Predatory Dinosaurs from the Sahara and Late Cretaceous Faunal Differentiation

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natural mechanism of aggregation.

The problem of the optimal path, for which $C_0$ is a minimum, has been solved exactly in two dimensions in the context of domain walls in random ferromagnets and directed polymers in a random medium (16). The Hurst exponent $H = \gamma / 2$. For directed, self-affine river basins, the values of $\gamma$ and $H$ can readily be deduced to be $\frac{4}{3}$ and $\frac{2}{3}$, respectively. These values are robust and do not change even if the minimization of the energy functional includes both directed and undirected networks (16).

For $\frac{1}{2} \leq \gamma < 1$, heterogeneities in the erosional properties are irrelevant, and the exponent values are the same as their homogeneous counterparts. Our proof relies on first observing that $\lim E \leq 1 + 2^y$ (Min E $\leq \Sigma \kappa^n$ for the tree for which $\Sigma \kappa^n$ is a minimum, but $\Sigma \kappa^n \leq \text{max} [\Sigma \kappa^n] \sim k_{\text{max}} \cdot 1^{1+2^y}$, where $k_{\text{max}}$ is the largest of the $k_v$ values) and then using Eq. 9 in conjunction with Eq. 3 to show that $H \geq 1$. Because $H > 1$ is not physically meaningful, the Hurst exponent remains unchanged at $H = 1$.

We have thus shown that OCNs with $\frac{1}{2} \leq \gamma \leq 1$ show three classes of behavior (Table 1). Our results indicate that the OCN, in its present form, does not describe the behavior of river basins. Rinaldo and co-workers (6) have carried out numerical studies of the $\gamma = \frac{1}{2}$ case. Their work, which was restricted to the statistics of local minima (and not the global minimum, as in our analysis), yielded exponents different from ours but in good accord with observational data.

**REFERENCES AND NOTES**


8. The effects of evaporation of the water are captured by a negative contribution to $R_0$. It can be shown that


12. Our finite-size scaling arguments and the notion of universality are similar to those in critical phenomena. See, for example, M. E. Fisher, Rev. Mod. Phys. 46, 587 (1974).

13. Directed networks are ones in which there is no local flow with a component away from the dominant downstream direction. Generally, the mean area (s) scales as $s_{\lambda}^{H}$, where $\lambda$ is the fractal dimension of the stream $d_1 = 1$. The fractal situation $d_1 > 1$ corresponds to $H = 1$, whereas as a self-affine geometry has $d_1 = 1$ and $H = 1$. All of our results hold for arbitrary networks without any restriction on their directness.

14. J. T. Hack, U.S. Geol. Surv. Prof. Paper 294-B (1957). The principal cause of the anomalous exponent of Hack is a matter of debate. Basin elongation occurs in the Scheidegger model (9, 10), but this model is yet untested with large sets of data. Alternatively, computer simulations (7) suggest that basin shapes have a similarity across scales.

15. This substitution is a generalization of the observation that the mean area is equal to the average distance to the outlet [B. M. Troutman and M. R. Karlinger, Water Resour. Res. 28, 563 (1992), and references therein].


17. We are indebted to A. Giacometti and I. Rodriguez-Iturbe and especially to A. Rinaldo for numerous stimulating discussions. This work was supported by grants from the Komitet Badan Naukowych, the National Aeronautics and Space Administration, the North Atlantic Treaty Organization, the National Science Foundation, and the Petroleum Research Fund administered by the American Chemical Society.

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**Predatory Dinosaurs from the Sahara and Late Cretaceous Faunal Differentiation**

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Late Cretaceous (Cenomanian) fossils discovered in the Kem Kem region of Morocco include large predatory dinosaurs that inhabited Africa as it drifted into geographic isolation. One, represented by a skull approximately 1.6 meters in length, is an advanced allosaurid referable to the African genus *Carcharodontosaurus*. Another, represented by a partial skeleton with slender proportions, is a new basal coelurosaur closely resembling the Egyptian genus *Bahariasaurus*. Comparisons with Cretaceous theropods from other continents reveal a previously unrecognized global radiation of carcharodontosauroid predators. Substantial geographic differentiation of dinosauir faunas in response to continental drift appears to have arisen abruptly at the beginning of the Late Cretaceous.

