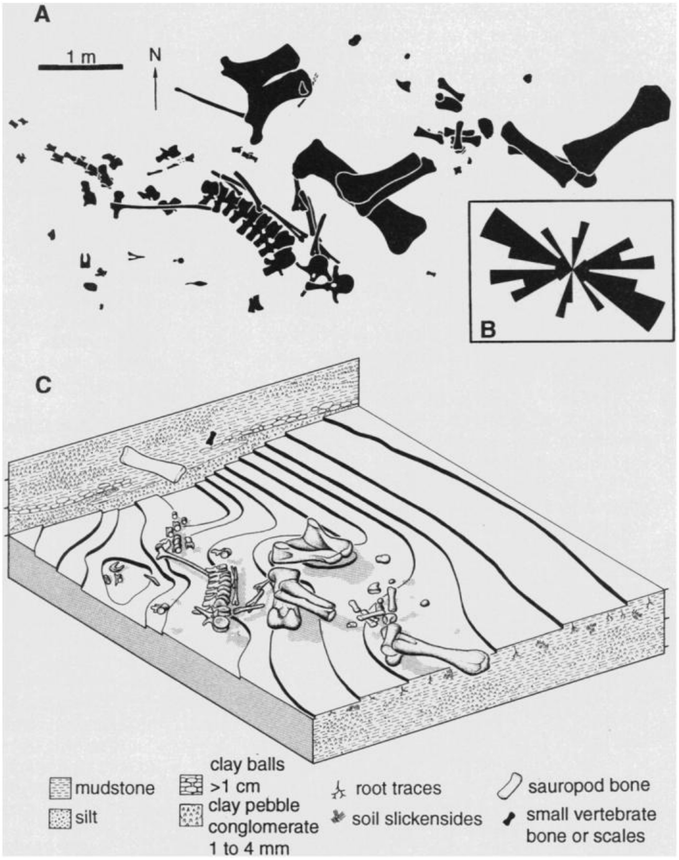

Fig. 5. Sauropod skeleton in mud-filled river channel at the Tamérat site. (**A**) Plan view of sauropod skeleton. (**B**) Mirror rose diagram showing the preferred bone orientation that arose from fluvial transport (n = 40, mean = 93.6°; current direction almost due west). (**C**) Scaled cut-away view showing the bones of the sauropod skeleton as they were found in the river channel, with the tail pointing downstream and dipping gently toward the channel floor. The skeleton is contained within only 79 cm of the channel deposit. A three-dimensional computer model of the bones and a 5-cm-step contour map of the channel floor were generated from coordinates on a site map and 93 depth measurements to the skeleton and channel floor. Light was cast on the model from the upper left creating shadows on the channel floor (*42*). Cross sections of channel floor and channel fill sediments are shown anteriorly and posteriorly, respectively (tick marks equal 50 cm).

REFERENCES AND NOTES

1. N. Jardine and D. McKenzie, *Nature* **235**, 20 (1972); J. Valentine and E. M. Moores, *J. Geol.* **80**, 167 (1972); E. H. Colbert, in *Implications of Continental Drift to the Earth Sciences*, D. H. Tarling and S. K. Runcorn, Eds. (Academic Press, London, 1973), pp. 395–412; J. Cracraft, *Annu. Rev. Ecol. Syst.* **5**, 215 (1974); C. B. Cox, *J. Biogeogr.* **1**, 75 (1974); D. A. Russell, *Can. J. Earth Sci.* **30**, 2002 (1993).
2. P. Taquet, *Cah. Paléontol.* (1976), p. 1.
3. L. L. Jacobs, D. A. Winkler, W. R. Downs, E. M. Gomani, *Palaeontology* **36**, 523 (1993).
4. A. F. de Lapparent, *Mém. Soc. Géol. France* **88A**, 1 (1960).
5. F. de Broin, C. Grenot, R. Vernet, *C. R. Acad. Sci.* **272**, 1219 (1971); F. de Broin *et al.*, *ibid.* **279**, 469 (1974); D. Russell, P. Taquet, H. Thomas, *C. R. Somm. Soc. Géol. Fr.* **5**, 205 (1976); M. Monbaron, *C. R. Acad. Sci.* **287**, 1277 (1978); P. M. Galton and P. Taquet, *Géobios* **15**, 147 (1982).

