THE ORIGIN AND EVOLUTION OF DINOSAURS

Paul C. Sereno

Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois 60637; e-mail: dinosaur@uchicago.edu

ABSTRACT

Phylogenetic studies and new fossil evidence have yielded fundamental insights into the pattern and timing of dinosaur evolution and the emergence of functionally modern birds. The dinosaurian radiation began in the Middle Triassic, significantly predating the global dominance of dinosaurs by the end of the period. The phylogenetic history of ornithischian and saurischian dinosaurs reveals evolutionary trends such as increasing body size. Adaptations to herbivory in dinosaurs were not tightly correlated with marked floral replacements. Dinosaurian biogeography during the era of continental breakup principally involved dispersal and regional extinction.

INTRODUCTION

After publication of seminal papers by Ostrom (1974, 1975, 1976a) and Bakker & Galton (1974) 20 years ago, it has become widely recognized that all dinosaurs evolved from a single common ancestor with birds as living descendants. Since then, modern phylogenetic research and new fossil evidence have yielded fundamental insights into the pattern and timing of dinosaurian evolution and the emergence of functionally modern birds.

Broad-scale application of cladistic methodology resulted in the first encompassing phylogenies for the two major clades of dinosaurs, Saurischia (Gauthier 1986) and Ornithischia (Sereno 1986). Smaller scale analyses followed along with the first comprehensive review of dinosaurian subgroups (Weishampel et al 1990) and compilation of dinosaurian literature and taxonomy (Chure & McIntosh 1989).

The quickening pace of field work over the last 20 years has brought to light a wealth of new fossil evidence, nearly doubling known dinosaurian diversity

435

(Dodson & Dawson 1991). Discoveries include complete skeletons of the earliest dinosaurs (Sereno & Novas 1992, Sereno et al 1993), well-preserved skeletons of Cretaceous dinosaurs on southern continents (Bonaparte et al 1990, Salgado & Bonaparte 1991, Powell 1992, Jacobs et al 1993, Sereno et al 1994, 1996, Coria & Salgado 1995), and exquisitely preserved skeletons of Cretaceous dinosaurs from central Asia (Russell & Dong 1993, Novacek et al 1994, Currie 1996).

Several aspects of dinosaurian paleobiology have been settled decisively. Tracksites (Ostrom 1972a, Thulborn & Wade 1984, Currie 1983) and monospecific bonebeds (Currie & Dodson 1984, Coombs 1990) have provided convincing evidence of gregarious behavior among large-bodied herbivores; embryos inside eggs have clarified the identity of several egg forms (Horner & Currie 1994, Norell et al 1994); and adult skeletons crouched over egg nests have provided evidence of brooding in theropods (Norell et al 1995, Dong & Currie 1996, Varricchio et al 1997). Controversy persists regarding parental care (Horner 1982, Geist & Jones 1996), growth rates, and physiology. Cross-age bone histology (Chinsamy 1990, Varricchio 1993) has substantiated other lines of evidence (Farlow 1993) that point toward fast growth rates and intermediate physiologies for most dinosaurs (Chinsamy 1994, Farlow 1990).

Remarkable discoveries of primitive birds from Cretaceous deposits in Asia (Sereno & Rao 1992, Zhou 1995, Hou et al 1995), Spain (Sanz & Bonaparte 1992), Argentina (Alvarenga & Bonaparte 1992, Chiappe & Calvo 1994), and Madagascar (Sampson et al 1996), as well as technological breakthroughs allowing intimate observation of flight performance in living birds (Jenkins et al 1988, Gatesy & Dial 1996a,b), have provided a new framework to understand the evolution of avian flight.

DINOSAURIAN ORIGINS

When did dinosaurs first appear? What did they look like? And for what reasons and at what pace did they become the dominant large-bodied land animals? Much of the fossil evidence relevant to these questions has come from a sequence of beds in northwestern Argentina that span the Middle and Late Triassic (Stipanicic 1983).

A Bipedal Radiation

Small slender-limbed bipedal archosaurs—the first vertebrates in the fossil record with a habitual bipedal posture—were discovered amidst a diverse fauna of larger crurotarsal archosaurs and basal synapsids in the Middle Triassic Chañares Formation in northwestern Argentina (Romer 1973), deposited between 235 and 240 million years ago. Just over one-half meter in length, *Marasuchus* and the functionally didactyl *Lagerpeton* were fleet-footed cursors

or saltators (Romer 1971, 1972, Bonaparte 1975, Sereno & Arcucci 1993, 1994). They share with dinosaurs a hinge-like ankle joint and a strong central triad of digits in the pes (foot), which demonstrate unequivocally that the dinosaurian radiation was rooted among small bipeds. All large-bodied dinosaurian quadrupeds, as a consequence, must have reverted to a four-legged posture.

Pterosaurs, the first vertebrate powered fliers, also have a hinge-like ankle joint and appear to have evolved from bipeds during the Middle Triassic (Gauthier 1986, Sereno 1991a). The evolutionary coincidence of bipedalism and powered flight suggests a potential functional connection, namely that the advent of bipedality may have released the forelimb from terrestrial locomotor constraints, which allowed its modification in other directions (Sereno 1991a).

Victors by Accident?

Explanations for major floral or faunal transitions, such as the rise of dinosaurs, are nearly always couched in competitive or opportunistic scenarios (Benton 1983), although neither are logically exclusive or necessarily distinguishable millions of years after the fact. Did dinosaurs out-compete their rivals (Charig 1984) or simply take advantage of vacant ecological space (Benton 1988)? Competitive scenarios invoke superior design; opportunistic scenarios argue that no such correlation exists. To the limited extent that such questions are testable by evidence from the fossil record, two questions must be answered: When and how suddenly did dinosaurian predators and herbivores dominate land faunas in terms of taxonomic diversity and abundance? And when did the most fundamental dinosaurian adaptations for carnivorousness and herbivory first appear? A classic competitive scenario predicts that dinosaurs would gradually dominate once their principal adaptations for carnivorousness and herbivory had evolved—a wedge-out, wedge-in model of faunal change.

The best record of the rise of dinosaurs comes from the Ischigualasto Formation in northwestern Argentina, which has yielded a Late Triassic (Carnian) vertebrate fauna dominated by rhynchosaurs, crurotarsal archosaurs, and gomphodont cynodonts (Bonaparte 1982, Rogers et al 1993). Nearly all dinosaur remains belong to the medium-sized predator *Herrerasaurus* (Reig 1963), initially regarded as the outgroup to other dinosaurs (Gauthier 1986, Benton 1990) but currently understood as a basal theropod (Sereno & Novas 1992, 1993, Novas 1993, Sereno 1993). Other dinosaurs are limited to well-preserved skeletons of a 1-m–long basal theropod, *Eoraptor* (Sereno et al 1993, 1998), and fragmentary jaws and limb bones of a primitive ornithischian, *Pisanosaurus* (Bonaparte 1976, Sereno 1991b).

By 230 million years ago, two of the three major clades of dinosaurs, Theropoda and Ornithischia, were recorded as fossils, and the third

(Sauropodomorpha) has been inferred to have existed by the presence of its sister group (Theropoda). The initial dinosaurian radiation, therefore, must have taken place prior to deposition of the Ischigualasto beds, probably during the Middle Triassic. Furthermore, dinosaurs did not predominate in abundance worldwide until late in the Triassic (Norian), some 215 million years ago, when prosauropods and coelophysoid ceratosaurs became the most common herbivores and predators, respectively. Ornithischians remained extremely rare until the Early Jurassic, about 200 million years ago. Thus for an initial period of at least 15 million years and probably significantly longer, dinosaurs were limited in diversity and abundance (Olsen & Sues 1986, Benton 1988).

Basic dinosaurian adaptations for predation and herbivory, in contrast, are already in place in the earliest known dinosaurs. Tooth-to-tooth wear facets, regarded by some as the key innovation behind ornithischian diversity during the Jurassic and Cretaceous (Norman & Weishampel 1985), are fully developed in *Pisanosaurus*. Similarly, classic predatory adaptations among theropods, such as the flexible joint in the lower jaw and the raking manus, are present in *Eoraptor* and *Herrerasaurus*. The substantial delay between the appearance of fundamental dinosaurian trophic adaptations and dinosaurian ascendancy toward the end of the Triassic is difficult to reconcile with a classic scenario of competitive advantage. We may never reliably determine the predominant causal agent(s) triggering the ascendancy of dinosaurs, but an opportunistic replacement, broadly similar to the mammalian replacement of nonavian dinosaurs at the end of the Cretaceous, is more consistent with current understanding of the fossil record.

