8. U. D. Larsen, J. Branebjerg, G. Blankenstein, in *Proceedings of the 2nd International Symposium on Miniaturized Total Analysis Systems µTAS '96* (Analytical Methods & Instrumentation, Base 1, 1996), pp. 228–230.
9. T. Laurell and J. Drott, *Biosens. Bioelectronics* **10**, 289 (1995).
10. D. E. Raymond, A. Manz, H. M. Widmer, *Anal. Chem.* **66**, 2858 (1994).
11. C. S. Effenhauser, A. Paulus, A. Manz, H. M. Widmer, *ibid.*, p. 2949.

12. Supported by SmithKline Beecham, Zeneca, and a grant from the Biotechnology and Biological Sciences Research Council (UK). We thank B. Robertson, for primers and templates used in this study, and A. Ivens. We also thank Hybaid for the loan of their PCR instrument and the Alberta Microelectronic Centre for the production of the microchips.

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Predatory Dinosaur Remains from Madagascar: Implications for the Cretaceous Biogeography of Gondwana

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Recent discoveries of fossil vertebrates from the Late Cretaceous of Madagascar include several specimens of a large theropod dinosaur. One specimen includes a nearly complete and exquisitely preserved skull with thickened pneumatic nasals, a median frontal horn, and a dorsal projection on the parietals. The new materials are assigned to the enigmatic theropod group Abelisauridae on the basis of a number of unique features. Fossil remains attributable to abelisaurids are restricted to three Gondwanan landmasses: South America, Madagascar, and the Indian subcontinent. This distribution is consistent with a revised paleogeographic reconstruction that posits prolonged links between these landmasses (via Antarctica), perhaps until late in the Late Cretaceous.

Dinosaurs underwent their greatest diversification during the Late Jurassic and Cretaceous. Although plate tectonics during this interval had a profound impact on the evolution of dinosaurs and coeval terrestrial faunas, this impact remains poorly understood, in part because of a paucity of fossil remains from southern continents. Recent expeditions have resulted in important dinosaurian discoveries on all major landmasses that once formed the southern supercontinent of Gondwana, and it is now possible to begin assessing the biogeographic history of dinosaurian clades, at least on a gross scale (*1*, *2*).

Current models of the sequence and timing of Gondwanan fragmentation are based predominantly on geophysical evidence and have yet to be rigorously tested with nonmarine fossils. Plate fragmentation can set minimum dates for the origin of particular terrestrial and freshwater clades if members are present on two or more landmasses. Conversely, phylogenetic patterns can provide increased paleogeographic resolution and serve as independent tests of tectonic models (*3*).

Here, we describe theropod dinosaur fossils from the Upper Cretaceous (?Campanian) Maevarano Formation, Mahajanga Basin, northwestern Madagascar (*4*). Fragmentary dinosaur remains have been reported from the Mahajanga Basin for more than a century (*5*), with three taxa erected during that period (*5*–*7*): a sauropod, *Titanosaurus madagascariensis*; a theropod, *Majungasaurus crenatissimus*; and a pachycephalosaur, *Majungatholus atopus*. Recent excavations in this same field area have yielded a rich diversity of fossil vertebrates, including abelisaurid theropods, titanosaurid sauropods, birds, crocodilians, snakes, turtles, fishes, frogs, and mammals (*8*–*10*). The fossils occur predominantly in coarse-grained sandstone facies, and a variety of indicators suggest a semiarid, seasonal depositional environment (*11*). Many specimens occur as disarticulated yet associated skeletons amassed into concentrations, likely representative of time-averaged assemblages (*11*).

One of the theropod specimens (FMNH PR 2100) includes a nearly complete skull (*12*)—among the best preserved and most complete dinosaur skulls known—and most of the tail. The skull is disarticulated and individual bones are virtually undistorted, allowing comprehensive and detailed study of all elements (Fig. 1). The external surface of many elements is covered in rugose sculpturing, and the skull roof is adorned with three median ornamentations: thickened, fused nasals; a low frontal horn; and a parietal eminence. The total skull length is 57 cm, and comparisons with a closely related taxon, *Carnotaurus sastrei* from Argentina (*13*), suggest a total adult body length of about 7 to 9 m. A second specimen (UA 8678) of the same taxon includes an incomplete and disarticulated skull, most of the precaudal axial column, and the left ilium. Several of the vertebrae and ribs, particularly in the cervical region, were recovered in articulation. The small size of the skull elements relative to those of FMNH PR 2100, combined with the lack of fusion between several vertebral centra and corresponding neural arches, indicates that this animal was immature at the time of death.

