The ascendency of dinosaurs on land near the close of the Triassic now appears to have been as accidental and opportunistic as their demise and replacement by therian mammals at the end of the Cretaceous. The dinosaurian radiation, launched by 1-meter-long bipeds, was slower in tempo and more restricted in adaptive scope than that of therian mammals. A notable exception was the evolution of birds from small-bodied predatory dinosaurs, which involved a dramatic decrease in body size. Recurring phylogenetic trends among dinosaurs include, to the contrary, increase in body size. There is no evidence for co-evolution between predators and prey or between herbivores and flowering plants. As the major land masses drifted apart, dinosaurian biogeography was molded more by regional extinction and intercontinental dispersal than by the breakup sequence of Pangaea.

The most important impact of this enriched perspective on dinosaurs may be its contribution to the study of large-scale evolutionary patterns. What triggers or drives major replacements in the history of life? How do novel and demanding functional capabilities, such as powered flight, first evolve? And how does the breakup of a supercontinent affect land-based life? The critical evidence resides in the fossil record—in the structure, timing, and geography of evolutionary radiations such as that of dinosaurs.

**Early Dinosaurs: Victims by Accident**

Did dinosaurs outcompete their rivals or simply take advantage of vacant ecological space? The ascendency of dinosaurs on land transpired after rapidly some 215 million years ago, before the close of the Triassic. Herbivorous prosauropods and carnivorous coelophysoid ceratosaurids spread across Pangaea, ushering in the “dinosaur era”: a 150-million-year interval when virtually all animals 1 m or more in length in dry land habitats were dinosaurs.

Dinosaurs, the descendants of a single common ancestor, first appeared at least 15 million years earlier but were limited in diversity and abundance (Fig. 1). Well-preserved skeletons discovered recently in 230-million-year-old rocks (mid-Carnian in age) give a glimpse of a land radiation already underway (12). The most fundamental adaptations for herbivory and carnivory among dinosaurs had already evolved. A novel means for slicing plant matter, utilizing inclined tooth-to-tooth wear facets, is fully developed in the meter-long herbivore *Pisanosaurus*, the oldest known ornithischian (Fig. 1, left; Fig. 2, node 1; Fig. 3A, feature 4). Jointed lower jaws and a grasping hyperextendable manus for subduing and eviscerating prey are present in the contemporary predators *Eoraptor* and *Herrerasaurus*, which are the oldest well-preserved theropods (Fig. 1, right; Fig. 2, node 2; Fig. 3B, features 11 and 12).
Fig. 1. Temporally calibrated phylogeny of Dinosauria, showing known temporal durations (solid bars), missing ranges (shaded bars), and ranges extended by fragmentary or undescribed specimens (dashed bars). At left is tabulated the number of recorded nonavian dinosaurian genera per stage and an estimated curve of generic diversity, taking into account available outcrop area (87). Basal or primitive taxa, in general, appear earlier in time than more derived members of a clade. Long missing ranges result from preservational bias against small body size (less than 2 m), which truncates the early record of many clades, and from intervals for which there is little corresponding exposed terrestrial rock (such as the Middle Jurassic). The shaded zone (bottom) indicates the initial stage of the dinosaurian radiation before their dominance of land faunas in taxonomic diversity and abundance.
Evidence, moreover, has implicated similar primary agents of extinction, namely global climatic change (seasonal aridity) (16) and, possibly, flood basalts associated with the opening of the Atlantic Ocean and extraterrestrial impacts (17).

Although the timing of end-Triassic extinctions remains less resolved than events at the end of the Cretaceous (18), dinosaurian and mammalian radiations cannot be explained as the result of niche subdivision, increased competition, or progressive specialization (escalation), or as taxonomic, taphonomic, or stochastic artefacts (19). These two great land radiations, the conventional signposts for the subdivision of Phanerozoic time, constitute opportunistic infilling of vacant ecospace after physical perturbation on a global scale.

**Ornithischians: Bird-Hipped Croppers**

Ornithischians processed plant matter by novel means. Vegetation was cropped by a horny bill and then sliced by tooth rows composed of expanded overlapping crowns with inclined wear facets (Fig. 3A, features 1 through 4). The predentary, a neomorphic bone, provided a stable platform for the lower bill while allowing the dentaries to rotate during (isognathus) occlusion (20). A holding space, or cheek, lateral to the tooth rows also suggests increased oral processing of plant matter (21).

