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REVIEW

The Evolution of Dinosaurs

Paul C. Sereno

The ascendancy 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.

During the past 30 years, intensified paleontological exploration has doubled recorded dinosaurian diversity (*1*) and extended their geographic range into polar regions (*2*). Exceptional fossil preservation has revealed eggshell microstructure (*3*), nesting patterns and brooding posture among predators (*4*), and epidermal structures such as downy filaments and feathers (*5*, *6*). Analysis of bone microstructure and isotopic composition has shed light on embryonic and posthatching growth patterns and thermophysiology (*7*). Footprint and track sites have yielded new clues regarding posture (*8*), locomotion (*9*), and herding among large-bodied herbivores (*10*). And the main lines of dinosaurian descent have been charted, placing the aforementioned discoveries in phylogenetic context (*11*).

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: Victors by Accident

Did dinosaurs outcompete their rivals or simply take advantage of vacant ecological space? The ascendancy of dinosaurs on land transpired rather rapidly some 215 million years ago, before the close of the Triassic. Herbivorous prosauropods and carnivorous coelophysoid ceratosaurs 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) provide 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 41; Fig. 3B, features 11 and 12).

Traditional scenarios for the ascendancy of dinosaurs that invoke competitive advantage (*13*) have difficulty accommodating the substantial temporal gap (15 million years or more) between the initial radiation of dinosaurs and their subsequent global dominance during the latest Triassic and Early Jurassic (*14*). Opportunistic replacement of a diverse array of terrestrial tetrapods (nonmammalian synapsids, basal archosaurs, and rhynchosaurs) by dinosaurs is now the most plausible hypothesis (*11*, *14*, *15*). This pattern is broadly similar to the replacement of nonavian dinosaurs by therian mammals at the end of the Cretaceous. Recent

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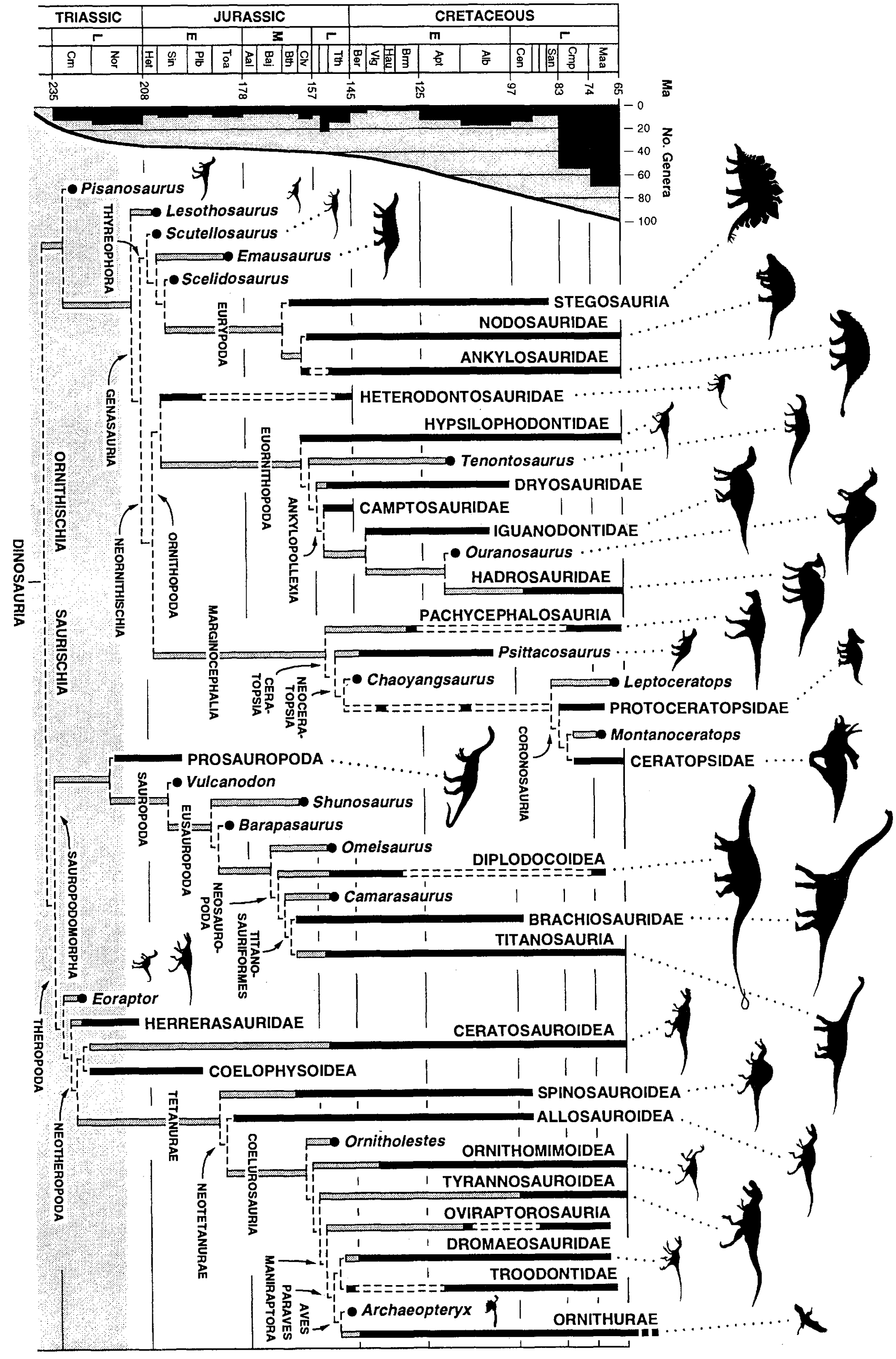