Although large theropod materials from the Maevarano Formation have generally been referred to *Majungasaurus crenatissimus* (*5*, *6*, *9*), the inadequacy of the holotype and neotype specimens (*14*) requires that this taxon be regarded as a *nomen dubium*. Comparison of the recently collected materials with the fragmentary holotype specimen of the putative Malagasy pachycephalosaur, *Majungatholus atopus*, demonstrates that *Majungatholus* is not a pachycephalosaur but rather a "domed" theropod (*15*). This finding has biogeographic significance in that it removes the only report of a pachycephalosaur from a Gondwanan landmass, thereby restricting occurrences of this dome-headed ornithischian clade to Laurasia. Thus, the materials described herein are referred to *Majungatholus atopus* and placed within the enigmatic theropod group Abelisauridae (*16*).

The skull of *Majungatholus atopus* is relatively short and broad, with large antorbital, laterotemporal, and external mandibular fenestrae (Fig. 1). The snout is blunt and relatively deep at the level of the nares, with elongate, thickened, and rugose nasals. A large, bilateral pneumatic foramen pierces the fused nasals, and computerized tomographic (CT) imaging demonstrates that this structure is virtually hollow, supported internally only by thin bony struts. The orbital fenestra is rounded dorsally, with processes of both the lacrimal and postorbital projecting into it ventrally, outlining the position of the eye. Just caudal to the nasals is a roughened, conical median projection arising from the frontals. CT imaging shows this frontal horn to be hollow as well. The holotype of

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Majungatholus has a similar, though broader and fully fused, median structure on the frontals that is also rugose. A third, smaller specimen (FMNH PR 2099), presumably even more immature than UA 8678, bears a low, divided, relatively smooth swelling atop partially fused frontals.

Behind the frontal horn of FMNH PR 2100 is a large projection of the parietals, diamond-shaped in dorsal view. This parietal eminence, formed by caudodorsal expansions of the parietals and supraoccipital, is about the same height as the frontal horn. The frontal and parietal ornamentations are separated by a deep, saddle-shaped trough that is floored by a median depression. The occiput displays the primitive theropod condition in being vertically oriented, but shares with other abelisaurids a high, broad, arching transverse nuchal crest. As in other abelisaurids, the mandibular rami are widely spaced, the mandibular symphysis is small, and contacts between the dentary and postdentary elements are relatively restricted (associated with enlargement of the external mandibular fenestrae). The teeth resemble those of other abelisaurids in being relatively low-crowned and blade-like (*13*).

The postcranial skeleton of *Majungatholus* exhibits a combination of autapomorphies, derived abelisaurid characters, and primitive ceratosaurian features (Fig. 2) (*16–18*). The postaxial cervical vertebrae have low and broad centra, abbreviated neural spines, and elongate, robust epipophyses. The ilium is relatively low, with a pronounced supracetabular shelf, an elongate postacetabular process, and a deep brevis fossa. Unlike the condition in other theropods, the cervical ribs are bifurcate distally and several are pierced proximally by multiple, enlarged pneumatic foramina.

Recent phylogenetic analyses (*17*) recognize two major clades within Theropoda, Ceratosauria and Tetanurae, with abelisaurids generally regarded as a Cretaceous radiation of ceratosaurs (Fig. 3). Abelisaurid synapomorphies of *Majungatholus* include external sculpturing of facial and cranial elements, a high and transversely expanded nuchal crest, and enlarged external mandibular fenestrae (*18*). Within Abelisauridae, *Majungatholus* and *Carnotaurus* share several derived features, including a stout postorbital, a large parietal eminence, and a triangular splenial with a straight caudal margin (*19*).