Major continental areas became increasingly isolated during the Late Cretaceous as non-avian dinosaurs underwent their final radiation. The influence of continental fragmentation on dinosaur evolution during this interval has remained uncertain because of uneven sampling of the fossil record. Late Cretaceous dinosaurean remains have been recovered principally from Asia and western North America and consist largely of coelurosaur predators and ornithischian herbivores (1). Although dinosauir bones of Late Cretaceous age have been reported from all major southern land areas including Antarctica (2–12), reasonably complete skeletons have been recovered only from South America (13), where abelisaur predators and titanosaurian herbivores flourished.

On continental Africa, the most complete remains of Late Cretaceous dinosaurs were discovered in Egypt and include the lower jaw and vertebrae of an unusual fin-backed theropod, *Spinosauros* (3); skull fragments and bones of another large theropod, *Carcharodontosaurus* (4); isolated bones of a third predator, *Bahariasaurus* (5); and bones of a large titanosaurian sauropod, *Aegyptosaurus* (6). In beds of similar age in Morocco, several bones of an enigmatic sauropod *Rhabditesaurus* were discovered (7). Phylogenetic interpretation of these remains (14–17) has been difficult because many of the bones are fragmentary and because the Egyptian collection was destroyed during World War II (18).

We describe new vertebrate remains from Late Cretaceous beds in the
Cladistic analysis of basal tetanurans places Carcharodontosaurus within the allosauroid clade (Fig. 4A) as recently suggested (17), allying it closely with Acrocanthosaurus from the Albian of North America (30) and Giganotosaurus from the Albian or Cenomanian of South America (31). Characters that unite these taxa as carcharodontosaurids include a broad orbital shelf (formed by the lacrimal and postorbital bones) and the squared anterior end of the lower jaw. In Carcharodontosaurus and Acrocanthosaurus, the cervical centra are particularly broad, and the anterior caudal vertebrae have small pleurocoels.

The new fossils also include a partial skeleton, several bones of which (the coracoid, femur, and fibula) are identical to bones referred to the Egyptian species Bahariasaurus ingens (5). These Egyptian bones, however, are not part of the holotypic specimen of B. ingens, which is based on other fragmentary postcranial elements (32). Therefore, we designate the Moroccan skeleton as the holotype of a new theropod, Deltadromeus agilis, gen. nov., sp. nov., to which we refer several of the Egyptian bones (33).

The limb bones in Deltadromeus are remarkably slender. Length/diameter ratios are similar to those in the smaller cœlurosaur Ornithomimus and are only 50 to 60% of the diameter of those in the equal-sized allosauroid Allosaurus (Table 1). The plate-shaped coracoid and proximal scapula in Deltadromeus are broader in other theropods that also show expansion of the acromial region (therizinosaurids, tyran- nosaurids, and deinonychosaurs). On the basis of the preserved portions of the humerus, radius, and ulna, the forelimb is not substantially reduced in length. The postcranial proportions of the hind limb bones lie between those for Allosaurus and Ornithomimus (Table 1).

The phylogenetic analysis suggests that Deltadromeus is an early derivative of the cœlurosaur radiation (Fig. 4A) and most closely resembles the smaller Late Jurassic taxon Ornitholestes (34). Its status as a
coelurosaur is based on the expansion of the coracoid, the reduction of the femoral fourth trochanter to a low ridge, and the presence of a large deep fossa on the proximal end of the fibula (Fig. 3, E, G, and H).

Late Cretaceous fossils from Africa are critical for the establishment of biogeographic patterns toward the end of the Mesozoic. During this time, an endemic fauna had arisen in Asia (central Asia and western North America) that consisted almost entirely of coelurosaurian predators and ornithischian herbivores (1). A complementary Gondwanan dinosaurian fauna composed of abelisaur and spinosaurid predators and titanosaurian sauropods has been described (35) but has yet to be clearly established on, and restricted to, southern continents other than South America (15, 36).

The dinosaur remains from Morocco support the following biogeographic conclusions:

1) During the Late Cretaceous, several large theropods achieved a trans-African distribution. The Moroccan material indicates that at least three large predators (Spinosaurs, Carcharodontosaurus, and Deltadromeus) ranged across northern Africa during the Late Cretaceous (Cenomanian).