Fig. 1. Temporally calibrated phylogeny of Dinosauria, showing known temporal durations (solid bars), missing ranges (shaded bars), and ranges extended by fragmentary or undescribed specimens (dashed bars). At left is tabulated the number of recorded nonavian dinosaurian genera per stage and an estimated curve of generic diversity, taking in to 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

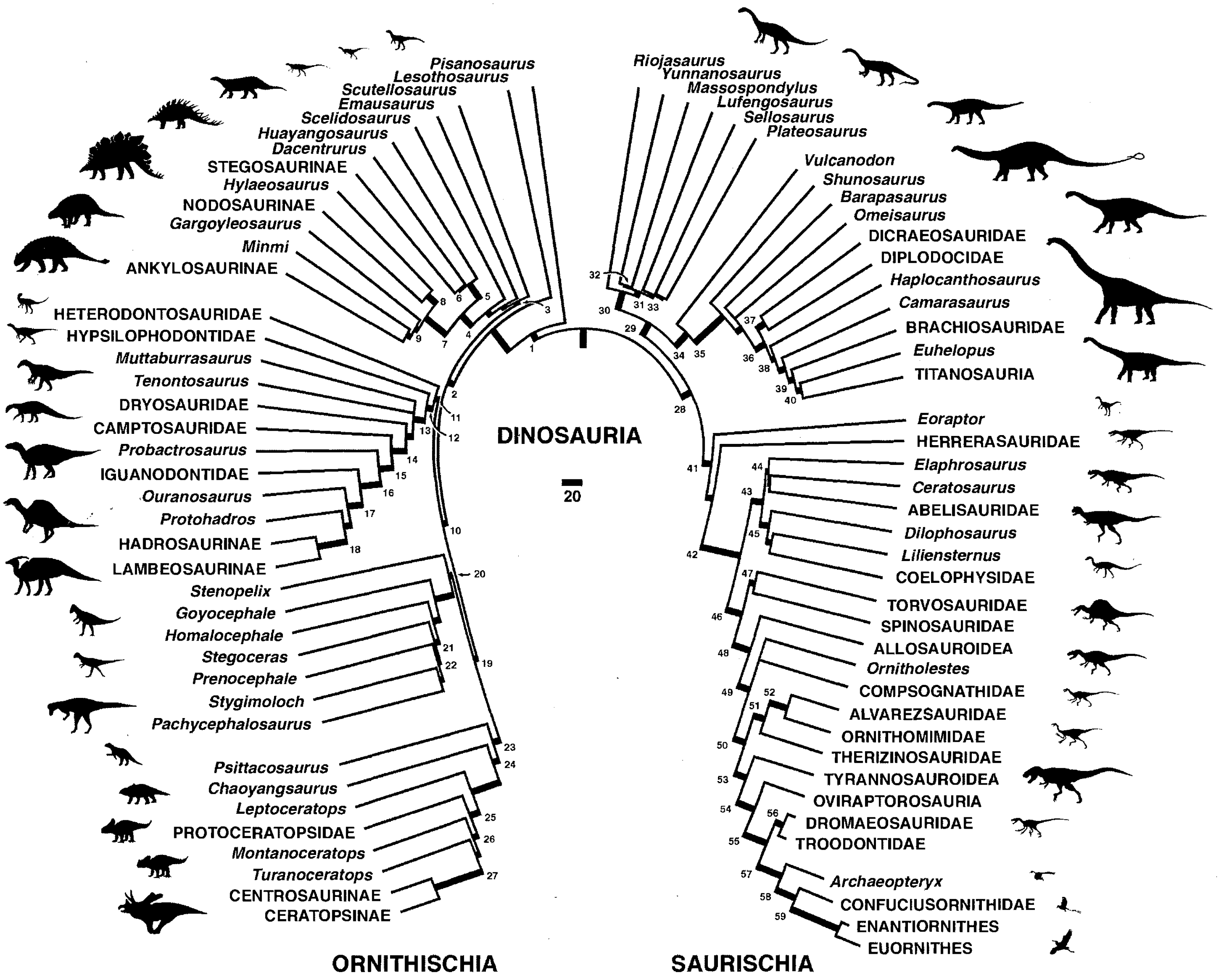

Fig. 2. Phylogeny of Dinosauria, showing the relationships among ornithischians (left) and saurischians (right). Thickened internal branches are scaled to reflect the number of supporting synapomorphies (scale bar equals 20 synapomorphies). Phylogenetic structure and internal branch lengths are based on minimum-length trees from maximum-parsimony analyses of approximately 1100 characters under delayed character-state optimization (Table 1). The evolution of hadrosaurids within Ornithopoda (nodes 11 through 18) and birds within Tetanurae (nodes 46 through 57) provide the best examples of sustained skeletal transformation. Numbered nodes are listed here, with normal and bold text indicating stem- and node-based taxa, respectively (*88*): 1, Ornithischia; 2, **Genasauria**; 3, Thyreophora; 4, **Eurypoda**; 5, Stegosauria; 6, Stegosauridae; 7, Ankylosauria; 8, Nodosauridae; 9, Ankylosauridae; 10, Neornithischia; 11, **Ornithopoda**; 12, Euornithopoda; 13, Iguanodontia; 14, **Ankylopollexia**; 15, Styracosterna; 16, **Hadrosauriformes**; 17, Hadrosauroidea; 18, **Hadrosauridae**; 19, **Marginocephalia**; 20, Pachycephalosauria; 21, **Pachycephalosauridae**; 22, Pachycephalosaurinae; 23, Ceratopsia; 24, Neoceratopsia; 25, **Coronosauria**; 26, Ceratopsoidea; 27, **Ceratopsidae**; 28, Saurischia; 29, **Sauropodmorpha**; 30, Prosauropoda; 31, **Plateosauria**; 32, Massospondylidae; 33, Plateosauridae; 34, Sauropoda; 