Ornithischians were extremely rare during
the Late Triassic; their remains consist largely of isolated teeth. The first well-preserved ornithischian skeletons are Early Jurassic in age (20, 22), by which time the major clades of ornithischians were already established (Fig. 1). The small-bodied bipeds *Pisanosaurus* and *Lesothosaurus* constitute successive sister taxa to other ornithischians (Fig. 2, node 1). The “bird-hipped” configuration of the pelvic girdle (with the pubis rotated posteriorly) characterizes *Lesothosaurus* and later ornithischians (Fig. 3A, feature 9). Possibly before the end of the Triassic, the remaining ornithischians split into armored thyreophorans and unarmored neornithischians, which include ornithopods and margiinocephalians (Fig. 1; Fig. 2, nodes 3, 10, 11, and 19). This phylogenetic scheme is based on few characters, which may indicate that these early divergences occurred within a short interval of time.

Thyreophoran body armor was originally composed of parasagittal rows of keeled scutes as in *Scutellosaurus* (23), a small Early Jurassic thyreophoran from western North America. More advanced thyreophorans, such as *Emausaurus* (24) and *Scelidosaurus* (25) from the Lower Jurassic of Europe, appear to have reverted to a quadrupedal posture, as evidenced by hoof-shaped manual unguals. The larger bodied stegosaurs and ankylosaurs constitute the “broad-footed” thyreophorans (Eurypoda), named for the spreading (versus compact) arrangement of metatarsals in their elephantine hind feet (Fig. 1; Fig. 2, node 4).

The earliest and most primitive stegosaurs, such as *Huayangosaurus* from the Middle Jurassic of China (26, 27), have reduced the lateral osteoderm rows while elaborating the pair flanking the midline into erect plates (over the neck) that grade into pointed spines (over the tail) (Fig. 1; Fig. 2, nodes 5 and 6). Stegosaurus more advanced than *Huayangosaurus* have low narrow skulls and long hindlimbs as compared to their forelimbs (27, 28).

Ankylosaurs elaborated the dermal armor of the trunk in another direction, filling the spaces between scute rows with smaller ossicles to create a solid shield over the neck and trunk. Several skull openings are closed by surrounding cranial bones and accessory ossifications, as in the basal ankylosaur *Gargoyleosaurus*, discovered recently in Upper Jurassic rocks in western North America (29) (Fig. 2, node 9). Before the close of the Jurassic, ankylosaurs had split into two distinctive subgroups—nodosaurids and ankylosaurs—both of which diversified for the most part on northern continents during the Cretaceous (30, 31). The nodosaurid skull is proportionately low and held with the snout tipped downward. Cranial sutures completely fuse with maturity, as in the North American genera *Pawpawsaurus* and *Panoplosaurus* (32). In most ankylosaurs, the skull is very broad, and the snout is gently domed. The wedge-shaped osteoderms that project from the back corners of the ankylosaur skull are short in basal forms such as *Gastonia*, *Shamosaurus*, and *Mmim* (33) but form prominent plates in other ankylosaurs. A terminal tail club, composed largely of two pairs of wedge-shaped osteoderms, also distinguishes all known ankylosaurs.

Ornithopods split into three distinct clades during the Jurassic: heterodontosaurids, hypsilophodontids, and iguanodontians (Fig. 1; Fig. 2, nodes 11 through 13). Heterodontosaurids, named for their prominent lower canines, were small fleet-footed ornithopods that first appear in the Early Jurassic. Although undoubted herbivores, heterodontosaurids have elongate forelimbs with large grasping hands tipped with treacherous claws, as seen in the southern African genera *Heterodontosaurus* and *Abrictosaurus* (34).

Hypsilophodontids, the most conservative ornithopods, underwent little modification during their long fossil record from the Middle Jurassic to the end of the Cretaceous (35). As a consequence, their monophyly is less certain (30, 36). Iguanodontians, in contrast, underwent marked transformation during the Late Jurassic and Early Cretaceous, from basal forms such as *Muttonburrrasaurus* and *Tenontosaurus* to more derived genera such as *Dryosaurus*, *Camptosaurus*, *Probactrosaurus*, and *Iguanodon* (37) (Fig. 2, nodes 13 through 17; Fig. 3A, features 5, 6, and 8). Ornithopods achieved their greatest diversity in the Late Cretaceous with the radiation of duck-billed hadrosaurs (38).