DINOSAURIAN DIVERSITY

The following outline of dinosaurian systematics and morphology is based on the phylogenetic relationships and age of 69 of the most significant genera and subgroups (Figures 1–4). Taxa are defined phylogenetically as either node- or stem-based groups (de Queiroz & Gauthier 1992, 1994; Table 1). These two kinds of phylogenetic definitions are most stable when implemented in combination, specifically when a node-based taxon is composed of two stem-based taxa. This definitional configuration, here termed a node-stem triplet, maximizes taxonomic stability and effectively maintains historically significant names in the face of new taxa or phylogenetic rearrangements. Nested node-stem triplets form the backbone of the higher-level classification used in this paper (Table 1). Dinosauria, for example, is defined as a node-based group composed of two stem-based groups, Ornithischia and Saurischia. Defined in this manner, Dinosauria will always be composed of Ornithischia and Saurischia regardless of future phylogenetic rearrangements among basal dinosaurs or the discovery of additional taxa (PC Sereno, unpublished data).
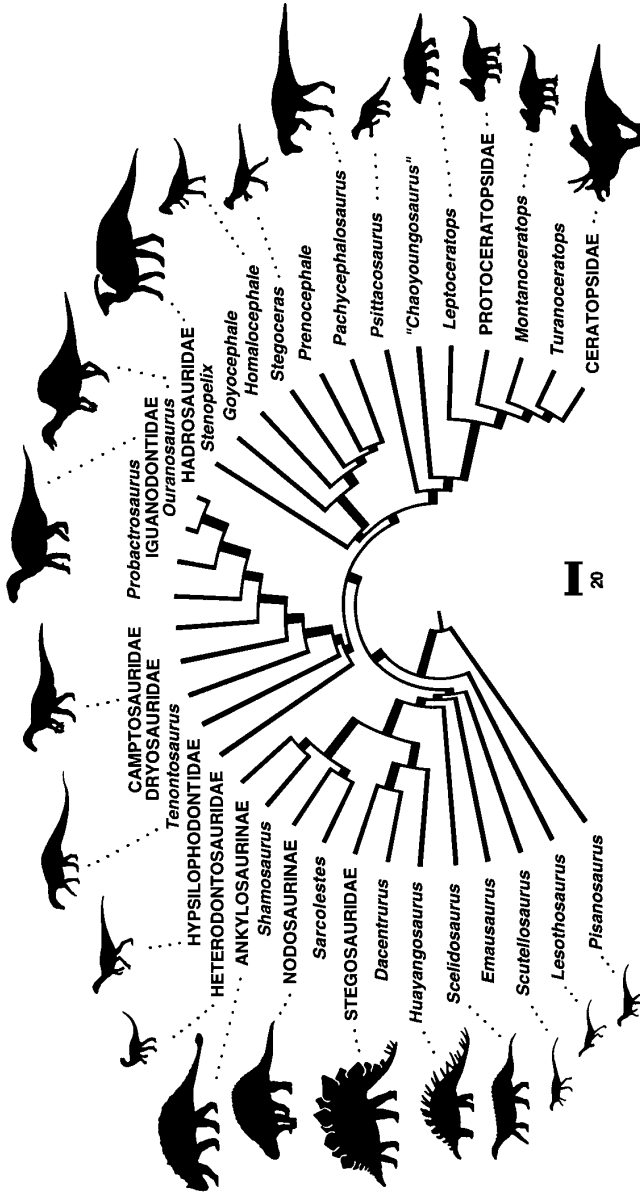
Figure 1 Phylogeny of Ornithischia, showing the relationships among 34 principal genera and subgroups. The cladogram is based on minimum-length trees from maximum parsimony analyses (Swofford 1993) of more than 300 characters, with internal branch lengths scaled according to the number of synapomorphies under delayed character-state optimization.

Figure 2 Calibrated phylogeny of Ornithischia (corresponding with Figure 1), showing known temporal ranges (*solid bar*), missing ranges (*cross-hatched*), and missing ancestral lineages (*cross-hatched*). Dashed temporal ranges are established on undescribed or fragmentary material.