35, Eusauropoda; 36, **Neosauropoda**; 37, Diplodocoidea; 38, Macronaria; 39, **Titanosauriformes**; 40, Somphospondyli; 41, Theropoda; 42, **Neotheropoda**; 43, Ceratosauria; 44, Ceratosauroidea; 45, Coelophysoidea; 46, Tetanurae; 47, **Spinosauroidea**; 48, **Neotetanurae**; 49, Coelurosauria; 50, **Maniraptoriformes**, 51, Ornithomimosauria; 52, Ornithomimoidea; 53, Tyrannoraptora; 54, **Maniraptora**; 55, Paraves; 56, **Deinonychosauria**; 57, **Aves**; 58, Ornithurae; 59, **Ornithothoraces**.

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 marginocephalians (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). Stegosaurs 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 ankylosaurid *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 ankylosaurids—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 ankylosaurids, the skull is very broad, and the snout is gently domed. The wedge-shaped osteoderms that project from the back corners of the ankylosaurid skull are short in basal forms such as *Gastonia*, *Shamosaurus*, and *Minmi* (*33*) but form prominent plates in other ankylosaurids. A terminal tail club, composed largely of two pairs of wedge-shaped osteoderms, also distinguishes all known ankylosaurids.

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 trenchant 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 *Muttaburrasaurus* 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 hadrosaurids (*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) (*11*). Some researchers have united 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 *Chaoyangsaurus* 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 posterodorsally 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 diplodocoids and macronarians, a clade composed of camarasaurids, 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