2) During the Early Cretaceous, large carcharodontosaurid predators underwent a global radiation. The close relationships between Carcharodontosaurus (African), Acrocanthosaurus (North American), and Gigantoraptor (South American) identify a carcharodontosaur radiation that had achieved a transcontinental distribution before the end of the Early Cretaceous (ca. 100 Ma) (Fig. 4B). Carcharodontosaurus may have been isolated on Africa during the Cenomanian (ca. 90 Ma), as paleogeographic reconstructions suggest, but its carcharodontosaurid progenitors were able to colonize northern and southern landmasses during the Early Cretaceous.

3) By the Late Jurassic, basal coelurosaurians had achieved a global distribution. Deltadromeus and recent discoveries of maniraptoran bones in Sudan and Argentina (37) document the presence of coelurosaurians on southern continents during the Late Cretaceous. The early divergence of a lineage that gave rise to Deltadromeus suggests that primitive coelurosaurians were present on southern continents before the close of the Jurassic.

4) At the beginning of the Late Cretaceous (Cenomanian), a distinctive dinosaurian fauna was present in Africa. Thus far, only Africa has yielded Late Cretaceous spinosaurids, primitive coelurosaurians like Deltadromeus, abundant small theropods with simple blade-shaped teeth, and a large iguanodontid (25). Although the sauropod Rebbachisaurus may share its closest relations with a South American form (38), the Moroccan dinosaurian fauna is distinct from Cenomanian faunas on South America and northern continental areas, where abelisaurids and titanosaurians (South America) and hadrosaurs, ankylosaurs, and deinonychosaurs (northern continents) are dominant (39).

![Fig. 2. Cranium and maxillary tooth (SGM-Din 1) and postaxial cervical vertebra (SGM-Din 3) of C. saharicus. Cranial reconstruction is shown in (A) left lateral and (B) dorsal views. Stipping indicates bone preserved on at least one side of the cranium. (C) Maxillary tooth from cranium in left lateral view, with magnified views of the posterior margin (right) and lateral surface (below). (D) Midcervical vertebra in (top) left lateral and (bottom) posterior views. Scale bar in (A) and (B), 50 cm; in (C), 5 mm (above) and 1 cm (below); in (D), 5 cm. Abbreviations: anto, antorbital fossa; ao, accessory pneumatic opening; di, diaphysis; f, frontal; j, jugal; l, lacrimal; lo, loral margin; m, maxilla; mf, maxillary fenestra; n, nasal; nfo, narial fossa; p, parietal; pa, parapophysis; pl, pleurocoel; po, postorbital; por, postorbital rugosity; poz, postzygapophysis; and so, supraoccipital.](image-url)

| Table 1. Length and minimum diameter measurements (in millimeters) and ratios in D. agilis (SGM-Din 2), Allosaurus fragilis (44), and Ornithomimus sp. (Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, uncataloged). Parentheses indicate estimation; dashes indicate missing information. |
|-----------------|-----------------|-----------------|-----------------|
| **Bone**        | **Deltadromeus** | **Allosaurus**  | **Ornithomimus** |
| **Length, diameter** |            |            |                |
| Midcaudal centrum | 130, 70        | —            | —              |
| Distal caudal centrum | 130, 35       | 90, 28       | —              |
| Humerus          | (328), 22      | 310, 38      | 418, 46        |
| Femur            | 740, 53        | 850, 96      | 485, 35        |
| Tibia            | (700), —       | 690, 72      | 300, 25        |
| Metatarsal II    | 417, 20        | 270, 42      | 332, 16        |
| Metatarsal III   | 450, 22        | 327, 40      | 311, 25        |
| Metatarsal IV    | 400, 20        | 275, 36      | 120, 7         |
| Digit II-phalanx 1 | 140, 8         | 120          | 68             |
| Digit II-ungual  | 80             | 80           | 52             |
| Digit III-phalanx 1 | 140            | 110          | —              |
| Digit IV-phalanx 1 | 98             | 75           | 40             |
| Digit IV-phalanx 3 | 98             | 75           | 40             |
| Digit IV-phalanx 3 | 52             | 30           | 22             |
| Digit IV-phalanx 4 | 37             | 29           | 21             |

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remains to be determined whether Africa's Cenomanian dinosaurian fauna persisted to the end of the Cretaceous.