Figure 3 Phylogeny of Saurischia, showing the relationships among 35 principal genera and subgroups. The cladogram is based on minimum-length trees from maximum parsimony analyses (Swofford 1993) of more than 400 characters, with internal branch lengths scaled according to the number of synapomorphies under delayed character-state optimization. Sauropod data based on Wilson & Sereno (1997).
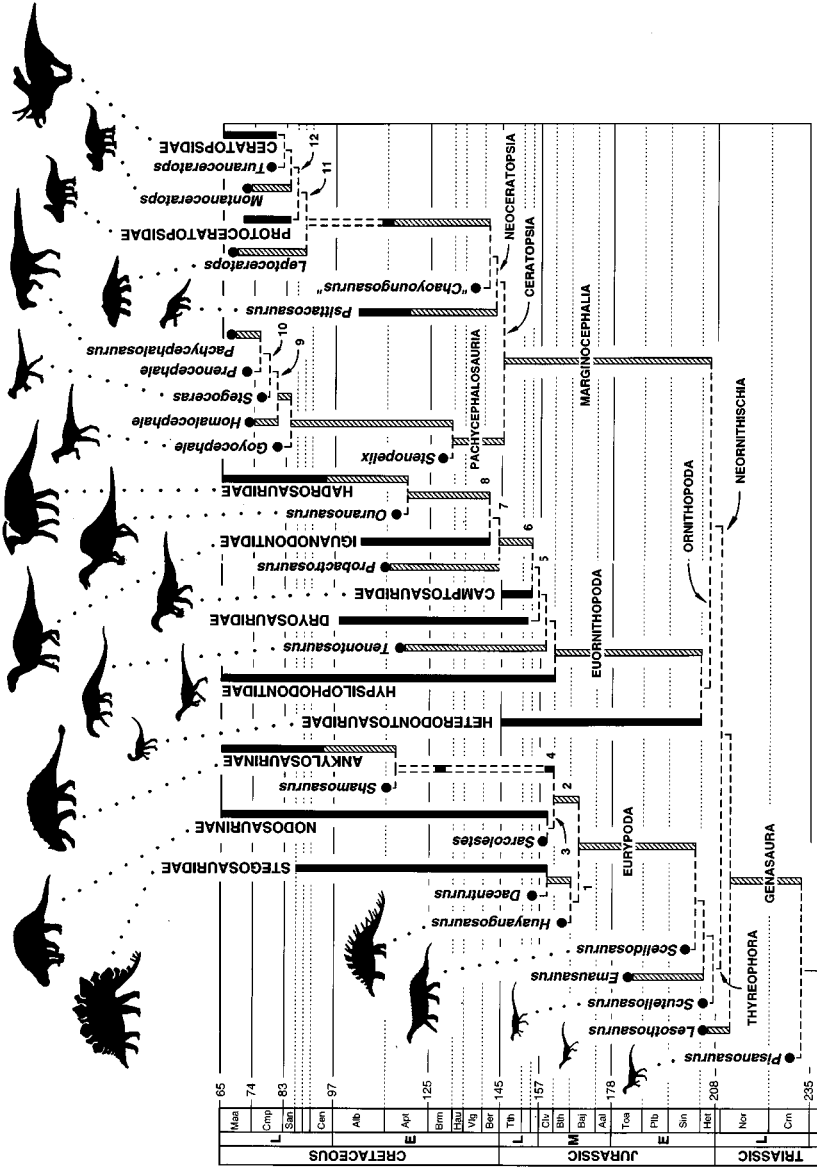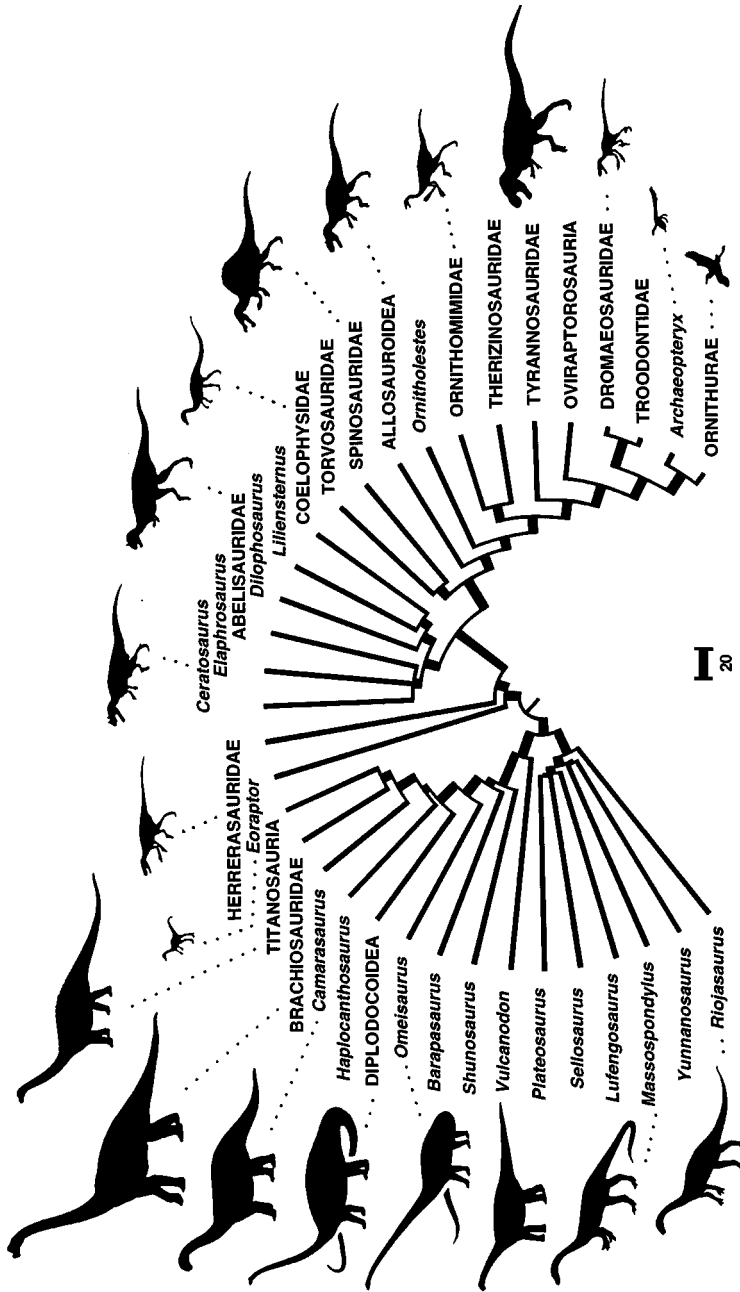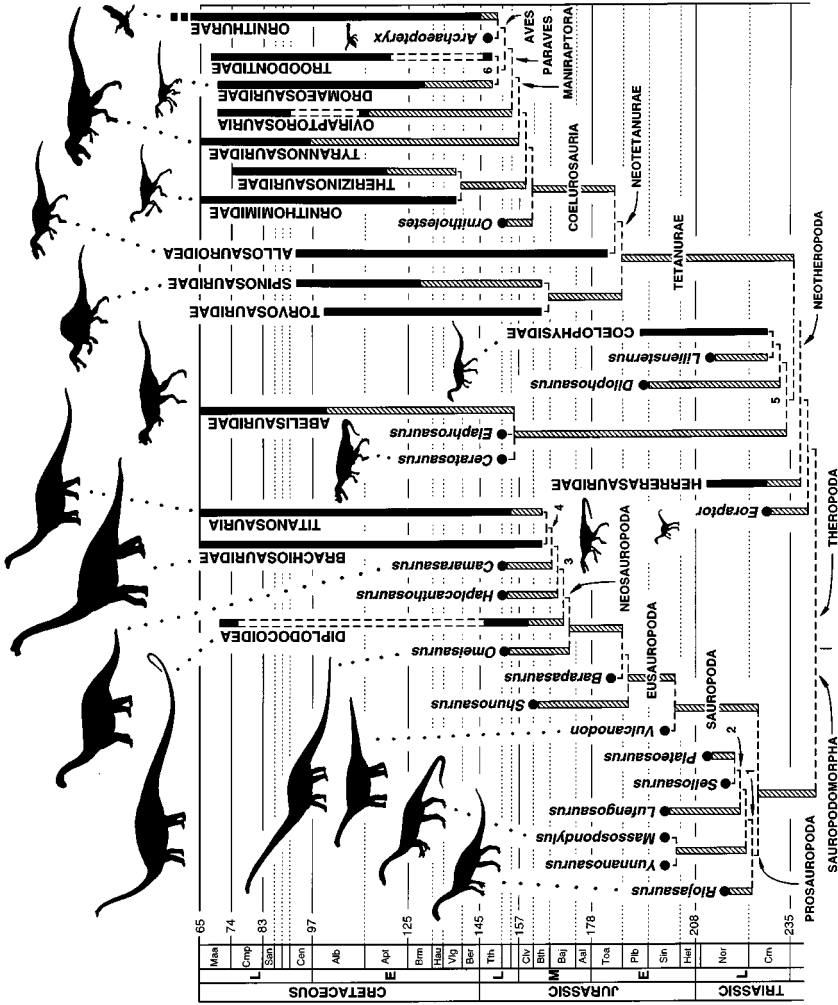
Figure 4 Calibrated phylogeny of Saurischia (corresponding with Figure 3), showing known temporal ranges (*solid bar*), missing ranges (*cross-hatched*), and missing ancestral lineages (*cross-hatched*). Dashed temporal ranges are established on undescribed or fragmentary material.

Table 1   Unranked higher-level classification of Dinosauria based on nested node-stem triplets[a]

Dinosauria (+230)[b]
  Ornithischia (+230)

    Genasauria (+210)
     Thyreophora (+210)

      Eurypoda (+165)
       Stegosauria (+165)
        Stegosauridae (+160)
         Stegosaurinae (+160)
       Ankylosauria (+165)
        Ankylosauridae (+95)
         Ankylosaurinae (+95)
        Nodosauridae (+160)
         Nodosaurinae (+110)
     Neornithischia (+200)

      Ornithopoda (+200)
       Heterodontosauridae (+200)
       Euornithopoda
        Hypsilophodontidae (+160)
        Iguanodontia
         Ankylopollexia (+155)
          Camptosauridae (+155)
          Styracosterna

           Hadrosauriformes (+140)
            Iguanodontidae (+140)
            Hadrosauroidea

             Hadrosauridae (+95)
              Hadrosaurinae (+85)
              Lambeosaurinae

     Marginocephalia (+210)
      Pachycephalosauria (+140)

       Pachycephalosauridae (+80)
        Stegoceras (+80)
        Pachycephalosaurinae
      Ceratopsia (+140)
       Neoceratopsia (+140)

        Coronosauria (+90)
         Protoceratopsidae (+90)
         Ceratopsoidea

          Ceratopsidae (+80)
           Centrosaurinae (+80)
           Chasmosaurinae

(*Continued*)

Table 1   (*Continued*)

Saurischia (+230)
  Sauropodomorpha (+230)
    Prosauropoda (+225)
      Plateosauria (+225)
        Plateosauridae (+215)
    Sauropoda (+225)
      Eusauropoda (+165)
        Neosauropoda (+165)
          Diplodocoidea (+165)
          Macronaria[c]
            Titanomorpha (+165)
              Brachiosauridae (+165)
              Titanosauria
  Theropoda (+230)
    Neotheropoda (+225)
      Ceratosauria (+225)
      Tetanurae
        Neotetanurae (+190)
          Allosauroidea (+190)
          Coelurosauria
            Maniraptora (+150)
              Oviraptorosauria (+150)
              Paraves[d]
                Deinonychosauria (+150)
                  Troodontidae (+150)
                  Dromaeosauridae
                Aves (+150)
                  Archaeopteryx (+150)
                  Ornithurae

[a]Boldface indicates node-based taxa; regular type indicates stem-based taxa. Node-stem triplets occur when a node-based taxon is composed of two stem-based subordinate taxa.
[b]Approximate minimum age of divergence (in millions of years) is given for node-based groups, for which it records the oldest ingroup, and for stem-based groups, for which it records either the oldest ingroup or the oldest member of its sister taxon (whichever is older). Node-stem triplets, therefore, typically have the same estimate for minimum age of divergence, and subordinate groups will have an equal or younger minimum age of divergence. (+, older than.)
[c]New taxon.
[d]Wilson & Sereno 1997.

Dinosauria

Loss of the postfrontal bone (also lost in crocodylomorphs) is the most notable cranial synapomorphy (shared-derived feature) common to all dinosaurs (Sereno & Novas 1992). Postcranial synapomorphies include ossified sternal plates, three sacral vertebrae (one dorsal vertebra incorporated), a functionally tridactyl manus (reduction of digit IV), and a distinct dorsally directed process on

the astragalus (ascending process). Most of these involve changes in the limb bones, the functional significance of which remains largely unknown.