6. E. Stromer, *Abh. Kgl. Bayer. Akad. Wiss., Math.-phys. Kl.* **28**, 1 (1915); *Abh. Bayer. Akad. Wiss., Math.-naturwiss. Abt., N.F.* **22**, 1 (1934).
7. ———, *Abh. Bayer. Akad. Wiss., Math.-naturwiss. Abt., N.F.* **9**, 1 (1931); *ibid.* **10**, 1 (1932).
8. Etymology: *Afro*, Africa (L.); *venator*, hunter (L.); *abaka*, from In Abaka, the Tuareg name for the area where the holotype was found; *ensis*, of a place (L.). The holotype is temporarily catalogued as UC OBA 1 at the University of Chicago. *Afrovenator abakensis* is diagnosed on the following autapomorphies: maxilla with lobe-shaped anterior margin of antorbital fossa; third cervical with a low, rectangular neural spine; very flat semilunate carpal; and metacarpal I with a broad flange for articulation against metacarpal II.
9. J. H. Madsen Jr., *Utah Geol. Min. Surv. Bull.* **109**, 1 (1976).
10. *Allosaurus* is based on USNM 4734 in the collections of the National Museum of Natural History [C. W. Gilmore, *Bull. U.S. Nat. Mus.* **110**, 1 (1920)]. This specimen and that of *Afrovenator* appear to be fully mature.
11. J. A. Gauthier, *Calif. Acad. Sci. Mem.* **8**, 1 (1986).
12. Tetanurae is the most strongly supported node in the analysis. This reflects the unrecorded early history of the tetanuran lineage, during which anatomical changes accumulated over a significant interval of time (Late Triassic to Early Jurassic) (Fig. 3B, node 3). Neotetanurae is supported by more character evidence than Torvosauroidea and Torvosauridae + Spinosauridae, which is due to the poor torvosauroid fossil record and homoplasy among basal tetanurans. Supporting synapomorphies include: **Tetanurae**: maxillary fenestra (*11*), lacrimal pneumatic excavation, slot in ventral process of lacrimal for jugal, jugal pneumatic excavation, prefrontal-frontal peg-in-socket articulation, basipterygoid processes as long as broad, posteriormost maxillary tooth positioned anterior to orbit (*11*), chevron bases with paired anterior and posterior processes, semilunate carpal with transverse trochlea, manual digit III reduced (metacarpal III shaft diameter 50% or less that of metacarpal II), manual digit IV absent (*11*), iliac-ischial articulation smaller than iliac pubic articulation, ischial obturator notch, femoral anterior trochanter blade-shaped (*11*), tibial distal end backing calcaneum, fibular distal end reduced (less than twice anteroposterior width at mid shaft), astragalar ascending process plate-shaped (*11*), astragalar cup for fibula reduced, astragalar distal condyles oriented anteroventrally, metatarsal III with hourglass-shaped proximal end and wedge-shaped mid shaft; **Neotetanurae**: promaxillary recess extends into maxillary anterior ramus, ectopterygoid pneumatic excavation invaginated laterally; splenial with notched anterior margin for internal mandibular fenestra, retroarticular surface of articular facing posteriorly, posterior chevrons L-shaped, furcula (fused clavicles), coracoid posterior process and fossa crescentic, iliac preacetabular process with notched anterior margin, iliac preacetabular fossa present, iliac pubic peduncle twice as long anteroposteriorly as broad transversely, pedal digit I-phalanges 1 + 2 subequal in length