5) The Moroccan fossils suggest, in conclusion, that substantial faunal exchange between major land areas may have continued well into the Early Cretaceous. Marked provincialism of dinosaurian faunas in North America, South America, and Africa appears to have abruptly arisen early in the Late Cretaceous, when dispersal routes between northern and southern

**Fig. 3.** Skeletal anatomy of *D. agilis* (SGM-Din 2). (A) Neural spines of anterior caudal vertebrae in left lateral view. (B) Midcaudal vertebra in left lateral view. (C) Midcudal chevron in left lateral view. (D) Skeletal reconstruction showing preserved bones (length of *D. agilis* approximately 9 m). (E) Scapulocoracoid and forelimb (composite left and right) in left lateral view. (F) Pubic foot in left lateral view. (G) Proximal left fibula in medial view. (H) Proximal femur (reversed from right) in left lateral view. (I) Tibia (reversed from right) in proximal view (anterior toward top). (J) Distal tibia, astragalus, and calcaneum (reversed from right) in anterior view. (K) Left metatarsals II to IV in anterior view. (L) Left metatarsals II to V in proximal view (anterior toward bottom). Scale bar in (A), 5 cm [also for (F), (G), (H), and (K)]; in (B), 5 cm [also for (I), (J), and (L)]; in (D), 1 m; in (E), 10 cm. Abbreviations: ac, acromium; ap, anterior process; as, astragalus; asp, ascending process; at, anterior trochanter; ca, calcaneum; cc, cnemial crest; dpc, deltopleural crest; ff, fibular fossa; ft, fourth trochanter; pp, posterior process; ra, radius; and ul, ulna.

**Fig. 4.** Phylogenetic and temporal relationships among basal tetanurans. (A) Strict consensus cladogram of eight minimum-length trees based on phylogenetic analysis of 63 characters in 14 terminal taxa (Table 2), with outgroup states based on *Eoraptor* and *Herrerasaurus*. The data are generally congruent (consistency index, 0.81; retention index, 0.84); more incomplete terminal taxa are less stable when trees several steps longer than the minimum are sampled (42). (B) Phylogram based on the cladogram and recorded temporal ranges as calibrated on a recent time scale (43). Error bars indicate age uncertainty. 1, Neotheropoda; 2, Tetanurae; 3, Neotetanurae; 4, Spinosauridae; 5, Alloosauridae; 6, Carcharodontosauridae; 7, Coelurosauria.
land areas were finally severed and when oceanic barriers had arisen between southern continents.

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rids, and maniraptorans. Ornithischians include an-
kylosaurs, hadrosaurs, pachycephalosaurs, and ceratopsians.

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for the largest tyrannosaur (138 cm and 120 cm; total, 229 cm). Skull length may thus be proportionately greater in carorachodontosaurs than in tyrannosaurs, which appear to have longer distal hind limbs segments.

29. Diagnostic features for C. saharicus. **Dentary**: Posterior to crown margin only slightly concave at mid-length and convex distally; enamel ornamentation, including transverse bands and groove-like wrinkles near crown margins. **Cranial**: Antorbital fenestra length 30%, and height 25%, of those of the cranial; ventral margin of antorbital fossa arched; prefrontal absent or co-ossified; postorbital venal ramus with robust lateral processes with groove and pit; postorbital-zygomatic arch articulation highly angulated; and paroccipital processes and basi- at tubera positioned far ventral to opisthotic condyle. **Postcranial**: Postaxial cervical vertebrae with kidney-shaped posterior articular faces, short neural spines, robust transverse processes, and strong ventral keels; anterior caudal vertebrae with pleurocoels; and distal caudal vertebrae with long anteroposteriorly compressed neural spines.

29. Storzer’s skeleton 1922 X46 provides an association between cranial and postcranial bones, including an exceptionally broad cervical vertebra and a pleurocoelous articular surface of the third vertebra (4). These vertebrae, in turn, overlap with skeleton 1922 X45 (Storzer’s “Spinosaurus B”), which provides additional information about the vertebrae column and pedicle flanges (5).


32. The histology of the spinous processes comprises broad dorsal vertebrae, a neural arch, three sacral vertebrae, a rib fragment, pubes, and the proximal portion of the ischium (29). Unlike the Moroskeletum, the shape of the pubis is broader, the public foot is divided in the midline, and the iliac peduncle of the ischium is proportionally narrower.