Ornithischia

The ornithischian skull and dentition underwent strong modification as an adaptation to an herbivorous diet. Ornithischian teeth are characterized by expanded crowns, marginal denticles, and wear facets born of tooth-to-tooth occlusion. The low subtriangular crowns of the earliest ornithischians exhibit this form and wear, which suggests that increased oral processing of plant material was a fundamental early ornithischian adaptation. Maxillary and dentary teeth, furthermore, are almost always inset medially, which creates a lateral holding, or "cheek," space for plant matter, and the jaw-closing adductor musculature inserts directly on the dentary (to the coronoid process).

The earliest well-preserved ornithischian skeletons are Early Jurassic in age, by which time it is clear that the major clades of ornithischians were already established (Figure 2). *Lesothosaurus*, a small cursorial biped, appears to be the sister taxon to other ornithischians, which are divided into armored thyreophorans and unarmored neornithischians (=Cerapoda; Sereno 1986). Neornithischians, in turn, branched early into ornithopods and marginocephalians. Early Jurassic thyreophorans (e.g. *Scutellosaurus, Emausaurus, Scelidosaurus*) do not depart far from the hypothetical ancestral lineage. Early Jurassic ornithopods, in contrast, consist entirely of a specialized subgroup of small-bodied forms: the fanged, long-limbed heterodontosaurids. Marginocephalians have the poorest early fossil record, of which the oldest representative dates back only to the Early Cretaceous (Figure 2).

In the traditional (precladistic) view of ornithischian descent, a central line of primitive ornithopods consisting of "fabrosaurids" and hypsilophodontids gave rise to all other ornithischian subgroups (Romer 1968, Thulborn 1971, Galton 1972). *Lesothosaurus* and hypsilophodontids, indeed, are among the most conservative of ornithischians. In cladistic perspective, nevertheless, *Lesothosaurus* is not ancestral to other ornithischians, and "fabrosaurids" constitute an artificial assemblage of early ornithischians, most of which are known only from isolated teeth (Sereno 1991b). Hypsilophodontids, likewise, are linked specifically with higher ornithopods (Iguanodontia) rather than with an assortment of ornithischian subgroups (Figure 1).

PISANOSAURUS AND *LESOTHOSAURUS*   Ornithischia, as the name indicates, was coined for the birdlike pelvic girdle, in which a rod-shaped pubis is rotated posteroventrally in line with the ischium. In *Pisanosaurus*, however, just enough of the pelvic girdle is preserved to suggest that posteroventral rotation may not characterize the earliest and most basal ornithischian (Sereno 1991b). The distal tibia and ascending process of the astragalus in

Pisanosaurus, likewise, are not compressed anteroposteriorly as in other or-nithischians (Novas 1989, Sereno 1991b). Little else is known about the earliest phase of ornithischian evolution during the Late Triassic.

By the Early Jurassic, the most basal form, *Lesothosaurus*, exhibits a broad range of ornithischian adaptations. The ornithischian cranium, which always has a very reduced antorbital opening, broad proportions, and a bill-covered snout, is in general less flexible (kinetic) than in most saurischians. The lower jaws, in contrast, join anteriorly in a mobile symphysis, which is capped by a neomorphic bill-covered bone (the predentary). The predentary provides a stable platform for the lower bill while permitting the dentary bones to rotate slightly about their long axes during bilateral occlusion (Crompton & Attridge 1986, Sereno 1991b). In this way, ornithischians evolved a bill-covered snout for cropping vegetation while maintaining the flexibility about the midline re-quired to produce high-angle, bilateral (isognathus), tooth-to-tooth wear facets. This fundamental mechanical role of the predentary, which appears to have been operative in the earliest ornithischians, has yet to be recognized as an or-nithischian adaptation (e.g. Weishampel 1984, Norman & Weishampel 1985).

The postcranial skeleton in *Lesothosaurus* (Thulborn 1972, Santa Luca 1984, Sereno 1991b) and more advanced ornithischians is characterized by marked transformation of the pubic bone, which is reduced to a slender posteroventrally directed rod that contacts the ischium at its distal end. In *Lesothosaurus* and all other ornithischians except stegosaurs, intertwined ossified tendons are present along the sides of the neural spines, which stiffen the trunk and anterior tail.

THYREOPHORA   Epidermal body armor is the most striking feature of thyreop-horans and consists initially of rows of low, keeled scutes. *Scutellosaurus*, the most primitive known thyreophoran, has several parasagittal rows of asymmet-rical scutes (Colbert 1981). The skull and postcranial skeleton in this Early Jurassic thyreophoran are little modified from that in *Lesothosaurus*. Its long tail and presumed facultative bipedal posture distinguish *Scutellosaurus* from all later thyreophorans.

Two Early Jurassic thyreophorans from Europe, *Emausaurus* and *Sceli-dosaurus*, form successive sister taxa to Eurypoda, or "broad-footed" thyreop-horans, a clade that consists of stegosaurs and ankylosaurs (Figures 1, 2). They reveal important information regarding the early evolution of thyreophorans. *Emausaurus*, a relatively small-bodied thyreophoran, has a broad subtriangu-lar palpebral bone firmly sutured to the orbital margin (Haubold 1990). The palpebral, usually rod-shaped and articulating in the upper corner of the orbit in most ornithischians, is fully incorporated into the skull roof in the larger-bodied thyreophoran *Scelidosaurus* (Owen 1861). The few preserved postcra-nial bones of *Emausaurus* suggest that it was an obligate quadruped, with

metacarpals subequal in length and hoof-shaped unguals, as in all more advanced thyreophorans. The armor consists of a combination of scutes similar to those in ankylosaurs and plates similar to, though shorter than, those in stegosaurs. *Scelidosaurus* exhibits several additional cranial features that link it with stegosaurs and ankylosaurs, such as the deep median keel on the palate. Thus, prior to the eurypod radiation during the Middle and Late Jurassic, early evolution within Thyreophora involved the incorporation of the palpebral in the skull roof, the assumption of an obligate quadrupedal posture with short metapodials and hoof-shaped unguals, and the differentiation of body armor.

Stegosaurs and ankylosaurs, although quite dissimilar in overall appearance, share many unusual features in the skull and skeleton. In the skull, two additional elements are added to the upper margin of the orbit. In the skeleton, the long preacetabular process of the ilium is deflected anterolaterally. The pes is very broad with a spreading, rather than compact, arrangement of the metatarsals, which is a unique condition among ornithischians. In these characteristics and others, *Scelidosaurus* is distinctly plesiomorphic and must be positioned outside Eurypoda.

Stegosaurs are easily recognized by the prominent row of parasagittal osteoderms that grade from short plates anteriorly to longer spines posteriorly. Another unusual dermal ossification, present in many stegosaurs, is a conical spine attached at a low angle to a plate-shaped base. Originally thought to reside over the pelvic girdle, the spine has been found in articulation over the shoulder girdle and has been termed the parascapular spine (Sereno & Dong 1992). Its absence in *Stegosaurus*, the most familiar stegosaur, constitutes a reversal. The dorsal vertebrae in stegosaurs are particularly diagnostic. Their neural arches appear as though they have been stretched dorsally and are devoid of ossified tendons, an exception among ornithischians. *Huayangosaurus*, from the Middle Jurassic of China, is the oldest and most primitive stegosaur, retaining premaxillary teeth and at least one lateral row of trunk scutes (Zhou 1984, Sereno & Dong 1992). Other stegosaurs show increasing disparity between fore and hind limbs, such that the humerus is less than two thirds the length of the femur (Dong et al 1983, Dong 1990, Galton 1990, Sereno & Dong 1992).

Ankylosaurs are easily recognized by their extensive body armor, which includes two rows of large plates that arch over the cervical region and a mosaic of smaller scutes that surround these plates and cover the trunk. The low ankylosaur skull lacks antorbital or supratemporal fenestrae and is extensively coossified. Early in their evolution, ankylosaurs split into two very distinct subgroups, nodosaurids and ankylosaurids (Coombs 1978, Sereno 1986, Coombs & Maryańska 1990). Nodosaurids are characterized by three cervical plate rows (rather than two) and an occipital condyle that deflects the skull anteroventrally at about 50° from the horizontal. Ankylosaurids are easily recognized by the

wedge-shaped dermal ossifications that adorn the back corners of the skull, the interlocking processes of the caudal vertebrae and chevrons, and the large terminal tail club. A patchwork of osteoderms sheath the front of the ankylosaurid skull and help to form a complex sinus system that occupies much of the domed snout (Coombs 1978, Coombs & Maryanska 1990).