to pedal digit III-phalanx 1; **Allosauroidea**: nasal participation in antorbital fossa, palatine with flange-shaped process for lacrimal, basioccipital excluded from the basal tubera, articular with pendant medial process; **Torvosauroidea**: anterior ramus of maxilla as long anteroposteriorly as tall, lacrimal anterior ramus dorsoventrally narrow, lacrimal foramen small and positioned at mid length along ventral ramus, postorbital ventral process broader transversely than anteroposteriorly, quadrate foramen reduced or absent; **Torvosauridae + Spinosauridae**: radius less than 50% of humeral length, manual digit I ungual elongate (three times height of proximal articular end).
13. F. von Huene, *Rev. Mus. La Plata* **29**, 35 (1926); S.-Y. Hu, *Vertebr. Palas.* **8**, 42 (1964); P. M. Galton and J. A. Jensen, *Brigham Young Univ. Geol. Stud.* **26**, 1 (1979); J. A. Jensen, *Great Basin Nat.* **45**, 710 (1985); B. B. Britt, *Brigham Young Univ. Geol. Stud.* **37**, 1 (1991).
14. A. J. Charig and A. C. Milner, in *Dinosaur Systematics: Perspectives and Approaches*, K. Carpenter and P. J. Crurrie, Eds. (Cambridge Univ. Press, Cambridge, 1990), pp. 127–140.
15. J. W. Stovall and J. Langston Jr., *Am. Midl. Nat.* **43**, 696 (1950).
16. Z. Dong, S. Zhou, Y. Zhang, *Palaeontol. Sinica* **23**, 1 (1983); X. Zhao and P. J. Currie, *Can. J. Earth Sci.* **30**, 2027 (1993); P. J. Currie and X. Zhao, *ibid.*, p. 2037.
17. W. R. Hammer and W. J. Hickerson, *Science* **264**, 828 (1994).
18. H. F. Osborn, *Bull. Am. Mus. Nat. Hist.* **35**, 733 (1916).
19. We agree with T. R. Holtz Jr. [*J. Paleontol.* **68**, 1100 (1994)] that tyrannosaurs are coelurosaurs and are not closely related to allosauroids (P. C. Sereno, unpublished data).
20. Fragmentary sauropod remains were first described from the Tiourarén beds as a new species, *Rebbachisaurus tamesnensis* (*4*). No type material was designated and no diagnostic features were mentioned. The assignment to the Moroccan genus *Rebbachisaurus* is incorrect because there are no overlapping bones (*R. garasbae* is based on a scapula). Lapparent's material appears to be consistent with additional bones collected in 1988 from the same area by a British Museum expedition [H. Gee, *Nature* **332**, 487 (1988)] and the skeleton mentioned in this report, none of which can be referred to *Rebbachisaurus* or any current genus or species.
21. Although Lapparent (*20*) considered his material to be a camarasaurid, in recent faunal reviews (*32*) it has been referred to the Diplodocidae. We are unaware of any character evidence in the original or newly discovered bones that would support assignment to Diplodocidae.
22. The fossiliferous beds near In Gall (Niger) were described recently as overbank deposits consisting predominantly of siltstone, with occasional caliche horizons and evidence of mudcracks [R. T. J. Moody and P. J. C. Sutcliffe, *Cret. Res.* **12**, 137 (1991)]. Geologic sections in dinosaur-bearing horizons, however, show that the beds consist almost entirely of mudstone and thin-bedded muddy limestone (Fig. 5C). Silt comprises only a minor component, far less than necessary for classification as a siltstone [P. D. Lundergard and N. D. Samuels, *J. Sed. Petrol.* **50**, 781 (1980)]. Furthermore, all of the dinosaur remains recovered along many kilometers of exposure were found in channel, rather than overbank, deposits. We also did not encounter any caliche deposits, mudcracks, or other indicators of periodic aridity.