33. **Etymology**: Delta (delta, Greek): dromenous, runner (Greek mythology). Named for the dactylfacies in which it was found and for the curvilinear proportions of its hind limbs. The holotypic skeleton (SM-N-Din 2) is in the collections of the Ministere de l’Energie et des Mines, Rabat, Morocco. Diagnosis: Anterior caudal vertebrae with broad quadrangular neural spines; coracoid and acromion broadly expanded anteroposteriorly; coracoid with shallow notch in anterior margin; iliac midshaft dorsally compressed; femur with accessory trochanter on distal shaft; femoral medial distal condyle with anterior extension; metatarsal IV distal condyle reduced. For more reference material (existing as figures only): Left coracoid, pubes, right femur, proximal right tibia, and left fibula (1912 VIII) (5). Femoral length (122 cm) is 1.5 times that of SM-N-Din 2, indicating that D. agilis grew to an adult body size within the range established for T. rex (40).


45. The following 63 synapomorphies correspond with scored character states (Table 2) that were used in the analysis of basal tetanuran relationships presented in Fig. 4. 1. Tetanurae: 1. maxillary fenestra; 2. lacrimal pneumatic excavation; 3. skull in ventral pro cesses of lacrimal for jugal; 4. jugal pneumatic excavation; 5. prefrontal-frontal pig-in-socket articulation; 6. posteriormost maxillary tooth positioned anterior to orbit; 7. maxillary tooth row anterior to orbit; 8. lacrimal pneumatic excavation; 9. skull in ventral processes of lacrimal for jugal; 10. maxillary tooth row anterior to orbit; 11. iliac-ischial articulation smaller than iliac-pubic articulation; 12. iliac obturator notch; 13. femoral antebrachial blade-shaped; 14. tibial distal end back calcaneum; 15. fibular distal end reduced (less than twice anteroposterior width at mid-shaft); 16. astragalar articulation process blade-shaped (state 1); 17. astragalar cup for fibula reduced; 18. astragalar distal condyle oriented anterovertebrally; 19. astragalar condyle with antebrachial groove; 20. metatarsals II and III with hourglass-shaped proximal end; 21. metatarsals III with wedge-shaped midshaft; 22. metatarsals IV with hourglass-shaped proximal end; 23. metatarsal IV distal condyle reduced; 24. astragalar condyle with antebrachial groove; 25. metatarsal IV distal condyle reduced; 26. posterior chevron L-shaped; 27. furcula (fused clavicles); 28. coracoid process posterior and fossa crescent-shaped; 29. iliac precoccygeal spine prominent; 30. ilial wing reduced; 31. ilial wing reduced; 32. ilial wing reduced; 33. ilial wing reduced; 34. ilial wing reduced; 35. ilial wing reduced; 36. ilial wing reduced; 37. radius less than 50% of humeral length; 38. man ual digit I ungual elongate (three times the height of proximal articular end). Allosauroidea (plus unresolved subgroups); 39. nasal participation in antorbital fossa; 40. excavated internal carotid artery canal; 41. basipterygoid process very short; 42. quadratojugal with broad articular flange for quadratojug al; 43. palatine with flange-shaped process for lacrimal; 44. basioccipital excluded from the basis tropica; 45. articular with pendant medial process; 46. quadratojugal short, head near mid-orbit; 47. angular twice maximum depth of angular (which equals a reduced external mandibular fenestra). Carcharodontosauridae (plus included node); 48. broad postorbital-lacrimal contact; 49. postorbital with suborbital flange; 50. dentary with squared, expanded anterior end; 51. pubic boc 30% of pubic length; 52. ventral extension of basioccipital; 53. midcervical centra (posterior articular facet) at least 50% broader than tall; 54. elevation of anterior face absent in midcaudal centra; 55. rudimentary caudal pleurocoels. Cleptosaurus (plus included node); 56. antorbital fossa anterior margin 40 to 50% of the anteroposterior width of fossa; 57. ectopterygoid pneumatic excavation subcircular; 58. caudal 15 and more posterior caudals with eorate prezygapophysal processes; 59. caudal end of postorbital process extends more than twice glenoid diameter; 60. ilial obturator flange triangular; 61. pubic obturator notch; 62. femoral fourth trochanter weak or absent; 63. fibular fossa occupying all of the masticial aspect of the proximal end.

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