ORNITHOPODA   Ornithopods fall into one of three distinct clades—Heterodontosauridae, Hypsilophodontidae, and Iguanodontia. The latter two are weakly joined as Euornithopoda (sensu Weishampel 1990a), based on the presence of an obturator process on the ischium and a few other characters (Sereno 1986, Weishampel & Heinrich 1992).

Heterodontosaurids are very small ornithopods (body lengths ≤1 m) known primarily from the Early Jurassic of southern Africa (Santa Luca 1980, Weishampel & Witmer 1990). A very small Early Jurassic heterodontosaurid has been discovered in western North America (Museum of Comparative Zoology, Harvard University; unpublished material), and *Echinodon* from the Late Jurassic of England also appears to be a heterodontosaurid, although formerly regarded as a "fabrosaurid" (Galton 1978) or thyreophoran (Coombs et al 1990). Heterodontosaurids are named for their heterodont dentition, which includes a short upper (premaxillary) canine and a longer lower (dentary) canine fitted to an arched diastema between the premaxilla and maxilla. Except for *Abrictosaurus*, all heterodontosaurids including *Echinodon* exhibit these dental features. In addition, the predentary is wedge-shaped and only loosely fitted to the convex ends of the dentaries. The gracile skeleton in heterodontosaurids has the elongate hind limb proportions of a cursor. The forelimbs are also unusually long in all heterodontosaurids in which they are preserved (contrary to Thulborn 1974, Weishampel & Witmer 1990) and are clearly adapted for grasping rather than weight support during locomotion, as evidenced by the elongate penultimate phalanges and narrow trenchant claws.

Hypsilophodontids, a more conservative group than heterodontosaurids with a long stratigraphic range from the Middle Jurassic to the end of the Cretaceous, comprise a half dozen well-known genera that are distinguished as a clade, and from each other, by only a few characters (Galton 1974, Sues & Norman 1990). The most diagnostic features are the short scapula (shorter than the humerus) and rod-shaped prepubic process, which are present in the earliest hysilophodontid, *Yandusaurus* (=*Agilisaurus*) from the Middle Jurassic of China (He & Cai 1984, Peng 1992).

Iguanodontians comprise a series of low-diversity sister taxa to hadrosaurids, a diverse, but morphologically tightly knit, array of genera that are currently restricted to the Late Cretaceous. The pectinate arrangement of nonhadrosaurid iguanodontians is supported by a broad range of data from the dentition, skull, and skeleton (Sereno 1986) and constitutes the best transformation series within

Ornithischia. Particularly significant modifications include the evolution of tooth batteries, a ligament-bound metacarpus, and digitigrade posture for the manus. Traditionally, Iguanodontidae has served as a repository for any large nonhadrosaurid ornithopod. Cladistic evidence in support of this traditional assemblage (Norman 1984, 1986), or some subset therein (Norman & Weishampel 1990), has failed to materialize. *Tenontosaurus* is the most basal iguanodontian (Sereno 1986, Forster 1990, Weishampel & Heinrich 1992), despite its rather late appearance in the mid Cretaceous of North America (Figure 2). Successively more-derived iguanodontians include *Dryosaurus* (Galton 1983) and *Camptosaurus* from the Late Jurassic and *Probactrosaurus* (Rozhdestvensky 1966), *Iguanodon* (Norman 1980, 1986), and *Ouranosaurus* (Taquet 1976) from the Early Cretaceous. Recently described from the Late Cretaceous of Argentina, *Gasparinisaura* is a late-surviving basal iguanodontian similar to *Dryosaurus* (Coria & Salgado 1996). *Rhabdodon* (=*Mochlodon*; Nopcsa 1902) and *Muttaburrasaurus* (Bartholomai & Molnar 1980) are less completely known genera from the mid and Late Cretaceous of central Europe and eastern Australia, respectively, and appear to represent basal iguanodontians less derived than *Camptosaurus*.

MARGINOCEPHALIA   Margin-headed dinosaurs, named for the parietosquamosal shelf that projects posteriorly over the occiput, comprise two very distinct clades, the thick-headed pachycephalosaurs and frilled ceratopsians (Figures 1, 2). Although marginocephalians first appeared in the Neocomian (earliest Cretaceous), they must have diverged from ornithopods by the Early Jurassic (Figure 2). Pachycephalosauria and Ceratopsia, in turn, probably also had diverged by the Middle Jurassic, given the low number of synapomorphies that unite Marginocephalia.

Stenopelix, the oldest known pachycephalosaur from the Early Cretaceous of Europe, shares with other pachycephalosaurs unusual features in the pelvic girdle and sacrum (Maryańska & Osmólska 1974, Sereno 1997). Unfortunately, no part of the skull is preserved. All other pachycephalosaurs have a significantly thickened frontoparietal portion of the skull roof, the posterior and lateral margins of which are ornamented with tubercles. In basal members, such as the Late Cretaceous Asian forms *Goyocephale* (Perle et al 1982) and *Homalocephale* (Maryańska & Osmólska 1974), the skull roof remains flat with open supratemporal fossae. In more advanced pachycephalosaurs, such as *Stegoceras* (Gilmore 1924, Sues & Galton 1987), a thickened dome composed of the frontoparietal appears during growth. In fully domed forms such as *Prenocephale*, the dome expands from the frontoparietal to the edge of the skull roof, incorporating all adjacent elements. The largest and most derived pachycephalosaurs evolved during the Maastrichtian (latest Cretaceous) in western North America. Their skulls are characterized by a cluster of swollen tubercles

on the posterolateral corners of the dome. In *Stygimoloch*, three of these tubercles extend from the cluster as short horn cores (Brown & Schlaikjer 1943, Giffin et al 1987).

Psittacosaurs, a tightly knit group of small-bodied parrot-beaked herbivores, occur exclusively in deposits of mid Cretaceous age in Asia (Sereno 1987, 1990). Other ceratopsians, or neoceratopsians, are abundant and diversified in Late Cretaceous deposits in western North America and Asia. These Late Cretaceous neoceratopsians include a series of small-bodied genera, formerly grouped together in Protoceratopsidae (Brown & Schlaikjer 1940, Sternberg 1951, Maryańska & Osmólska 1975), and a diverse family of large-bodied ceratopsids restricted to western North America (Hatcher et al 1907, Lull 1933, Dodson & Currie 1990, Sereno 1997). All neoceratopsians are quadrupedal and are characterized by enlargement of the skull relative to the skeleton. Most neoceratopsians have a greatly expanded marginocephalian shelf as a thin posterodorsally directed shield, composed primarily of the parietal. In ceratopsids, the dentition is specialized for vertical shearing rather than transverse cutting (as in hadrosaurids) and consists of compact dental batteries composed of stacks of two-rooted teeth. Ceratopsids diverged quickly into two distinct subfamilies, the deep-snouted centrosaurines (Sampson 1995) and the long-frilled chasmosaurines (Lehman 1990).

Sauropodomorpha

All sauropodomorphs, the second branch of dinosaurian herbivores, have an enlarged external naris and taller crowns than those of most ornithischians. In the postcranial skeleton, all sauropodomorphs have an enlarged first pedal ungual, which exceeds the length of any other pedal phalanx. Marked lengthening of the neck does not characterize sauropodomorphs as a whole but rather arose several times within Sauropodomorpha.

During the Late Triassic, sauropodomorphs split into two distinct clades, Prosauropoda and Sauropoda (Figures 3, 4). Prosauropods, the first global radiation of dinosaurian herbivores, are often abundant in Upper Triassic and Lower Jurassic deposits. Sauropods, in contrast, have yet to be recorded in Triassic rocks and are rare in rocks of Early Jurassic age. By the Middle Jurassic, however, prosauropods had gone extinct and the sauropod radiation was under way (Figure 4). *Vulcanodon*, from the earliest Jurassic of southern Africa (Raath 1972, Cooper 1984), and several later basal sauropods (He et al 1988, Zhang 1988) constitute successive sister taxa to neosauropods, a group that peaked in diversity in the Late Jurassic. Neosauropods include diplodocoids and a more varied clade that includes camarasaurids, brachiosaurids, and titanosaurs (Upchurch 1995, Calvo & Salgado 1995, Wilson & Sereno 1997).