23. S. Wenz, *Colloq. Int. C. N. R. S. Probl. Actu. Paleontol.-Evol. Vertebr.* **218**, 175 (1975); E. Buffetaut and P. Taquet, *Nature* **280**, 486 (1979); E. Buffetaut, *Geol. Rundsch.* **70**, 611 (1981); H. Gee, *Nature* **332**, 487 (1988).
24. J. G. Maisey, Ed., *Santana Fossils: An Illustrated Atlas* (TFH, Neptune, NJ, 1991).
25. The Tiourarén beds and the fossiliferous horizons at Gadoufaoua (GAD 5) are separated by several distinct lithologic units (*2*).
26. J. G. Maisey, in *Biological Relationships between Africa and South America*, P. Goldblatt, Ed. (Yale Univ. Press, New Haven, CT, 1993), pp. 435–454.
27. R. Molnar, *Mém. Soc. Géol. France* **139**, 131 (1980); E. Buffetaut and J.-C. Rage, in *The Africa–South America Connection*, W. George and R. Lavocat, Eds. (Clarendon, Oxford, 1993), pp. 87–99.
28. J. F. Bonaparte, F. E. Novas, R. A. Coria, *Contrib. Sci. Nat. Hist. Mus. L. A. County* **416**, 1 (1990); J. F. Bonaparte and F. E. Novas, *Ameghiniana* **21**, 259 (1985); J. E. Powell, thesis, Univ. Nacional Tucumán, Argentina (1986).
29. J. F. Bonaparte and Z. Kielan-Jaworowska, in *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, P. J. Currie and E. H. Koster, Eds. (*Occas. Pap. 3*, Tyrrell Museum of Palaeontology, 1987), pp. 24–29.
30. F. von Huene and C. A. Matley, *Mem. Geol. Surv. India* **21**, 1 (1933); S. Chatterjee, *J. Paleontol.* **52**, 570 (1978). W. Janensch [*Palaeontographica* (*Suppl. 7*) **1**, 1 (1925); *ibid.* **1**, 279 (1929)] suggested that the Late Jurassic African theropod, *Elaphrosaurus bambergi*, might be a tetanuran (that is, closely related to *Ornitholestes* or ornithomimids) as have later authors [D. A. Russell, *Can. J. Earth Sci.* **9**, 375 (1972); P. M. Galton, *Palaeontol. Z.* **56**, 265 (1982)] (*18*), except G. S. Paul [*Predatory Dinosaurs of the World: A Complete Illustrated Guide* (Simon and Schuster, New York, 1988) p. 265] and T. R. Holtz Jr. (*19*). We agree that *Elaphrosaurus* is a derived ceratosaur based on the absence of several tetanuran synapomorphies and the presence of synapomorphies of Ceratosauria and subgroups (postaxial cervical and dorsal vertebrae with posterior pleurocoel, mid cervical centra with length four times diameter of anterior face, fusion of sutures in the pelvic girdle, pendant supraacetabular shelf, brevis fossa with broad distal end, postacetabular process with concave posterior margin, large ischial antitrochanter, femoral trochanteric shelf, and fused astragalocalcaneum) (P. C. Sereno, unpublished data).
31. M. Borsuk-Bialynika, *Palaeontol. Polon.* **37**, 5 (1977); C. W. Gilmore, *U.S. Geol. Surv. Prof. Pap.* **210C**, 1 (1946). We agree with the recent reassessment of *Opisthocoelicaudia* as a titanosaurid [O. Gimenez, *Ameghiniana* **30**, 154 (1993)] rather than a camarasaurid as originally described.
32. J. S. McIntosh, in *The Dinosauria*, D. B. Weishampel, P. Dodson, H. Osmólska, Eds. (Univ. of California Press, Berkeley, 1990), pp. 345–401.