During Late Cretaceous times, the top predators in most Laurasian terrestrial ecosystems were the large-bodied tyrannosaurids, which suggests that this tetanuran clade may have originated after the split between Laurasia and Gondwana. Earliest Late Cretaceous (Cenomanian) paleoenvironments in northern Africa appear to have been dominated by the lesser known but equally giant carcharodontosaurids, as well as spinosaurids and coelurosaurs (Fig. 3) (*20*). Carcharodontosaurids are also present in early Late Cretaceous deposits of Argentina (*20*), indicating a minimum origination date in the Early Cretaceous, circa 120

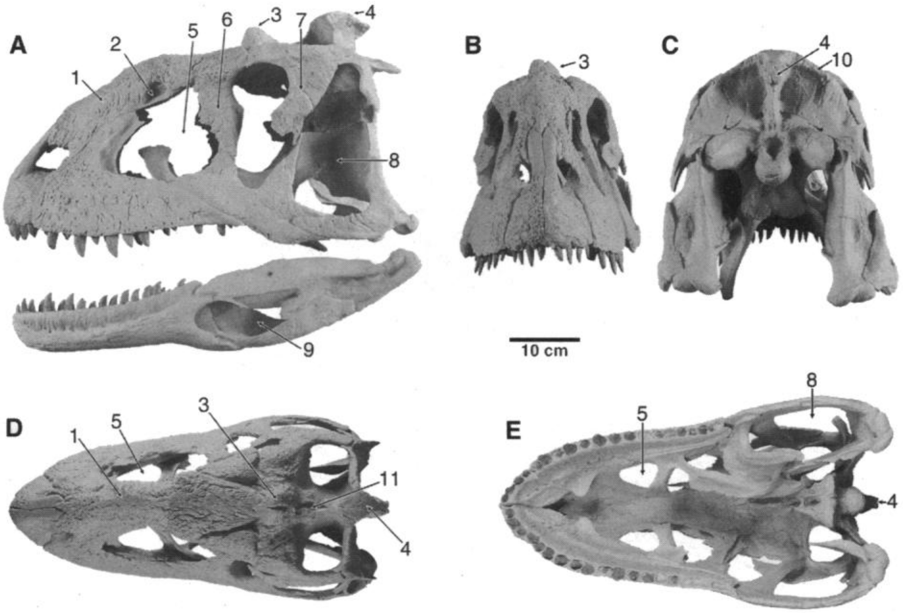


Fig. 1. Reconstruction of the skull and lower jaws of *Majungatholus atopus*, based on preserved elements of FMNH PR 2100 (*12*). (**A**) Left lateral view of skull and lower jaws; (**B**) rostral view of skull; (**C**) occipital view of skull; (**D**) dorsal view of skull; (**E**) palatal view of skull. Numbered features: 1, thickened nasals; 2, pneumatic foramen of nasal; 3, frontal horn; 4, parietal eminence; 5, enlarged antorbital fenestra; 6, lacrimal with suborbital process; 7, postorbital with suborbital process; 8, enlarged laterotemporal fenestra; 9, enlarged external mandibular fenestra; 10, nuchal crest; 11, median depression between frontal horn and parietal eminence. All elements were molded and cast, and then reassembled as shown.