Marginocephalians, a group characterized by a bony shelf on the posterior margin of the skull, are composed of two distinct subgroups: the thick-headed pachycephalosaurs (39, 40) and frilled ceratopsians (41, 42). Both clades are known exclusively from northern continents and primarily from the Upper Cretaceous of western North America and Asia (Fig. 1; Fig. 2, nodes 20 through 27). In all pachycephalosaurs, the skull roof is thickened and ornamented with lateral and posterior rows of tubercles. In primitive forms such as *Goyocephale*, the skull roof is flat with open supratemporal fenestrae. In more derived forms, the frontoparietal portion of the skull roof thickens further into a dome, which eventually incorporates all elements of the skull roof. The largest of these domed forms, *Pachycephalosaurus* and *Stygimoloch*, have swollen tubercles or horns projecting from the posterior corners of the skull (40) and constitute the only ornithischians to maintain an obligatory bipedal posture at large body size (more than 1 ton) (41). Some researchers have unified flat-headed pachycephalosaurs as a clade (43), but this condition is primitive, with some flat-headed genera being more closely related to domed forms (11, 30).

Psittacosaurids, the most primitive ceratopsians, are small-bodied parrot-beaked herbivores from Asia assigned to the single genus *Psittacosaurus*. As in all ceratopsians, the anterior margin of the psittacosaurid snout is capped by the rostral, a neomorphic bone sheathed by the upper bill. Although they show remarkably little skeletal variation, psittacosaurids persisted throughout most of the Early Cretaceous.

Remaining ceratopsians (neoceratopsians) also date back to the earliest Cretaceous of China and include *Chaoyangosaurus* and *Archaeoceratops* (42). *Archaeoceratops* and more derived neoceratopsians are distinguished by very large skulls relative to their postcranial skeletons and may have already reverted to a quadrupedal posture. In Late Cretaceous neoceratopsians, such as the abundant Asian form *Protoceratops*, the posterior margin of the skull extends postodorally as a thin shield pierced by a pair of fenestrae. Ceratopsids, a diverse subgroup of large-bodied neoceratopsians, were restricted to western North America, ranging from Mexico to the north slope of Alaska. Their many cranial and postcranial modifications include slicing dental batteries composed of stacked columns of two-rooted teeth and postorbital horns and frill processes of variable length and shape (41).

Sauropodomorphs: Long-Necked Titans

Sauropodomorphs constitute the second great radiation of dinosaurian herbivores. Although their origin is as ancient as that of ornithischians, their diversification followed a different time course (44, 45). As a group, sauropodomorphs are united by only a few characteristics, such as an enlarged narial opening and an unusual position for the longest pedal claw—on the first digit, or hallux, rather than the middle toe (Fig. 3C, features 21 and 29). Unlike ornithischians, there are no singleton genera at the base of the clade. By the Late Triassic, sauropodomorphs had already split into two distinctive groups: prosauropods and sauropods (Fig. 2, nodes 29, 30, and 34). Prosauropods diversified rapidly with only minor skeletal modification to become the dominant large-bodied herbivores on land from the Late Triassic through the Early Jurassic. Sauropods, in contrast, were rare in the Early Jurassic, when ornithischians appear to have undergone their major radiation, but diversified rapidly during the Middle Jurassic after prosauropods had gone extinct (Fig. 1). A succession of basal sauropods lies outside the main neosauropod radiation, which split during the Middle Jurassic into diplocodoids and macronarians, a clade composed of camarasaurs, brachiosaurids, and titanosaurs (Fig. 2, nodes 37 through 40). Neosauropods became the dominant large-bodied herbivores during the Middle and Late Jurassic and, on
southern continents, throughout the Cretaceous as well (44, 45).

Traditionally, prosauropods were viewed as an ancestral (paraphyletic) assemblage that gave rise to sauropods, a hypothesis with some appeal given the absence of any record of sauropods during the Triassic. Several unique features, however, unite all prosauropods, such as a twisted pollex (thumb) tipped
by a large claw that points inward (11, 46). *Riojaszaurus*, a Late Triassic prosauropod from South America, is one of only a few basal prosauropods that retain a short neck (47). Other contemporaneous prosauropods and younger genera from the Early Jurassic, such as *Massospondylus*, have proportionately longer cervical vertebrae, as does the well-known European genus *Plateosaurus* (47). Prosauropods were remarkably uniform in skeletal design despite their broad distribution across Pangaea. As a consequence, their interrelationships are poorly established.