33. R. E. Molnar, T. F. Flannery, T. H. Rich, *Alcheringa* **5**, 141 (1981); J. F. Bonaparte, *Ann. Paléontol.* **72**, 247 (1986).
34. The age of divergence between sister groups must be as early as, or earlier than, the first record of either sister group. The presence of an allosaurid in the Early Jurassic (*17*), for example, indicates that its successive sister taxa (Sinraptoridae, Coelurosauria) also must have diverged by the Early Jurassic, even though the first record of these taxa is Late Jurassic. These missing (or "ghost") sister lineages may not have acquired all of the synapomorphies that unite known members of the sister taxon [W. Hennig, *Phylogenetic Systematics*, (Univ. of Illinois Press, Urbana, 1966), pp. 163–169; M. A. Norell, in *Extinction and Phylogeny*, M. J. Novacek and Q. Wheeler, Eds. (Columbia Univ. Press, New York, 1992)].
35. P. M. Galton, *Nature* **268**, 230 (1977).
36. P. Taquet, *C. R. Acad. Sci.* **299**, 217 (1984).
37. A. G. Smith, D. G. Smith, B. M. Funnell, *Atlas of Mesozoic and Cenozoic Coastlines* (Cambridge Univ. Press, Cambridge, 1994), p. 41.
38. Terminal taxa include *Afrovenator* and six suprageneric taxa with the following characteristics: **Ceratosauria** (Abelisauroidea, Ceratosauroidea): posterior pleurocoel in cervicals and dorsals, pelvic girdle with fused sutures, iliac brevis fossa with broad distal end, iliac postacetabular process with concave posterior margin, femoral trochantric shelf, fused astragalocalcaneum; **Torvosauridae** (*Eustreptospondylus*, *Torvosaurus*): antorbital fossa with very narrow ventral margin on maxilla, broad antorbital excavation posterior to promaxillary fenestra, deep jugal posterior process, pubis and ischium with broad proximal shafts; **Spinosauridae** (*Baryonyx*, *Spinosaurus*): elongate prenarial snout, specialized anterior dentition (increase in number of premaxillary teeth, terminal rosette), and increase in height of the dorsal neural spines; **Allosauridae** (*Acrocanthosaurus*, *Allosaurus*, *Cryolophosaurus*, *Monolophosaurus*): quadrate short with head level with the middle of the orbit, deep anterior ramus of surangular, and small diameter of the external mandibular fenestra; **Sinraptoridae** (*Sinraptor*, *Yangchuanosaurus*): maxilla with two accessory pneumatic excavations, external nares with marked inset of the posterior margin, postorbital with bulbous anteriorly projecting rugosity, squamosal with flange that covers the quadrate head in lateral view; **Coelurosauria** (*Ornitholestes*, Therizinosauridae, Ornithomimidae, Tyrannosauridae, Caenagnathidae, Deinonychosauria, Aves): increase in the width of the anterior margin of the antorbital fossa, six sacral vertebrae (that is, vertebrae that attach to the pelvic girdle), transition point in tail located at approximately the fifteenth caudal vertebra, ischium less than 70% of pubis, triangular ischial obturator flange, and pubis with an obturator notch (also *Allosaurus*).
39. P. C. Sereno *et al.*, *Nature* **361**, 64 (1993).
40. D. L. Swofford, PAUP 3.1 (Illinois Natural History Survey, Champaign, IL, 1993).
41. W. B. Harland *et al.*, *A Geologic Time Scale* (Cambridge Univ. Press, Cambridge, 1989).