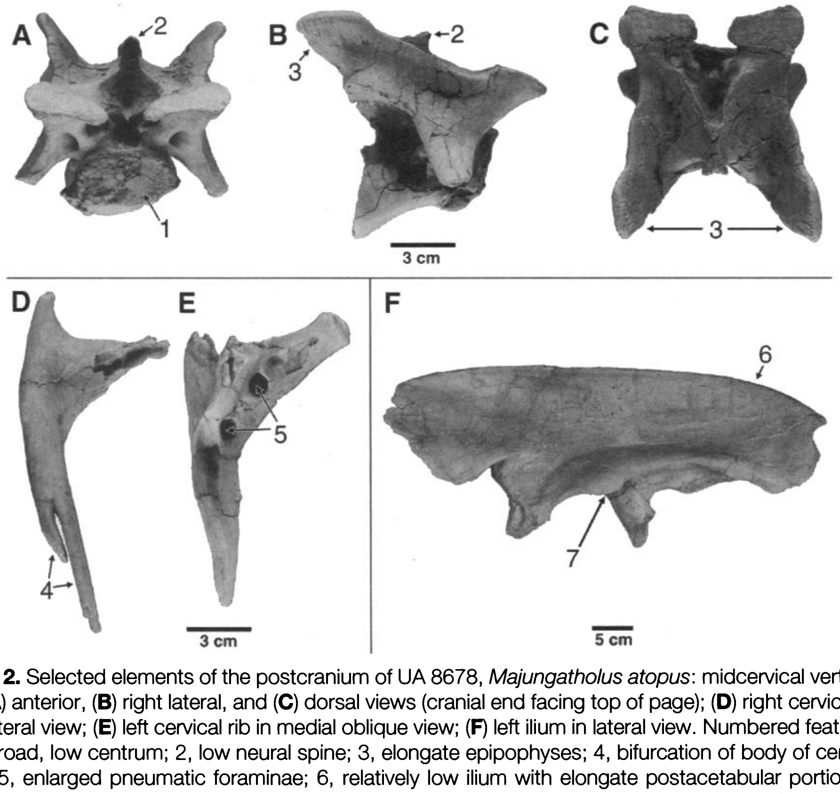


Fig. 2. Selected elements of the postcranium of UA 8678, *Majungatholus atopus*: midcervical vertebra in (**A**) anterior, (**B**) right lateral, and (**C**) dorsal views (cranial end facing top of page); (**D**) right cervical rib in lateral view; (**E**) left cervical rib in medial oblique view; (**F**) left ilium in lateral view. Numbered features: 1, broad, low centrum; 2, low neural spine; 3, elongate epipophyses; 4, bifurcation of body of cervical rib; 5, enlarged pneumatic foraminae; 6, relatively low ilium with elongate postacetabular portion; 7, pronounced supracetabular crest. The thin, elongate cervical rib shaft is broken away in (E) and only partially preserved in (D).

million years ago (Ma), before the isolation of Africa (*21*). The group may have been present in the Cretaceous of North America (*20*), though this contention is disputed (*22*). Abelisaurids show several derived features thought to characterize carcharodontosaurids, including broad postorbital-lacrimal contact and postorbital with suborbital flange (*23*). It is uncertain whether these characteristics evolved independently in the two groups, or whether they indicate a common ancestry.

Although abelisaurids were reported from the Late Cretaceous of Europe (*24*) and northern Africa (*25*), these materials are scanty and their phylogenetic affinities require confirmation from more complete, diagnostic material (*26*). The only fossils clearly attributable to this group have been recovered from South America, Madagascar, and India, and only from late Late Cretaceous horizons (Fig. 3) (*23*). The Indian fossils include at least two abelisaurid taxa, referred to as *Indosuchus* and *Indosaurus* (*27*, *28*), but the lack of associations among the fragmentary, isolated remains makes this sample problematic (*29*). The South American abelisaurid fossils are more informative, with two taxa (*Abelisaurus* and *Carnotaurus*) represented by nearly complete skulls (*13*, *28*, *30*).

Fig. 3. Summary of phylogenetic, temporal, and biogeographic relationships of nonavian theropod genera from the Cretaceous of Gondwana (*2*, *17*, *20*, *35*, *36*). Taxa include most named genera recovered from Cretaceous deposits on Gondwanan landmasses.