The close relationship between all prosauropods and sauropods was clouded for many years by the erroneous association of prosauropod bones with the jaws

of predatory archosaurs (rauisuchians) from the same deposits (von Huene 1932, Young 1951). That mix-up (see Galton 1985a, Benton 1986) resulted in the long-standing notion that some prosauropods were "carnosaurs" (Colbert 1964). Other prosauropods, particularly the so-called melanorosaurids, have been regarded as more closely related, or even ancestral, to sauropods (Colbert 1964, Charig et al 1965, Cruickshank 1975, Bonaparte & Pumares 1995). The first cladistic hypothesis of higher-level sauropodomorph phylogeny also concluded that prosauropods were paraphyletic (Gauthier 1986). More recently, however, Prosauropoda has been regarded as a monophyletic sister group to sauropods (Galton 1989, Sereno 1989), as evidenced in particular by the twisted pollex (thumb) and other aspects of the hand.

Traditional (precladistic) higher-level sauropod systematics has been dominated by a dichotomous scheme that separates sauropods with broad nares and spatulate crowns (Camarasauridae or Brachiosauridae) from those with elevated nares and narrow crowns (Titanosauridae or Atlantosauridae) (Janensch 1929, von Huene 1932, Romer 1966, Steel 1970, Bonaparte 1986). This hypothesis, recast more recently in cladistic terms (Gauthier 1986, Upchurch 1995), suggests that sauropods diverged into brachiosaurid-camarasaurid and diplodocoid-titanosaur clades. An opposing view has recently been forwarded that separates diplodocoids from all others and links brachiosaurids with titanosaurs (Calvo & Salgado 1995, Wilson & Sereno 1997). These major differences notwithstanding, all recent cladistic hypotheses agree that diplodocoids, camarasaurids, brachiosaurids, and titanosaurs constitute a monophyletic group (Neosauropoda) that excludes more primitive sauropods such as *Vulcanodon*, *Barapasaurus*, and *Omeisaurus* (Jain et al 1979, Cooper 1984, He et al 1988, Zhang 1988).

PROSAUROPODA   Prosauropods are facultative bipeds with a body-size range that overlaps that of the smallest sauropods. Despite a temporal range of at least 30 million years (Late Triassic through Early Jurassic, Figure 4), prosauropods undergo little skeletal change. Most variation occurs within the skull, which in overall proportions is either narrow as in *Plateosaurus* (Galton 1984, 1985b) or broad and low as in *Massospondylus* (Attridge et al 1985, Gow et al 1990). Relative to body size, prosauropods have very small skulls, which are delicately constructed. Gut-processing with gastroliths seems to have played an important role in prosauropods because their crowns, which typically are delicate lanceolate-shaped blades, are not characterized by tooth-to-tooth wear facets, unlike those of ornithischians and sauropods. Perhaps as a consequence, the skull in prosauropods is delicately built and much less transformed than in ornithischians and sauropods.

New evidence suggests that all prosauropods may have had a narrow horny beak at the end of the upper and lower jaws. A raised bony platform for the upper half of such a beak is clearly present on the premaxillae in *Riojasaurus*

from the Late Triassic of Argentina (Bonaparte & Pumares 1995), and a similar, but more subtle, platform is present in *Plateosaurus* (PC Sereno, unpublished data). In the lower jaw of prosauropods, the first tooth is inset from the end of the dentary to accommodate a narrow lower beak.

Prosauropods had diversified before the close of the Triassic (Figure 4). With the exception of *Riojasaurus* from the Late Triassic of Argentina and "*Gyposaurus*" (Young 1941) from the Early Jurassic of China, most belong to an advanced subgroup with elongate cervical vertebrae. The jaw articulation is dropped below the tooth rows in a subset of these long-necked prosauropods, which includes *Sellosaurus* and *Plateosaurus* from the Late Triassic of Europe (Galton 1984, 1985), *Coloradisaurus* from the Late Triassic Argentina (Bonaparte 1978), and *Lufengosaurus* from the Early Jurassic of China (Young 1951).

BASAL SAUROPODA   *Vulcanodon*, known primarily from a partial skeleton from the earliest Jurassic of southern Africa, is the most primitive sauropod discovered to date (Raath 1972, Cooper 1984). The quadrupedal proportions of the limbs, their columnar construction, the partially pronated forearm, and strengthened proportions of the first and fifth digits in the pes are features shared with all later sauropods (Wilson & Sereno 1997). Other aspects of the skeleton in *Vulcanodon* are distinctly primitive and similar to that in prosauropods, such as the platelike pubis and compact digitigrade metatarsus. In later sauropods, the metatarsals have a spreading plantigrade configuration with a reduced number of phalanges. *Shunosaurus* and *Omeisaurus*, from the Middle and Late Jurassic of China, respectively, are more advanced than *Vulcanodon* but do not appear to belong to the neosauropod radiation (Zhang 1988, He et al 1988). In *Shunosaurus* and later sauropods, the neck is lengthened from 10 to 12 or more vertebrae by incorporation of trunk vertebrae into the neck. In *Omeisaurus*, the centra of the neck and trunk are hollowed by deep lateral excavations (pleurocoels) that characterize all neosauropods. Early sauropod cranial modifications, which are present in both *Shunosaurus* and *Omeisaurus*, include partial retraction of the external nares to a position above the antorbital opening and precise tooth-to-tooth occlusion. The latter capability, unique among dinosaurian herbivores, must be invoked to explain the regular V-shaped wear facets that form along the edges of the spatulate crowns in *Shunosaurus*, *Omeisaurus*, and many later sauropods; lower and upper crowns interlock precisely upon occlusion (Wilson & Sereno 1997). The enamel on the crowns in these and other sauropods has a characteristic wrinkled texture, the function of which is not known. During the Early Jurassic, in summary, the stage was set for an explosive radiation of sauropods that would rapidly become the dominant large-bodied herbivores for the remainder of the period and, on many continents, during the Cretaceous as well.

NEOSAUROPODA   Neosauropods comprise four principal subgroups: diplodo-
coids, camarasaurids, brachiosaurids, and titanosaurs, all of which have a
bound, strongly transversely arched, digitigrade metacarpus. Diplodocoids,
the most highly modified of neosauropods, are easily recognized by the eleva-
tion of the external nares to a position above the orbits, the profound rotation
of the posterior portion of the skull, the squared muzzle, the slender cylindrical
crowns, and the bifid neural spines in the neck and trunk. *Diplodocus* and its
close Late Jurassic relatives *Apatosaurus* and *Barosaurus* compose the long-
necked, long-tailed family Diplodocidae (Hatcher 1901, Holland 1906, Lull
1919, Gilmore 1936, Janensch 1935–36, Berman & McIntosh 1978), whereas
the Late Jurassic genus *Dicraeosaurus* and the bizarre tall-spined Early Creta-
ceous genus *Amargasaurus* compose the short-necked family Dicraeosauridae
(Janensch 1929, 1935–36, Salgado & Bonaparte 1991, Salgado & Calvo 1992).

Camarasaurids, known mainly from the Late Jurassic genus *Camarasaurus*
(Osborn & Mook 1921, Gilmore 1925, Madsen et al 1995) are short-necked
sauropods with broad spatulate crowns in robust jaws and with bifid neural
spines in cervical and anterior trunk vertebrae. In general, camarasaurids de-
part less than the other subgroups from the ancestral neosauropod condition.
Brachiosaurids, best known from the Late Jurassic genus *Brachiosaurus* (Riggs
1904, Janensch 1935–36, 1950), have an expanded pectoral girdle and length-
ened forelimb relative to the pelvic girdle and hind limb, respectively. Despite
its length, the neck is composed of only 13 single-spined vertebrae. *Nemeg-
tosaurus* (Nowinski 1971) and *Quaesitosaurus* (Kurzanov & Bannikov 1983)
from the Late Cretaceous of Asia are probably brachiosaurids (Wilson & Sereno
1997) or basal titanosaurs (Calvo 1994), although they were originally described
as diplodocoids. The spatulate crowns in *Nemegtosaurus* bear V-shaped facets
and, though narrower, are very similar to those in *Brachiosaurus*.

Titanosaurs, best known from Cretaceous deposits in South America although
present worldwide during this period, are nearly all short-necked sauropods that
are easily recognized by their broad sternum and coracoid, anteriorly expanded
iliac blade, stocky limb proportions, absence of ossified carpals or phalanges,
and short tail composed of proceolous caudals. No complete titanosaur skull
has yet been recovered. The dentition is characterized by narrow cylindrical
crowns truncated by high-angle wear facets, except in some Early Cretaceous
titanosaurs that have weakly spatulate crowns. Except in the Asian titanosaur
Opisthocoelicaudia (Borsuk-Bialynika 1977), most titanosaurs have simple low
neural spines and a peculiar biconvex first caudal centrum (Gilmore 1946).
Some advanced forms, such as *Saltasaurus*, were armored with scutes, which
are characterized by a rugose or woven surface texture (Powell 1992).