42. The skeletal bones and the channel floor contour map were modelled using Form Z 2.1 (auto.des.sys, Columbus, OH, 1992). Lighting and bone shadows were generated with StudioPro (Strata, St. George, UT, 1993).

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An Experimental Study of Inbreeding Depression in a Natural Habitat

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Inbreeding is known to lead to decreased survival and reproduction in captive populations of animals. It is also important to know whether inbreeding has deleterious effects in natural habitats. An estimate was made of the effects of inbreeding in white-footed mice, *Peromyscus leucopus noveboracensis*, derived from a wild population. This study demonstrates that inbreeding had a significant detrimental effect on the survivorship of mice reintroduced into a natural habitat. This effect was more severe than the effect observed in laboratory studies of the population.

Inbreeding adversely affects captive animals in a number of ways (*1*–*5*). However, captive animals are not exposed to many of the causes of mortality afflicting natural populations, such as predation, weather extremes, food stress, and epidemic disease. Deleterious effects of inbreeding have been demonstrated in natural populations of plants (*6*) and a few species of invertebrates (*7*) and fish (*8*), but the mobility and long generation lengths of mammals and other tetrapods have made it difficult to estimate the effect of inbreeding on survivorship in natural populations of these animals (*5*). This difficulty has led some researchers to question whether estimates of inbreeding depression made in captive populations can be used to predict the effects of inbreeding in nature or, indeed, whether natural populations experience inbreeding depression at all (*9*). Worldwide habitat destruction has forced many formerly natural populations into captivity for survival [such as the black-footed ferret *Mustela nigripes* (*10*)], and some captive populations have been inbred by necessity (*11*). The continued survival of many species depends on captive propagation before reintroduction (*12*), but inbreeding may compromise the fitness of reintroduced animals (*7*).

We developed a mark-release-recapture experiment to measure the effects of inbreeding on survivorship in a natural habitat. White-footed mice, *Peromyscus leucopus noveboracensis*, were collected from an area in which they were abundant and were used to found a laboratory population (*13*). Inbred and noninbred descendants of the wild-caught mice were released back into the field site from which the progenitors had been captured (Fig. 1) and were surveyed by trapping (*14*). A census of the field site in 1990 before the release resulted in only three captures during 1350 trap nights (0.002 mice per trap night). In 1988, when the progenitors of the laboratory population were collected, 0.163 mice per trap night had been captured by the same trapping protocol, suggesting that the population density had decreased. This decrease in population density may have been a direct result of the collection of the founders of the laboratory population but was more likely a result of some other, unknown process. This situation provided an opportunity to measure the effects of inbreeding in a natural setting that would allow new animals to become established without strong competition from an existing resident population (*15*).

Of the 786 animals released, 123 (15.7%) were recaptured at least once (Table 1). Mice were recaptured up to eight times for a total of 170 recaptures. Some were recaptured as long as 127 days after release, suggesting that many of the laboratory-bred mice became successfully established in the natural habitat. The low capture rate for wild mice can partially explain the high recapture rate for lab-reared animals. With few resident mice to force dispersal from the site, the reintroduced population quickly became established. Recapture histories for individual mice are available over the Internet (*16*) or from the authors.

Movement did occur among trapping areas and probably into nontrapped areas of the field site as well (Fig. 1). Most mice were recaptured within 50 m of the site of release. Of the 29 mice recaptured on a different trapline from their release site, 10 males and 6 females were inbred and 7 males and 6 females were noninbred. There is no significant effect of sex and inbreeding status on the tendency to move between areas (goodness of fit test based on log-linear models: $G = 1.464$, $P > 0.4$, with 2 df and expected frequencies calculated from the recapture data in Table 1). Thus, inbred mice do not move among the three release sites at a significantly

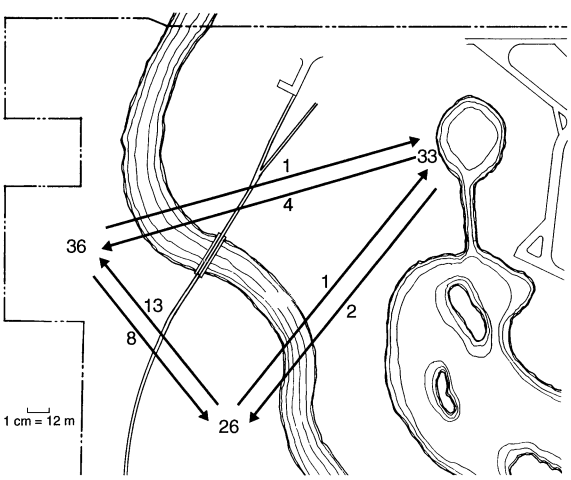

Fig. 1. Map of field site. Numbers at the ends of arrows represent the number of mice that were recaptured in the same area in which they were originally released. Numbers on directional arrows represent mice that were recaptured in a different area from the one in which they were released. Numbers on the figure sum to 124 because one mouse was recorded in all three areas. The field site comprised nonpublic areas of the Chicago Zoological Park, Brookfield, Illinois. All three areas are within a mixed deciduous forest. The broken line represents a fenced boundary between forested and nonforested areas. Wavy lines are water-depth contours. An old railroad bed and wooden bridge are indicated by solid lines.

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