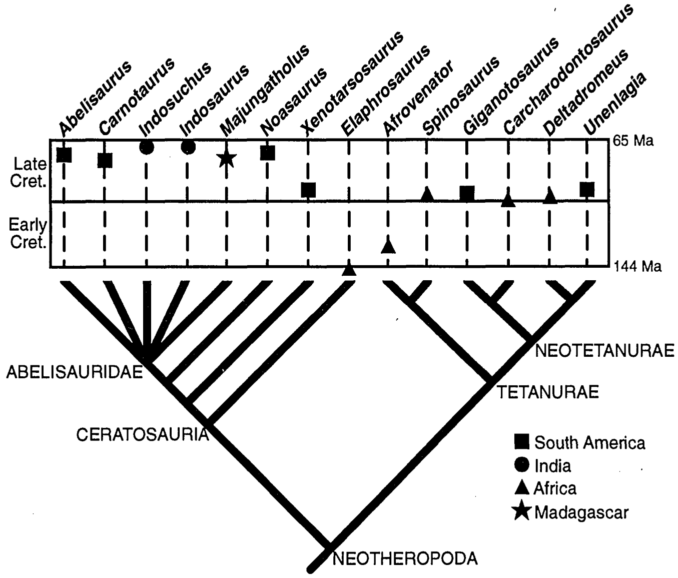
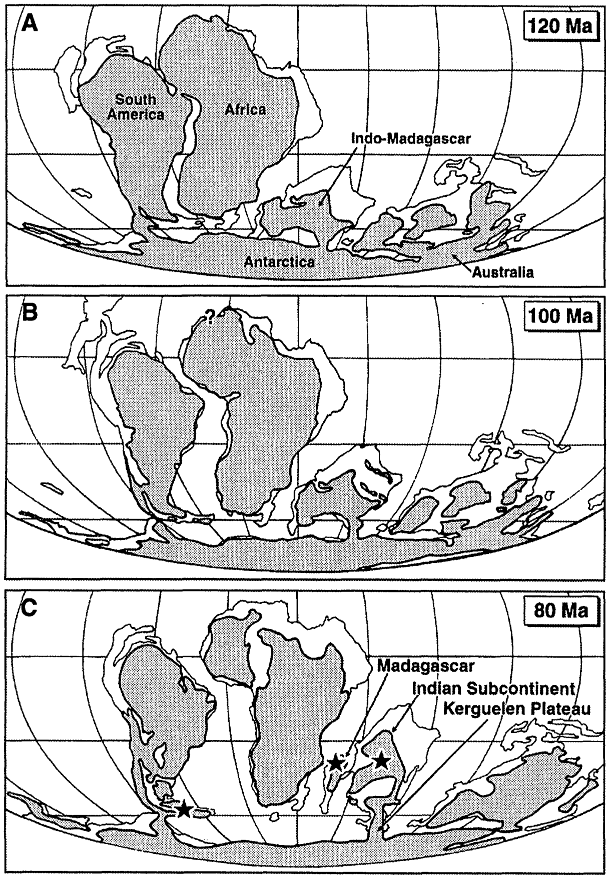


Fig. 4. Revised paleogeographic reconstruction of the fragmentation of Gondwana during the Cretaceous (*21*). (**A**) During the Early Cretaceous (circa 120 Ma), plate tectonic activity severed subaerial connections between Africa and South America, fully isolating Africa, while connections were maintained among other Gondwanan landmasses. (**B**) At the close of the Early Cretaceous, subaerial links were retained among Gondwanan landmasses exclusive of Africa. (**C**) These continental links persisted until sometime in the middle to late Late Cretaceous (perhaps as late as 80 Ma). Madagascar and the Indian subcontinent were attached to Antarctica via an isthmus comprising several terranes, including the Kerguelen Plateau. Stars indicate confirmed records of abelisaurid theropods.



Most paleogeographic reconstructions depict the Cretaceous as the most active interval of Gondwanan fragmentation, with Indo-Madagascar separating from Antarctica by about 125 Ma, South America separating from Africa before 100 Ma, and Madagascar separating from the Indian subcontinent at 85 to 90 Ma (*31*). Separation of South America and the Antarctic Peninsula occurred in the Oligocene (*31*). Ignoring ecological influences, this sequence of fragmentation would predict that the elements of the Late Cretaceous terrestrial biota of South America would be more similar to those of Africa than to those of Indo-Madagascar.

In contrast to these paleogeographic reconstructions, Hay *et al.* (*21*) postulated a subaerial link between Indo-Madagascar and Antarctica across the Kerguelen Plateau that persisted until as late as 80 Ma, much later than the final separation between South America and Africa (Fig. 4). The Kerguelen Plateau is thought to have been emplaced after the rifting between Indo-Madagascar and Antarctica (*21*, *32*). This revised reconstruction would predict a greater similarity of the Late Cretaceous terrestrial biota between South America and Indo-Madagascar (via Antarctica) than between South America and Africa. Also, from the time of its physical isolation from South America, Africa should exhibit increasing endemism.

The known distribution of abelisaurids (Argentina, Indian subcontinent, and Madagascar), like that for gondwanathere mammals (*10*), is consistent with at least two major biogeographic hypotheses: (i) Abelisaurids originated before the major continental fragmentations of the Early Cretaceous, and spread throughout most of Gondwana and perhaps into Laurasia. In keeping with this scenario, the current absence of documented African abelisaurids is attributable to poor sampling, differential extinction, or both. (ii) Abelisaurids originated sometime in the Early Cretaceous after the tectonic isolation of Africa. If so, abelisaurids never existed on Africa but rather dispersed between South America and Indo-Madagascar via Antarctica, making use of the postulated land bridge across the Kerguelen Plateau. Both views are equally probable given the data at hand.