No phylogenetic arrangement of these four neosauropod subgroups is
free of homoplasy. Analysis of a broad survey of characters suggests that

camarasaurids brachiosaurids, and titanosaurs form a clade of large-nosed neosauropods, in which the maximum diameter of the nares exceeds that of any other cranial opening (Macronaria; Wilson & Sereno 1997). Now it is clear that cylindrical crowns, elongate cervical vertebrae, additional cervical vertebrae, and bifid neural spines all arose more than once in sauropod evolution. Because all four neosauropod subgroups are present and geographically widespread by the Late Jurassic, the basal divergences among neosauropods must have taken place during, or prior to, the Middle Jurassic (Figure 4).

Theropoda

Unlike many ornithischians and sauropodomorphs, theropods remained habitual bipeds throughout their evolution. Predatory adaptations that arose in the earliest theropods include a flexible bite (midmandibular joint), a long and powerful three-fingered hand modified for grasping and raking, and a dynamic balancing tail stiffened distally by overlapping processes (prezygapophyses). Theropod bones have larger medullary cavities than in other dinosaurs, a feature taken to its extreme in avians. Hollowing of skeletal components, including elaborate pneumatic diverticulae within the bones of the skull in most theropods, reduces bone weight.

Eoraptor and *Herrerasaurus*, the oldest dinosaurs known from complete skeletons, constitute successive sister taxa to neotheropods, which had split early in the Late Triassic into ceratosaurs and tetanurans. Ceratosaurian predators dominate during the Late Triassic and Early Jurassic, but from the Middle Jurassic to the end of the Cretaceous, tetanurans are more diverse on all continents (except possibly on South America). Tetanurans split during the Jurassic into allosauroids and coelurosaurs.

During the Cretaceous, the fortunes of these three clades—ceratosaurs, allosauroids, and coelurosaurs—varied geographically as the continents drifted apart. In South America, abelisaurid ceratosaurs appear to have predominated by the Late Cretaceous. In Africa, the largest predator, *Carcharodontosaurus*, is an allosauroid, which lived alongside other tetanurans (*Spinosaurus*) and coelurosaurs (*Deltadromeus*). In central Asia and western North America, nonavian coelurosaurs dominate all Late Cretaceous faunas. Avian coelurosaurs, known during the Late Jurassic from the single genus *Archaeopteryx*, had already achieved a global distribution early in the Cretaceous (Chiappe 1995a).

Based primarily on body size, the traditional (precladistic) division of theropods into "carnosaurs" and "coelurosaurs" (Colbert 1964) is no longer tenable because body size clearly increased and decreased on several occasions during theropod evolution. Furthermore, removing ceratosaurs (Molnar et al 1990) does not salvage the traditional size-based dichotomy. Recent advances in understanding theropod evolution include the (*a*) discovery of the basal theropod *Eoraptor* and repositioning of herrerasaurids as basal theropods (Sereno

& Novas 1992, Sereno et al 1993, Novas 1993), (*b*) realization that remaining theropods are divisible into ceratosaurs and tetanurans (Gauthier 1986, Rowe 1989, Rowe & Gauthier 1990), (*c*) discovery of South American abelisaurids and recognition of their status as Cretaceous ceratosaurs (Bonaparte et al 1990), (*d*) partitioning of basal tetanurans (Sereno et al 1994, 1996, Holtz 1994), and (*e*) recognition of coelurosaurs as a monophyletic clade (Gauthier 1986) that includes tyrannosaurs (Holtz 1994) and birds. The relationships among coelurosaurs has yet to be settled decisively (Gauthier 1986, Holtz 1994, Sereno 1995).

EORAPTOR AND *HERRERASAURUS*   All bones in the skeleton of 1-m–long *Eoraptor* are hollowed by internal cavities, including the vertebrae, ribs, chevrons, and tarsals (Sereno et al 1998). The vertebral centra, in particular, are remarkably hollow, with walls often no more than 1 mm thick. The skull in *Eoraptor* (Sereno et al 1998) and *Herrerasaurus* (Sereno & Novas 1993), in contrast, lacks the elaborate craniofacial pneumatic spaces that characterize later neotheropods (Witmer 1995). The skeleton in *Herrerasaurus* is distinctly more advanced than that in *Eoraptor* (Novas 1993, Sereno et al 1993, 1997), with the grasping, raking function of the manus enhanced by proportionately long penultimate phalanges and trenchant unguals. The expanded distal end of the pubis, or pubic foot, characterizes herrerasaurids and nearly all later theropods, including primitive birds.

Herrerasaurus is closely related to *Staurikosaurus*, from similar age deposits in Brazil (Colbert 1970, Galton 1977); to *Chindesaurus*, from latest Triassic deposits in North America (Long & Murry 1995); and probably to *Agrosaurus*, from the Late Triassic of Australia (Seeley 1891, Molnar 1991a). Herrerasaurids may constitute the first global radiation of theropods.

CERATOSAURIA   Ceratosaurs are united principally by features in the pelvic girdle and hind limb (Gauthier 1986, Rowe 1989, Rowe & Gauthier 1990). One involves the peculiar dimorphic form of the femoral anterior trochanter (sigmoidal or blade-shaped), which, along with more subtle proportional differences, distinguish the sexes in skeletons of *Coelophysis* (Colbert 1989) and *Syntarsus* (Raath 1990). This sexual dimorphism is also present in *Ceratosaurus* and *Dilophosaurus*. Another ceratosaurian feature involves a distinct pattern of skeletal fusion in the pelvic girdle, tarsus, and metatarsus (Rowe 1989).

Ceratosaurs split early into two lineages, the ceratosauroids and coelophysoids. Ceratosauroids, which first appear in the Late Jurassic of western North America (*Ceratosaurus*; Gilmore 1920) and eastern Africa (*Elaphrosaurus*; Janensch 1925), are represented by the family Abelisauridae in Late Cretaceous deposits in South America (*Abelisaurus, Carnotaurus, Naosaurus*; Bonaparte & Novas 1985, Bonaparte et al 1990), India (*Indosuchus*; Chatterjee 1978), and

Madagascar (*Majungasaurus*; Depéret 1896). *Carnotaurus*, the best-known abelisaurid, has an extremely short skull, as in *Indosuchus* and *Majungasaurus*, with unusual wedge-shaped frontal horns. The diminutive forelimbs in *Carnotaurus* may eventually be shown to characterize other abelisaurids.

Coelophysoids, the only neotheropods recorded from the Late Triassic, survived until the end of the Early Jurassic and include medium-sized *Dilophosaurus* (Welles 1984, Hu 1993) and *Liliensternus* (von Huene 1934), as well as a tightly knit group of small-bodied coelophysids, such as *Coelophysis, Syntarsus, Procompsognathus*, and *Segisaurus*, that appear to have achieved a global distribution by the end of the Triassic (Camp 1936, Ostrom 1981, Colbert 1989, Raath 1969, 1990, Rowe 1989, Sereno & Wild 1992). Coelophysoids are characterized by their long skulls, crescentic nasolacrimal crests, and overhanging (apparently mobile) premaxillae.

BASAL TETANURAE   Basal tetanurans include torvosaurids, spinosaurids, a diverse clade of allosauroids, and several genera of less certain affinities (*Afrovenator, Piatnitzkyasaurus, Compsognathus*). Tetanurans exhibit several advanced characters that include a relatively short (preorbital) maxillary tooth row; pneumatized lacrimal and jugal, transversely expanded distal tibia; tall ascending process on the astragalus; and others (Gauthier 1986, Holtz 1994, Sereno et al 1996).

Basal tetanurans, with the exception of *Compsognathus* (Ostrom 1978), are large-bodied theropods, some of which are more closely related to coelurosaurs than others. Torvosaurids (*Torvosaurus, Eustreptospondylus*; von Huene 1923, Galton & Jensen 1979, Britt 1991), *Chilantaisaurus* (Hu 1964), and possibly the bizarre piscivorous spinosaurids (*Spinosaurus*, *Baryonyx*; Stromer 1915, Charig & Milner 1990) are the most primitive tetanurans, tentatively united on the basis of an extraordinarily short forearm (less than half humeral length) and an unusually long thumb ungual (Sereno et al 1996). The phylogenetic relationships of other basal tetanurans, commonly referred to as megalosaurs (Waldman 1974), are even less certain.