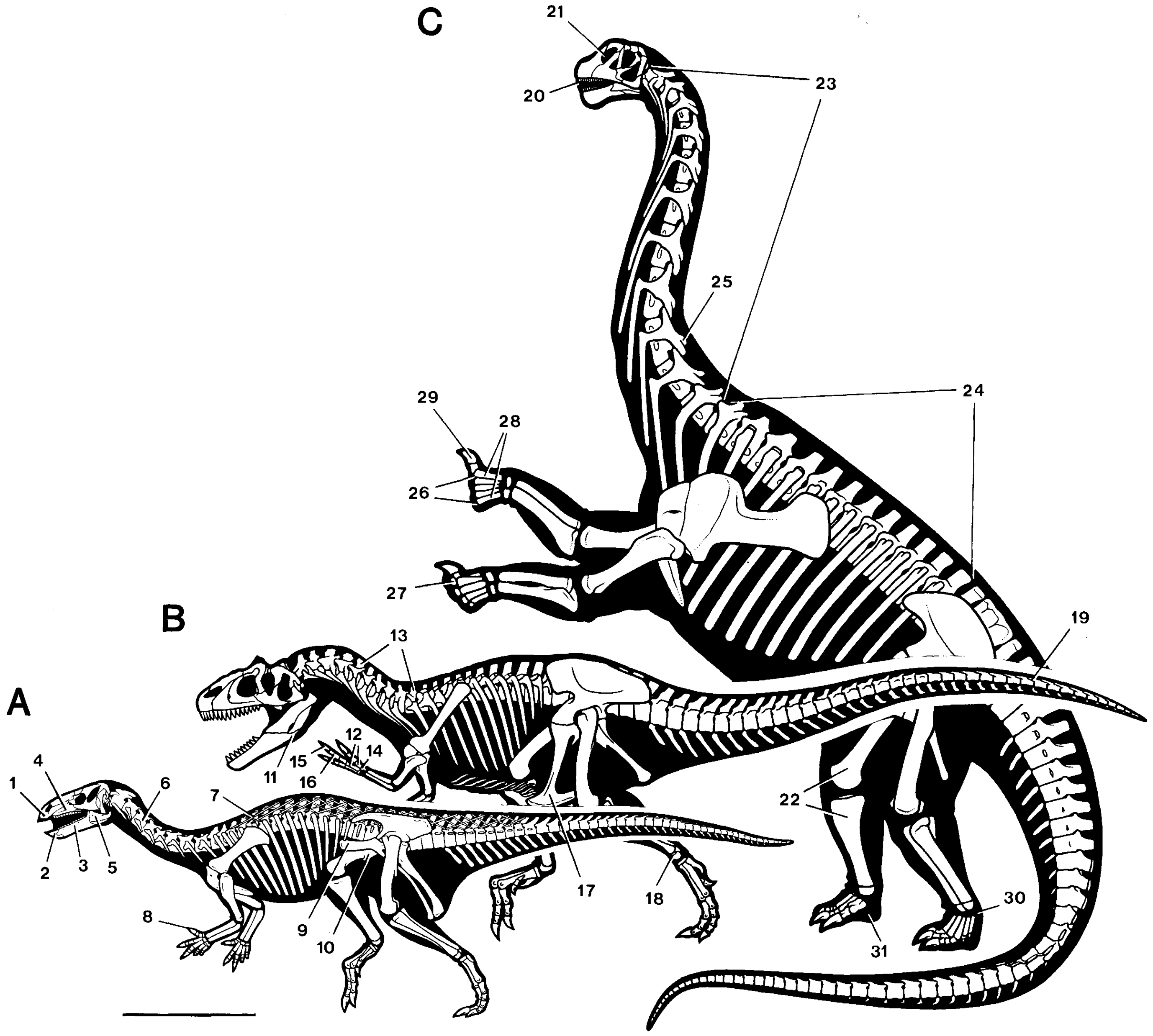

Fig. 3. Skeletal innovation in the three major clades of dinosaurs (Ornithischia, Theropoda, and Sauropodomorpha) as shown by contemporaneous species from the Upper Jurassic (Kimmeridgian) Morrison Formation of North America. Labeled features evolved at various nodes as described in the text. Scale bar, 1 m. (**A**) *Camptosaurus dispar*, an ornithischian. (**B**) *Allosaurus fragilis*, a theropod. (**C**) *Camarasaurus lentus*, a sauropodomorph [after (*44*)]. Skeletal innovations are as follows: **1**, horny beak for cropping; **2**, predentary bone for lower bill support; **3**, cheek depression for oral processing of plant matter; **4**, leaf-shaped crowns with wear facets and asymmetrical enamel for shearing plant matter; **5**, coronoid process for attachment of robust jaw-closing muscles; **6**, opisthocoelous cervicals with reduced neural spines for flexibility; **7**, ossified tendons to stiffen trunk; **8**, rigid digit I with subconical ungual for defense; **9**, pubis with prepubic process and posteroventrally directed postpubic process opening posterior trunk; **10**, pendant fourth trochanter for enhanced caudal hindlimb retractors; **11**, intramandibular joint for flexible bite; **12**, metacarpal extensor depressions for manual raking; **13**, hollow skeleton to reduce bone weight; **14**, semilunate carpal simplifying wrist action to maneuver large hands; **15**, manual digit II longest, emphasizing inner digits; **16**, long penultimate phalanges enhancing grasping capability; **17**, pubic foot for body support at rest; **18**, astragalar ascending process uniting tibia and tarsus; **19**, elongate prezygapophyses unite distal tail forming a dynamic stabilizer; **20**, crowns with regular V-shaped wear facets indicate precise occlusion for slicing vegetation; **21**, nares enlarged and retracted; **22**, columnar limb posture for weight support at large body size; **23**, 12 or more opisthocoelous cervical vertebrae composing a longer neck; **24**, 11 or fewer dorsal vertebrae shortening the trunk; **25**, bifurcate neural spines accommodating a robust median elastic ligament; **26**, arched ligament-bound metacarpus for digitigrade manual posture; **27**, manual/pedal phalanges reduced in number for a more fleshy foot pad; **28**, manual digits I and V weight-bearing to broaden support; **29**, manual digit I ungual enlarged possibly for intraspecific rivalry; **30**, distal tarsals unossified increasing shock-absorbing cartilage in joints; **31**, elephantine pes for weight support at large body size.