Reconstructions of dinosaur biogeography initially focused on distinctions between Laurasian and Gondwanan faunas (*33*). More recently, it has been argued that dinosaur faunas were relatively cosmopolitan until the beginning of the Late Cretaceous, at which time the isolation of continental landmasses by oceanic barriers resulted in an abrupt shift toward marked provincialism (*20, 34*). Recent paleogeographic and paleontological data, including those presented here for abelisaurid theropods, suggest an alternative hypothesis: African faunas became increasingly endemic during the Cretaceous after Africa's isolation from South America, whereas retention of subaerial connections among the remaining Gondwanan landmasses resulted in relatively extensive cosmopolitanism for the associated terrestrial faunas, perhaps until late in the Late Cretaceous.

REFERENCES AND NOTES

1. J. Le Loeuff, *Cretaceous Res.* **12**, 93 (1991); D. Russell, *Can. J. Earth Sci.* **30**, 2002 (1993); J. Le Loeuff, in *The Encyclopedia of Dinosaurs*, P. J. Currie and K. Padian, Eds. (Academic Press, New York, 1997), pp. 51–56.
2. P. C. Sereno, *Annu. Rev. Earth Planet. Sci.* **25**, 435 (1997).
3. L. Grande, *Paleobiology* **11**, 234 (1985); K. C. Beard, *Bull. Carnegie Mus. Natl. Hist.* **34**, 5 (1998); A. Hallam, *An Outline of Phanerozoic Biogeography* (Oxford Univ. Press, New York, 1994).
4. Exact locality coordinates for the theropod specimens are on file in the Field Museum of Natural History (FMNH), Chicago, and the Université d'Antananarivo (UA), Madagascar.
5. C. Depéret, *Bull. Soc. Geol. Fr.* **24**, 176 (1896).
6. R. Lavocat, *Bull. Mus. Natl. Hist. Nat. (Paris)* **27**, 256 (1955).
7. H.-D. Sues and P. Taquet, *Nature* **279**, 633 (1979); H.-D. Sues, *J. Paleontol.* **54**, 954 (1980).
8. D. W. Krause, J. H. Hartman, N. A. Wells, in *Natural Change and Human Impact in Madagascar*, B. Patterson and S. Goodman, Eds. (Smithsonian Institution Press, Washington, DC, 1996), pp. 3–43; C. A. Forster, L. M. Chiappe, D. W. Krause, S. D. Sampson, *Nature* **382**, 532 (1996); S. D. Sampson, D. W. Krause, C. A. Forster, *Nat. Hist.* **106**, 24 (1997); C. A. Forster, S. D. Sampson, L. M. Chiappe, D. W. Krause, *Science* **279**, 1915 (1998).
9. S. D. Sampson, D. W. Krause, P. Dodson, C. A. Forster, *J. Vertebr. Paleontol.* **16**, 601 (1996).
10. D. W. Krause, G. V. R. Prasad, W. von Koenigswald, A. Sahni, F. E. Grine, *Nature* **390**, 504 (1997).
11. R. R. Rogers, S. D. Sampson, E. M. Roberts, *J. Vertebr. Paleontol.* **17** (suppl. 3), 71A (1997).
12. All elements of the skull of FMNH PR 2100 are represented on at least one side, and most are complete and undistorted. The only missing elements are the left premaxilla, right pterygoid, right ectopterygoid, and right vomer. In Fig. 1, the left premaxilla has been reconstructed on the basis of the preserved right premaxilla.
13. J. F. Bonaparte, F. E. Novas, R. A. Coria, *Contrib. Sci. Nat. Hist. Mus. Los Angeles Cty.* **416**, 1 (1990).
14. The original theropod materials recovered from the Maevarano Formation, including isolated teeth and caudal vertebrae, were assigned to *Megalosaurus crenatissimus* (*5*). However, no single holotype specimen was named from this collection, and none of the specimens appear to be diagnostic to the generic level. A partial dentary was subsequently made the holotype of the species and was placed into a new genus, *Majungasaurus* (*6*). However, comparison of the latter specimen with dentaries of other abelisaurids failed to reveal diagnostic characters. The jaw is fragmentary, and the dentition does not appear to differ significantly from that in the Indian abelisaurid materials.