The columnar posture of the limbs and the partial pronation of the forearm in the earliest known sauropods, *Vulcanodon* from southern Africa (48), suggest that moderate-sized early sauropods had already adopted an obligatory quadrupedal stance during locomotion (Fig. 3C, feature 22). *Shunosaurus* and *Omeisaurus*, from the Middle Jurassic of China, preserve the earliest complete sauropod skulls (49). The spatulate crowns show a regular pattern of V-shaped wear facets that is common among primitive sauropods. Regular wear facets are the product of precise tooth-to-tooth occlusion, a remarkable adaptation in animals that were continuously replacing their teeth (11, 44, 50). Mammals evolved sophisticated occlusal precision during this same interval but did so at the cost of nearly eliminating tooth replacement. Two notable features that evolved early in sauropod evolution include the retraction of the external nares to a position above the antorbital opening and the increase in the number of cervical vertebrae from 10 to at least 12 (Fig. 3C, features 21 and 23) (44).

Neosauropods and several genera that lie just outside this diverse radiation are easily recognized by the digitigrade (rather than plantigrade) posture of the manus, in which the ligament-bound metacarpals are arranged in a tight arc and oriented nearly vertically (Fig. 3C, feature 26). Within Neosauropoda, Diplodocoidae (Fig. 2, node 37) includes the highly modified diplodocids, which have retracted the external nares to a position above the orbits. The muzzle of the diplodocid skull is squared and lined with a reduced number of slender cylindrical crowns that are similar in form to those in derived titanosaurs (although truncated by high-angle wear facets rather than the near-vertical facets that characterize the narrow crowns of advanced titanosaurs) (50). North American representatives, such as *Diplodocus*, have particularly long necks and tails, the former composed of 15 elongate vertebrae and the latter composed of 80 vertebrae that taper to a whiplash end.

Other neosauropods include *Camarasaurus*, a basal genus with broad spatulate crowns and a relatively short neck; and brachiosaurids, a long-necked subgroup with proportionately long forelimbs (51). Titanosaurs, best known from Upper Cretaceous rocks in South America but present worldwide during the Cretaceous, are characterized by a particularly broad pectoral region and wide-gauge posture (8), stocky limbs that lack ossified carpal and phalanges, and a short tail composed of prococelous vertebrae (52). Titanosaur teeth are either weakly spatulate or cylindrical, and some advanced genera, such as *Saltasaurus*, have large scutes embedded in the skin over the trunk.

Sauropod phylogeny is marked by parallel evolution of narrow cylindrical crowns, bifid (forked) neural spines in the presacral column, and elongation of the cervical column (44, 45, 53). The traditional union of the narrow-crowned diplodocids and titanosaurs (54) has been abandoned in the face of recent cladistic analyses, based on a broad selection of characters and taxa, that unite brachiosaurids and titanosaurs (44, 45).

**Theropods: Bipedal Predators**

All theropods, including birds, are obligatory bipeds. Distinctive predatory adaptations arose in the earliest theropods, *Eoraptor* and *Herrerasaurus*. Foremost among these is the flexible lower jaw with a sliding joint midway along its length and an elongate hand reduced to three functional digits that are specialized for grasping and raking (Fig. 3B, features 11, 12, and 16) (12). These early predators constitute successive sister taxa to all later theropods, or neotheropods, which split into ceratosaurids and tetanurans before the close of the Triassic (Fig. 2, nodes 42, 43, and 46). During the Late Triassic and Early Jurassic, the great majority of theropods were ceratosaurids. By the Middle Jurassic, in contrast, tetanurans had diversified on all continents and had split into two major groups, the allosaurids and coelurosaurids, the latter giving rise to birds before the end of the Jurassic (11, 55–57) (Fig. 1).

*Eoraptor* (12), a 1-m-long cursorial biped, more closely approximates the common ancestor of dinosaurs than does any other taxon discovered to date. Its jaws and raptorial hands nevertheless exhibit modifications shared with other theropods (Fig. 2, node 41). *Herrerasaurus*, a medium-sized theropod (12), exhibits additional locomotor adaptations such as a balancing tail, the distal half of which is stiffened by overlapping vertebral processes (Fig. 3B, feature 19).