by a large claw that points inward (*11*, *46*). *Riojasaurus*, 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 sauropod, *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, Diplodocoidea (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 carpals and phalanges, and a short tail composed of procoelous 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 diplodocoids 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 are 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 ceratosaurs 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 ceratosaurs. By the Middle Jurassic, in contrast, tetanurans had diversified on all continents and had split into two major groups, the allosauroids and coelurosaurs, 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, ceratosaurs 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 ceratosauroids and coelophysoids (Fig. 2, nodes 43 through 45). First recorded in the Late Jurassic, ceratosauroids (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 *Syntarsus*) that are similar to the common North American genus *Coelophysis* (*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 allosauroid *Cryolophosaurus*, was discovered in Lower Jurassic rocks on Antarctica and is quite similar to allosauroids from Upper Jurassic rocks on several continents (*61*). During the Cretaceous, allosauroids 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 "megalosaurids" are restudied.

Nonavian coelurosaurs include a diverse array of small-to-medium-sized predators, such as the ostrichlike ornithomimids, deep-snouted oviraptorosaurs, and sickle-toed deinonychosaurs (*63*). Coelurosaurs also include two clades, the therizinosaurids and tyrannosauroids, whose more derived members grew to very large body sizes (*64*). Coelurosaurs 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 Coelurosauria (*56*), but opinions differ on the monophyly of most, or all, coelurosaurs that have an especially narrow middle metatarsal (the "arctometatarsalian" 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 alvarezsaurids (*65*) as avians.

The phylogeny shown here (Fig. 2, nodes 49 through 57; Table 1) supports and extends the conclusions of an early cladistic survey (*55*). Except for a few basal genera, coelurosaurs are divided into ornithomimosaurs and tyrannoraptorans, the former including alvarezsaurids and, with less support, therizinosaurids (Fig. 2, nodes 51 and 52). Tyrannoraptorans, in turn, diversified as tyrannosauroids, oviraptorosaurs, deinonychosaurs, and birds (*63*). *Caudipteryx* is interpreted here as a basal oviraptorosaur rather than an immediate avian outgroup (*6*). Deinonychosauria, the monophyly of which is here maintained (Fig. 2, node 56), and birds are united by many synapomorphies, including a powerful sickle-clawed digit in the pes. This eviscerating digit, first described in *Deinonychus*, is present but considerably muted in *Archaeopteryx* and the basal ornithurine *Confuciusornis* (66) and is well developed in *Rahonavis* (*67*), a close relative of *Archaeopteryx*.

Evolution of Feathers, Perching, and Flight

For use in understanding the evolution of vertebrate flight, the early record of pterosaurs and bats is disappointing: Their most primitive representatives are fully transformed as capable fliers. The early avian record, in contrast, provides the rare opportunity to tease apart the sequence of modifications that led to powered flight and its early refinement (Fig. 4).

In the past decade, spectacular fossil discoveries in lacustrine rocks in northern China and central Spain (*5*, *6*, *66*, *68*) and in fluvial rocks elsewhere (*67*, *69*) have provided critical new evidence for the evolution of avian flight and perching and the origin of feather structure and arrangement. Cladistic analyses of character data (*55–57*, *65*, *68*, *69*) (Table 1) have endorsed Ostrom's hypothesis (*70*) that birds are specialized coelurosaurs, a conclusion also supported by egg size, eggshell microstructure, and nesting patterns (*3*, *4*). There is no longer any morphological "gap" in skeletal data: The number of changes at Aves (Fig. 2, node 57) is fewer than occur at more basal nodes within Theropoda or at nodes within Aves. Flagging opposition to the understanding of birds as coelurosaurian descendants (*71*) has yet to take form as a testable phylogenetic hypothesis (*72*).