15. The holotype specimen of *Majungatholus atopus* (MNHN.MAJ 4), housed in the Muséum National d'Histoire Naturelle, Paris, consists of a partial skull roof with a frontal "dome" (*7*). Several characteristics of this specimen (for example, lack of radiating arrangement of bony trabeculae in dome; dome occurring wholly within frontals rather than incorporating parietals; rugose ornamentation) are not present in any members of Pachycephalosauria. Conversely, MNHN.MAJ 4 has several theropod characteristics (for example, long, divided olfactory tracts) as well as derived features present in FMNH PR 2100. Most importantly, the frontal "dome" of the holotype is equivalent to the frontal "horn" in FMNH PR 2100.
16. Diagnostic characters for *Majungatholus atopus*: thickened, fused, highly pneumatic nasals with large, bilateral foramina; frontals with median hornlike projection; cervical ribs bifurcate distally; cervical ribs with multiple enlarged pneumatic foraminae proximally (diameter > 10 mm).
17. J. A. Gauthier, *Mem. Calif. Acad. Sci.* **8**, 1 (1986); T. Holtz, *J. Paleontol.* **68**, 1100 (1994); P. Sereno, *Neues Jahrb. Geol. Palaeontol. Abh.*, in press. Ceratosauria includes at least two groups, Coelophysoidea and Ceratosauroidea. Coelophysoids (for example, *Coelophysis*, *Syntarsus*, *Dilophosaurus*) are known from the Late Triassic and Early Jurassic of Africa, Europe, and North America. Ceratosauroids are thus far represented by two genera (*Ceratosaurus* and *Elaphrosaurus*), from the Late Jurassic of North America and Africa, and by the Cretaceous abelisaurids, known from South America, Madagascar, and the Indian subcontinent. Tetanurae includes more derived theropods such as Allosauroidea (allosaurids, spinosaurids, carcharodontosaurids) and Coelurosauria (for example, dromaeosaurids, ornithomimids, troodontids, and tyrannosaurids, as well as birds), which together are represented on all major landmasses.
18. Synapomorphies of Abelisauridae observable in *Majungatholus atopus* include **Cranial**: External sculpturing of craniofacial elements; premaxilla with reduced to absent palatal process; maxilla-jugal contact elongate; rostral process of lacrimal strongly reduced or absent; lacrimal with pronounced suborbital process; broad lacrimal-postorbital contact; long axis of postorbital oriented rostroventral-caudodorsal; postorbital with pronounced suborbital process; high, transversely broad nuchal crest with large squamosal contributions; medial alveolar border of premaxilla, maxilla, and dentary bearing fused interdental plates with series of vertical ridges and grooves; hypertrophied external mandibular fenestra and associated weak contacts between dentary and postdentary elements. **Postcranial**: Postaxial epipophyses elongate.
19. Synapomorphies of *Majungatholus* and *Carnotaurus* include **Cranial**: Postorbital rostrocaudally elongate; postorbital with stepped-down ventrolateral fossa; dorsally placed median fossa in saddle-shaped depression overlapping contact of frontals and parietals; enlarged, caudodorsally projecting parietal eminence supported ventrally by stout supraoccipital; laterally directed paroccipital processes with upturned distal ends; stout, triangular splenial with straight caudal margin (*13*).
20. P. C. Sereno *et al.*, *Science* **272**, 986 (1996).
21. W. W. Hay *et al.*, in *The Evolution of Cretaceous Ocean/Climate Systems*, *Geol. Soc. Am. Spec. Pap.*, E. Barrera and C. Johnson, Eds., in press.
22. P. J. Currie, personal communication.
23. F. E. Novas, in *The Encyclopedia of Dinosaurs*, P. J. Currie and K. Padian, Eds. (Academic Press, New York, 1997), pp. 1–2. Derived features shared by Abelisauridae and Carcharodontosauridae include rugose sculpturing on external surface of facial elements, broad postorbital-lacrimal contact, postorbital with suborbital flange, and ossified interorbital region.
24. E. Buffetaut, P. Mechin, A. Mechin-Salessy, *C. R. Acad. Sci. Paris* **306**, 153 (1988); H. Astibia *et al.*, *Terra Nova* **2**, 460 (1990); J. Le Loeuff and E. Buffetaut, *Geobios* **25**, 585 (1991).