Although some question remains regarding their monophyly, ceratosaurids are united by features of the pelvic girdle and hindlimb, including some that are sexually dimorphic (58). Before the close of the Triassic, ceratosaurs split into two subgroups: the ceratosaurs, including *Eoraptor*, and coelophysoids (Fig. 2, nodes 43 through 45). First recorded in the Late Jurassic, ceratosaurids or “neoceratosaurs” include the Late Jurassic genera *Elaphrosaurus* and *Ceratosaurus*. The group persisted into the Cretaceous in Europe and on several southern continents (South America, India, and Madagascar), where they are represented by the unusual short-snouted, horned genera *Carnotaurus*, *Indosuchus*, and *Majungatholus* (58). Coelophysoids include the medium-sized *Dilophosaurus* and *Liliensternus*, as well as a diverse array of small-bodied predators (such as *Procompsognathus*, *Segisaurus*, and *Sternosuchus*) that are similar to the common North American genus *Coe- lophysis* (59).

Nearly all basal tetanurans are large-bodied, large-headed forms, formerly grouped together (with large-headed ceratosaurs and tyrannosaurids) as “carnosaurs.” Torvosaurids and the piscivorous crocodile-snouted spinosaurids appear to constitute an early side branch within Tetanurae (60). The oldest tetanuran, the crested allosaurid *Cryolophosaurus*, was discovered in Lower Jurassic rocks on Antarctica and is quite similar to allosaurids from Upper Jurassic rocks on several continents (61). During the Cretaceous, allosaurids reached body sizes rivaling those of the largest tyrannosaurids (57, 62). Many skeletal features characterize tetanurans, such as the peculiar semilunate wrist bone that constrains movement of the manus and the tall plate-shaped ascending process on the astragalus that immovably unites the shin bone and proximal tarsals (Fig. 3B, features 14 and 18). Further clarification of basal relationships within Tetanurae is anticipated, as genera such as *Afrovenator*, *Neovenator*, and others formerly referred to as “megalosauroids” are restudied.

Nonavian coelurosaurids include a diverse array of small-to-medium-sized predators, such as the ostrichlike ornithomimids, deep-snouted oviraptorosaurs, and sickle-toed deinonychosaurs (63). Coelurosaurids also include two clades, the therizinosaurids and tyrannosaurids, whose more derived members grew to very large body sizes (64). Coelurosaurids are characterized by an increase in the number of sacral vertebrae, a reduction in thigh retraction during locomotion, and an increased stiffening of the distal half of the tail—features that are further developed in birds.

Coelurosaurian interrelationships have remained controversial because of conflicting distributions for several salient features and differences in character data and analysis. Consensus has been reached that tyrannosaurids belong within Coelurosaurs (56), but opinions differ on the monophyly of most, or all, coelurosaurids that have an especially narrow middle metatarsal (the “artometatarsal” condition). Other major points of controversy include the position of therizinosaurids, the monophyly of Deinonychosauria (dromaeosaurids plus troodontids), the position of the feathered *Caudipteryx* among nonavians, and the interpretation of alvarez-
Evolutionary Tempo and Morphologic Scope

How does the land-based radiation of nonavian dinosaurs sketched above compare with its successor, the Cenozoic radiation of therian mammals? Several similarities make the comparison particularly enlightening: The most recent common ancestor for each radiation lay at the minimum end of the range in body size for the clade; that ancestor lived 15 million years or more before the clade’s domination of land habitats (79); each clade underwent significant taxonomic diversification before the clade’s domination of land habitats; and each clade rather suddenly inherited significant vacant ecospace in the aftermath of mass extinctions.

These similarities render the differences between these radiations all the more remarkable. The Cenozoic diversification of therian mammals was explosive: The rate of origination and standing diversity of species rose dramatically in the first few million years (80); the range of body size expanded by three orders of magnitude in the first few million years, approaching the maximum range attained within land mammals (81); substantial morphologic disparity quickly emerged, as two dozen distinctive adaptive designs (recognized as orders) appear in the fossil record within the first 15 million years (82); these adaptive designs included gliders, swimmers, burrowers, saltators, and cursors (excluding bats for fair comparison to nonavian dinosaurs) that invaded dry land, marshland, tropical, arboREAL, freshwater, and oceanic habitats.