Cooptation of structures that originally evolved for another purpose (*73*) has played a larger role than was previously thought in early avian evolution. Features formerly understood as strictly avian, such as vaned feathers and their tandem arrangement on the manus and forearm as primaries and secondaries, are now known among flightless nonavian coelurosaurs (Fig. 4, node 4) (*6*). In the oviraptorosaur *Caudipteryx* (*6*), for example, the short symmetrical primaries and secondaries clearly had no flight function, and the rectrices at the distal end of its bony tail are better suited for display than for any aerodynamic function. Given the absence of basic flight-related features in its skeleton (such as a laterally facing glenoid), there is no evidence of flight function in the ancestry of *Caudipteryx*. Vaned feathers and their arrangement as primaries, secondaries, and rectrices therefore must have originally evolved for other functions (such as thermoregulation, brooding, or display). Other features formerly associated only with birds are now known to have arisen deeper in theropod phylogeny, such as a down-like body covering (*5*, *74*), a broad plate-shaped sternum, ossified sternal ribs and uncinate processes (Fig. 4, nodes 3 through 5), and substantial enlargement of the forebrain (*75*).

The refinement of flight capability and maneuverability and the evolution of a fully opposable digit for perching proceeded rapidly once primitive avians were airborne (Fig. 4, node 6). Within 10 million years after the appearance of *Archaeopteryx*, body size shrank to that of a sparrow, well below the size range of nonavian coelurosaurs (Fig. 4, node 8). Modifications during this interval had a major impact on flight and perching performance, such as the evolution of alular feathers on the first digit of the manus, a fully opposable hallux in the pes, and a fused pygostyle at the end of the tail (Fig. 4, nodes 7 and 8). The crow-sized basal ornithurine *Confuciusornis* (*66*), known from thousands of specimens from earliest Cretaceous sites in northern China, is destined to become the best-known basal avian. Slightly younger sparrow-sized birds, such as *Sinornis* (*68*), *Concornis*, and *Iberomesornis* (*76*), document the enantiornithine radiation that dominated avifaunas for the remainder of the Cretaceous (*77*).

Controversy surrounds two taxa that were initially proposed as avians more advanced than *Archaeopteryx*: *Protoavis* (*78*) and the alvarezsaurids (*65*). *Protoavis* is widely regarded as a composite of several nonavian species, and the short-armed flightless alvarezsaurids, such as *Mononykus* and *Shuvuuia*, have been interpreted alternatively as the sister group to ornithomimids (Fig. 2, node 52).

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.shl. Abbreviations: CI, consistency index; RI, retention index.

Analysis	Number of terminal taxa	Number of characters	Number of minimum-length trees	CI, RI
Basal Dinosaria	15	146	1	0.81, 0.89
Thyreophora	19	119	27	0.87, 0.94
Ornithopoda	14	149	1	0.94, 0.97
Marginocephalia	19	155	1	0.90, 0.96
Prosauropoda	11	32	6	0.97, 0.98
Sauropoda	13	116	1	0.80, 0.86
Ceratosauria	13	60	1	0.91, 0.94
Tetanurae	20	220	3	0.85, 0.86
Basal Aves	6	100	1	0.97, 0.98