25. D. A. Russell, *Bull. Mus. Natl. Hist. Nat. (Paris)* **18**, 349 (1996).
26. The putative abelisaurid materials from Europe include a dentary and several isolated postcranial elements from the Late Cretaceous of France (*24*). Several of these appear to be derived from ceratosaurian theropods yet lack diagnostic abelisaurid features. The Moroccan materials (*25*) include isolated, partial jaw elements thought to resemble those of abelisaurids, yet once again there are no definitive characters supporting this designation.
27. F. von Huene and C. A. Matley, *Mem. Geol. Surv. India* **21**, 1 (1933); S. Chatterjee, *J. Paleontol.* **52**, 570 (1978); _____ and D. K. Rudra, *Mem. Queensl. Mus.* **39**, 489 (1996).
28. J. F. Bonaparte, *Hist. Biol.* **5**, 1 (1991).
29. The described materials of Indian abelisaurids appear to represent at least two taxa, *Indosaurus* and *Indosuchus*, from the Late Maastrichtian Lameta deposits (*27, 28*). Both taxa were erected on fragmentary brain cases. Although the collection includes numerous additional cranial and postcranial elements, the great majority were surface collected as isolated specimens. Thus, assigning particular elements to one or the other taxon is problematic until associations are established, particularly between cranial and postcranial elements.
30. J. F. Bonaparte and J. E. Powell, *Mem. Soc. Geol. Fr.* **139**, 19 (1980); J. F. Bonaparte and F. E. Novas, *Ameghiniana* **21**, 259 (1985).
31. A. M. Ziegler, C. R. Scotese, S. F. Barrett, in *Tidal Friction and the Earth's Rotation II*, P. Brosche and J. Sundermann, Eds. (Springer-Verlag, Berlin, 1982), pp. 240–252; E. J. Barron, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **59**, 207 (1987); C. R. Scotese, L. M. Gahagan, R. M. Larson, *Tectonophysics* **155**, 27 (1988); C. R. Scotese, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **87**, 493 (1991); W. C. Pitman III, S. Cande, J. LaBreque, J. Pindell, in *Biological Relationships Between Africa and South America*, P. Goldblatt, Ed. (Yale Univ. Press, New Haven, 1993); A. G. Smith, D. G. Smith, B. M. Funnell, *Atlas of Mesozoic Coastlines* (Cambridge Univ. Press, Cambridge, 1994).
32. B. C. Storey, *Nature* **377**, 301 (1995).
33. J. F. Bonaparte and Z. Kielan-Jaworowska, in *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, P. J. Currie and E. H. Koster, Eds. (Occasional Paper 3, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, 1987), pp. 24–29.
34. P. C. Sereno, J. A. Wilson, H. C. E. Larsson, D. B. Dutheil, H.-D. Sues, *Science* **266**, 267 (1994).
35. F. E. Novas, in *The Encyclopedia of Dinosaurs*, P. J. Currie and K. Padian, Eds. (Academic Press, New York, 1997), pp. 678–689.
36. A. Ardolino and D. Delpino, in *X Congreso Geologico Argentino, Actas III* (San Miguel de Tucuman, Argentina, 1987), pp. 193–196.

37. We thank B. Rakotosamimanana, P. Wright, B. Andriamihaja, the Institute for the Conservation of Tropical Environments staff, the people of Berivotra, and all expedition members for assistance with field work; G. Buckley, J. Flynn, and W. Simpson (FMNH) for preparation support; P. Currie and G. Olshevsky for anatomical and nomenclatural discussions; R. Coria and D. Fastovsky for manuscript reviews; K. Passaglia, V. Heisey, and J. Holstein for preparation of specimens; M. Stewart and J. Weinstein for photography; and B. Chen and R. Day for assistance with CT scanning. The figures were composed by L. Betti-Nash. Access to comparative materials was kindly provided by P. Taquet (Museum National d'Histoire Naturelle, Paris); S. Cumbaa, K. Shepherd, and C. Kennedy (Canadian Museum of Nature, Ottawa); S. Chatterjee (Texas Tech University, Lubbock); D. Rudra and S. Bandyopadhyay (Indian Statistical Institute, Calcutta); and S. Sen Gupta (Geological Survey of India, Calcutta). Supported by NSF and The Dinosaur Society.

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