The radiation of nonavian dinosaurs, by comparison, was sluggish and constrained: Taxonomic diversification took place at a snail’s pace (Fig. 1, left); standing diversity, which may have totaled 50 genera or less during the first 50 million years, increased

Table 1. Summary of cladistic analyses (76) that support the calibrated phylogeny of Dinosauria shown in Fig. 2. Characters and taxon/character-state matrices are available at www.sciencemag.org/feature/data/1041760.sht. Abbreviations: CI, consistency index; RI, retention index.

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<th>Number of minimum-length trees</th>
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Fig. 4. Major stages in the evolution of modern avian skeletal design and function. Many skeletal innovations of critical functional importance for flight arose for other purposes among early theropods, including (1) the hollowing of all long bones of the skeleton (Theropoda) and removal of pedal digit I from its role in weight support; (2) evolution of a rotary wrist joint to efficiently deploy a large grasping manus; (3) expansion of the coracoid and sternum for increased pectoral musculature and plumaceous feathers for insulation (89); (4) the presence of vaned feathers arranged as primaries, secondaries, and rectrices for display or brooding or both; (5) shortening of the trunk and increased stiffness of the distal tail for balance and maneuverability. Archaeopteryx remains a pivotal taxon, documenting (6) the acquisition of basic flight and perching function before the close of the Jurassic (laterally facing shoulder joint, split propulsion-lift wing with asymmetric feathers, and reversed hallux). Key refinements of powered flight and perching in later birds include (7) the deep thorax with strut-shaped coracoid and pygostyle; (8) the triosseal canal for the tendon of the principal wing rotator (the supracoracoideus muscle), alular feathers for control of airflow at slow speeds, rectriceal fan for maneuverability and braking during landing, and fully opposable hallux for advanced perching; and (9) the elastic furcula and deep sternal keel for massive aerobic pectoral musculature (90). Ornithothoracine birds diverged early as Enantiornithes ("opposite birds") (68, 77), which prevailed as the predominant avians during the Cretaceous, and Euornithes ("true birds"), which underwent an explosive radiation toward the close of the Cretaceous that gave rise to all living avians (Neornithes, or "new birds").
slowly during the Jurassic and Cretaceous, never reaching mammalian levels; maximum body size for herbivores and carnivores was achieved more than 50 million years after the dinosaurian radiation began (Fig. 1); only 8 to 10 distinctive adaptive designs emerged (recognized as suborders), and few of these would have been apparent after the first 15 million years of the dinosaur radiation (Fig. 1); adaptive designs that never evolved include gliders, burrowers, saltators, or taxa specifically adapted to marshland, arboreal, freshwater, or oceanic habitats (excluding birds for the purpose of comparison).

The dinosaurian radiation differs from that of Cenozoic therians in other ways that may have influenced tempo and adaptive scope: (i) during the basal radiation, Earth’s land surface was united as a supercontinent rather than subdivided into smaller land masses; (ii) the ancestor was a terrestrial biped rather than a terrestrial (or arboreal or fossorial) quadruped; and (iii) during basal divergences, body mass was greater by at least an order of magnitude. An undivided supercontinent is difficult to invoke as a significant constraint on taxonomic diversification or morphologic disparity in dinosaurs, given that all of the major dinosaurian subgroups had diverged before the onset of significant breakup in the earliest Cretaceous (Figs. 1 and 5A). Bipedal posture cannot be invoked as an evolutionary constraint, because early avians with this posture rapidly invaded arboreal, freshwater, and marine habitats before the close of the Cretaceous.

Greater body mass and its ecological, physiological, and life-history correlates, however, may well have played a major role in shaping the dinosaurian radiation. Larger body size in mammals is correlated with lower standing diversity, greater species longev-

**Fig. 5.** Dinosaurian paleobiogeography. (A) Temporally calibrated area-gram showing the breakup of Pangaea into 10 major land areas by the end of the Cretaceous. Checkered bars indicate high-latitude connections that may have persisted into the Late Cretaceous. Five paleogeographic reconstructions (91) divide continental areas (outlines) into dry land (black) and shallow (epieric) seas (unshaded). (B) Continent-level vicariance hypothesis for the carcharodontosaurs Acrocanthosaurus, Gigantor- tosaurus, and Carcharodontosaurus, which lived on North America, South America, and Africa, respectively, approximately 90 to 110 Ma. (C) Polar dispersal across Beringia (double-headed arrow) must be invoked to explain the geographic distribution of ceratopsians and other dinosaurian subgroups during the Late Cretaceous. Checkered branches show dispersal from Asia to North America in three lineages, which is one of two equally parsimonious dispersal scenarios for ceratopsians (given this cladogram and an Asian origin for Ceratopsia). Globe shows Maastrich-
ity, and greater habitat specificity (83), which may account for the slower rate of taxonomic diversification and more restricted range of morphologic disparity among nonavian dinosaurs. In these regards, avians more closely resemble therian mammals.