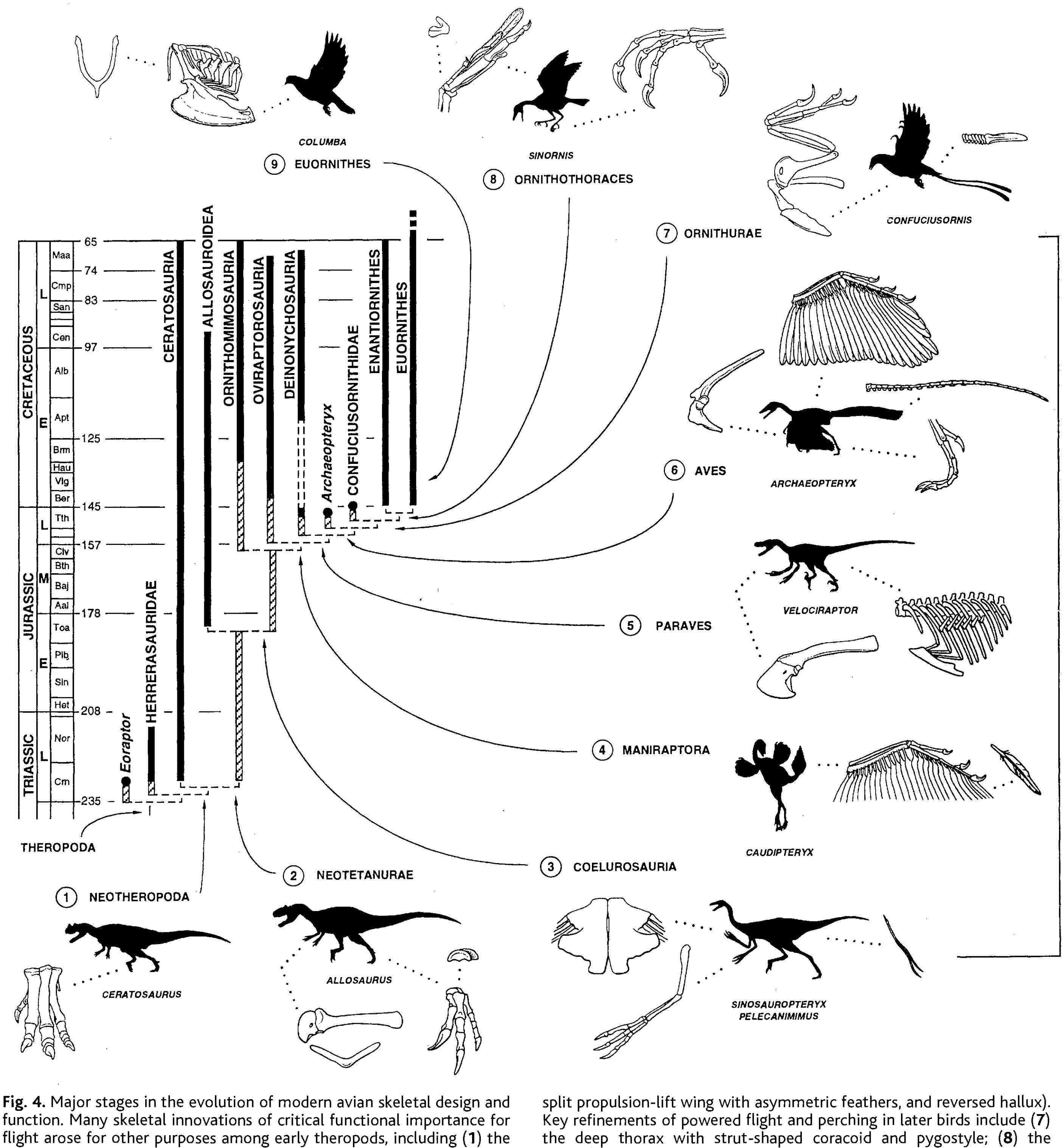

Fig. 4. Major stages in the evolution of modern avian skeletal design and function. Many skeletal innovations of critical functional importance for flight arose for other purposes among early theropods, including (**1**) the hollowing of all long bones of the skeleton (Theropoda) and removal of pedal 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 plumulaceous 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-

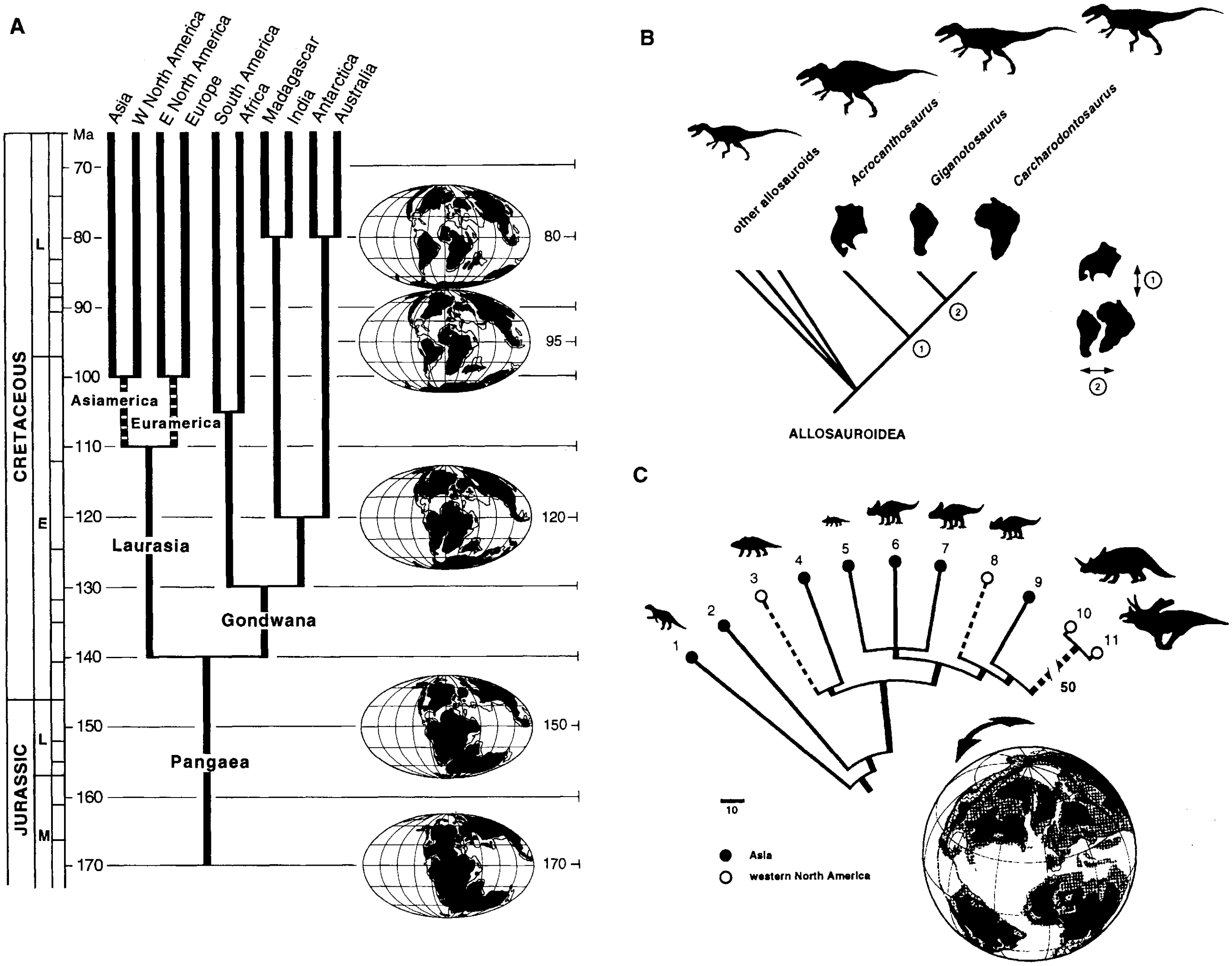

Fig. 5. Dinosaurian paleobiogeography. (**A**) Temporally calibrated areagram showing the breakup of Pangaea into 10 major land areas by the end of the Cretaceous. Checkered bars indicate high-latitude connections that may have persisted into the Late Cretaceous. Five paleogeographic reconstructions (*91*) divide continental areas (outlines) into dry land (black) and shallow (epieric) seas (unshaded). (**B**) Continent-level vicariance hypothesis for the carcharodontosaurids *Acrocanthosaurus*, *Giganotosaurus*, 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 Maastrichtian (70 Ma) paleogeography divided into orogenic belts (inverted Vs), lowlands (black), and shallow and deep seas (gray and white, respectively). Internal branch lengths of the cladogram are scaled according to the number of supporting synapomorphies under delayed character-state transformation. Scale bar indicates 10 synapomorphies (with the long ceratopsid branch shortened). 1, *Psittacosaurus*; 2, *Chaoyangsaurus*; 3, *Leptoceratops*; 4, *Udanoceratops*; 5, *Microceratops*; 6, *Bagaceratops*; 7, *Protoceratops*; 8, *Montanoceratops*; 9, *Turanoceratops*; 10, Chasmosaurinae; 11, Ceratopsinae.

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 cervicals, 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 accretive (*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 *Confuciusornis* are smaller than any mature nonavian dinosaur; and sparrow-to-starling–sized ornithothoracines mark the bottom of the trend, which certainly played a key role in the evolution of avian perching and powered flight (Fig. 4, nodes 5 through 8).

The study of limb proportions in dinosaurian herbivores and contemporary predators, as in mammalian ungulates and their predators, suggests that pursuit predation was not a major influence in the evolution of locomotor capabilities (*85*); large dinosaurian herbivores are most often graviportal irrespective of the locomotor capability of contemporary predators. Study of the dentitions of dinosaurian herbivores during the angiosperm radiation of the Late Cretaceous likewise does not reveal any clear co-evolutionary pattern (*11*).

Dinosaurs and Drifting Continents

The breakup of the supercontinent Pangaea provides an extraordinary case study for the operation of large-scale biogeographic processes. Before the close of the Jurassic, rifting opened the Tethyan Sea between the northern and southern land masses Laurasia and Gondwana. Further breakup occurred during the Cretaceous, with the opening of the Atlantic Ocean and the spread of shallow seas on the continental margins. Subdivision of the once continuous land surface of the supercontinent can be represented by a calibrated areagram (Fig. 5A).

The fossil record shows that the relatively uniform dinosaurian faunas of the Late Triassic and Jurassic gave way to highly differentiated faunas during the Cretaceous. Faunal differentiation is governed by three processes: vicariance and regional extinction enhance 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 areagram established independently on the basis of geologic evidence (Fig. 5A). Carcharodontosaurid 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 carcharodontosaurids 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 areagram 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. Ceratosauroid and allosauroid 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 (tyrannosauroids). 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.

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