Evolutionary Trends and Coevolution

Recurring phylogenetic trends among dinosaurs include incorporation of osteoderms in the skull, narial enlargement and retraction, reduction and loss of teeth, increase in neck length and number of cervicalis, increase in the number of sacrals, miniaturization of the forelimb, reduction and loss of external digits in the manus, and posterior rotation of the pubis.

Judging from the body size and trophic adaptations of dinosaurian outgroups, the ancestral dinosaur was a bipedal carnivore closely resembling the 1-m-long early theropod Eoraptor. Anagenetic trends (84) toward substantially greater body mass occurred within six clades, four of which assumed facultative or obligatory quadrupedal posture (Thyreophora, Ornithopoda, Ceratopsia, and Sauropoda) (11). For dinosaurs as a whole, these trends are acceotive (84), with upper values being attained in different clades at different times during the Jurassic and Cretaceous.

The only sustained trend toward decreased body mass occurred during the evolution of birds. The ancestral neotetanuran was probably a predator the size of Allosaurus, weighing 3 to 5 tons (Fig. 4, node 2). Basal maniraptorans are considerably smaller (20 to 100 kg); crow-sized basal avians such as Archaeopteryx and Concodiusornis are smaller than any mature non-avian dinosaur; and sparrow-to-starling–sized birds. The ancestral neotetanuran was probably an extraordinary case study for the evolution of the Late Triassic and Jurassic gave way to highly differentiated faunas during the Cretaceous. Fossil differentiation is governed by three processes: vicariance and regional extinction enhancement, faunal differentiation, and dispersal reduces it (11).

Vicariance, or the splitting of lineages in response to geographic partitioning, is a plausible hypothesis when a three-taxon cladogram matches an areagam established independently on the basis of geologic evidence (Fig. 5A). Carcharodontosaur predators from three continents, for example, show a pattern of relationships that mirrors the breakup sequence of Pangaea (Fig. 5B). The breakup events, in addition, predate the predators, which come from rocks of mid- to Late Cretaceous age [Albian to Cenomanian, 110 to 90 million years ago (Ma)]. Continent-level fragmentation of Pangaea thus could have generated this phylogenetic pattern, assuming that primitive carcharodontosaurs were broadly distributed before the breakup. Vicariance at this scale, however, does not appear to have been a major factor in the differentiation of Cretaceous dinosaurs, both because phylogenetic patterns among taxa of Cretaceous age are not consistent with the areagam and because the age of relevant taxa often predates the relevant breakup event (11).

Regional extinction, or the disappearance from one or more geographic regions of a taxon whose former presence is clearly demonstrated by fossils, seems to have played a major role in the marked differentiation of Late Cretaceous dinosaurian faunas. Ceratosaur and allosaurid predators, for example, were present on both northern and southern continents during the Jurassic and Early Cretaceous, but by the Late Cretaceous were replaced in North America and Asia by large-bodied coelurosaurs (tyran saurosaurids). Similarly, titanosaurian herbivores were present on northern and southern continents during the Early Cretaceous. During the Late Cretaceous, titanosaurs were almost completely replaced as large-bodied herbivores in North America and Asia by hadrosaurids.

Dispersal, or the crossing of geographic barriers, reduces faunal differentiation that might arise in response to geographic isolation. Intercontinental dispersal during the Cretaceous is best documented between western North America and Asia. A polar dispersal route between these land areas allowed periodic bidirectional exchange, as evidenced by the phylogenetic relationships of clades with representatives on both land areas (Fig. 5C). Dispersal between northern and southern continents across the Tethyan Sea also occurred during the Cretaceous, as shown by phylogenetic patterns in spinosaurid predators and hadrosaurids (86). Intercontinental dispersal clearly contributed to biogeographic patterns during the latter half of the Mesozoic.

Future discoveries are certain to yield an increasingly precise view of the history of dinosaurs and the major factors influencing their evolution.

References and Notes