Allosauroids form a distinct, long-lived clade of somewhat more advanced tetanurans that share a small number of cranial characters (Sereno et al 1996), such as construction of the braincase (the exclusion of the basioccipital from the basal tubera) and a pendant process near the jaw joint (on the articular bone). Allosauroids include the crested genus *Cryolophosaurus* from Antarctica [the earliest well-dated tetanuran (Hammer & Hickerson 1994)], the crested genus *Monolophosaurus* from China (Zhao & Currie 1993), the broader-snouted *Allosaurus* from North America (Madsen 1976), the highly pneumatized sinraptorids from China (*Yangchuanosaurus*, *Sinraptor*; Dong et al 1983, Currie & Zhao 1993a), and the late-surviving carcharodontosaurids from

the Cretaceous of North America (*Acrocanthosaurus*; Stovall & Langston 1950), South America (*Giganotosaurus*; Coria & Salgado 1995), and Africa (*Carcharodontosaurus*; Stromer 1931, Sereno et al 1996).

COELUROSAURIA   Coelurosaurs are small- to large-bodied theropods that are united by several features in the skull, vertebrae, and limb bones. Three features that are potentially related to the cursorial capabilities of most coelurosaurs include the extended sacrum (six sacral vertebrae), more extensive stiffening of the tail, and reduced femoral fourth trochanter (Gauthier 1986, Sereno et al 1996). Coelurosaurs comprise the basal genera *Ornitholestes* (Osborn 1916) and *Deltadromeus* (Sereno et al 1996), the long-clawed therizinosaurids (Perle 1979, Clark et al 1994) and ornithomimids (Osmólska et al 1972), tyrannosaurids, and maniraptorans (including birds) (Figures 3, 4).

Many derived features link tyrannosaurids and maniraptorans, despite marked differences in their forelimb length and body size. The prefrontal bone is extremely reduced or absent, the supratemporal fossae are separated in the midline only by a sagittal crest, an extra fenestra is present on the palate between the palatine and pterygoid, and the short ischium lacks the distal foot (Osborn 1905, 1912, Molnar 1991b). The fossil record of tyrannosaurids, currently limited to large-bodied genera from the Late Cretaceous of North America and Asia, is presumed to extend back to the Late Jurassic (Figure 4), when members of this lineage were probably considerably smaller.

Maniraptorans include oviraptorosaurs, deinonychosaurs, and birds, and they are characterized by an ulna with a curved shaft and an ischium with a broad obturator notch and reduced distal symphysis. The toothless skull in oviraptorosaurs is extremely modified, with elevated external nares, a palate that extends below the cheek margin, and a fused dentary symphysis (Osmólska 1976, Barsbold et al 1990). The skeleton, which is less modified than the skull, has an unusually short tail (40 or fewer vertebrae). Oviraptorosaurs comprise two distinct families: the caenagnathids and oviraptorids. Caenagnathids, known primarily from the western North American genus *Caenagnathus*, have proportionately longer skulls, although little of the cranium has been recovered. Asian oviraptorids (*Oviraptor, Conchoraptor, Ingenia*) have extremely short, deep snouts that rival the truncated facial proportions seen in certain species of psittacosaurs. *Oviraptor*, unlike other oviraptorids, has a pneumatic median crest composed of the premaxilla and nasals. Abundant in Upper Cretaceous deposits in Asia, oviraptorosaurs must have diverged as early as the Late Jurassic, given the minimum age of their sister taxon (Figure 4).

Deinonychosaurs, named after the enlarged sickle-shaped ungual on the second digit of the pes, are medium-sized coelurosaurs closely related to birds (Ostrom 1969). Deinonychosaurs comprise two distinct families, Troodontidae

and Dromaeosauridae, both of which have relatively long, low skulls with teeth that have smaller serrations on the anterior carina. The tail in deinonychosaurs is stiffened by chevrons with unusual bifurcate anterior and posterior processes. The pes is functionally didactyl, and body weight is borne solely by digits III and IV. The distal condyles of metatarsals III and IV, as a result, are expanded to accommodate the load.

Troodontids, by comparison, have a more slender build with proportionately longer limbs and more moderate enlargement of the second pedal digit (Barsbold 1974, Osmólska 1987, Osmólska & Barsbold 1990, Russell & Dong 1993). Recurved teeth with large *Troodon*-like serrations from the Upper Jurassic Morrison Formation (Chure 1994) may document the earliest troodontid. Otherwise, a nearly perfect skeleton of a new troodontid, *Sinornithoides*, from the Lower Cretaceous of Inner Mongolia provides the earliest record of the family (Russell & Dong 1993). In known troodontids, the fibula fails to reach the calcaneum, and the metatarsus is particularly narrow and compact, with reduction of the shaft of metatarsal II (Wilson & Currie 1985). The highly modified troodontid skull has a rounded U-shaped snout with an increased number of smaller teeth and a large hollowed pneumatic space on the ventral aspect of the braincase (Currie & Zhao 1993b).

Dromaeosaurids are more diverse and abundant than troodontids and are first recorded in Lower Cretaceous deposits (Barremian-Aptian) in western North America (Ostrom 1969, 1976a, Kirkland et al 1993). The skull is characterized by a Y-shaped quadratojugal and horizontal mandibular condyles, as seen in the most primitive known genus *Dromaeosaurus* (Currie 1995). Many other features are present in a derived subset of dromaeosaurids that includes *Deinonychus* and *Saurornitholestes* from western North America and *Velociraptor* from Mongolia. The cervical series follows a tight sigmoid curve from the trunk to the skull, which elevates the skull above the trunk. The tail, also more specialized than that in troodontids, forms a stiffened beam, united by hypertrophied prezygapophyses and anterior processes of the chevrons, which extend across as many as ten vertebrae (Ostrom 1969, 1976a).

Coelurosaurian interrelationships are currently unsettled owing to the conflicting distributions of several important skeletal novelties. The specialized eviscerating second pedal digit, for example, is present in troodontids and dromaeosaurs and supports deinonychosaurian monophyly (Gauthier 1986) or the monophyly of Deinonychosauria plus Aves (Paraves; see Table 1), as it occurs in some basal avians (PC Sereno, unpublished data). The splint-shaped proximal end of metatarsal III, on the other hand, is present in most ornithomimids, tyrannosaurids, and troodontids, which have been united as "Arctometatarsalia" (Holtz 1994). Within this group, ornithomimids and troodontids were united (as "Bullatosauria") on the basis of an inflated parasphenoid (Holtz 1994),

although this condition also occurs in therizinosaurids. Of these features, some have arisen more than once within Coelurosauria because there is no phylogenetic arrangement free of homoplasy (i.e. parallel acquisition or loss). The character evidence at hand favors deinonychosaurian monophyly (Figures 3, 4), but only a comprehensive consideration of character evidence will convincingly resolve coelurosaurian relationships.

EARLY AVIAN DIVERSITY

The debate over avian origins—i.e. whether birds are the descendants of theropod dinosaurs (Huxley 1870a, Ostrom 1974, 1975, 1976b) or are more closely related to crocodylomorphs or more remote diapsid reptiles (Heilmann 1926, Walker 1972, Tarsitano & Hecht 1980)—has been resolved over the last decade. Proponents of the theropod hypothesis have marshalled considerable cladistic evidence favoring the interpretation of birds as specialized coelurosaurs (Thulborn 1984, Cracraft 1986, Gauthier 1986, Holtz 1994). Opponents of this view (Martin et al 1980, Tarsitano & Hecht 1980, Feduccia & Wild 1993), in contrast, have yet to frame their opinions as a phylogenetic hypothesis with specific outgroups and itemized character evidence (Witmer 1991).

In this review, Aves and "avian" refer to a node-based group composed of *Archaeopteryx*, Passeriformes, and their common ancestor and all descendants (following traditional usage). Ornithurae, or "stiff-tailed" birds, is defined here as a stem-based group including all avians more advanced than *Archaeopteryx* (Gauthier 1986, Cracraft 1986, Sereno & Rao 1992).

Archaeopteryx and Other Basal Avians

The skeletal anatomy of *Archaeopteryx*, the oldest and most basal avian yet discovered, has been documented in detail by restudy of skeletons found in the nineteenth century (Ostrom 1972b, 1976b, Wellnhofer 1974, Hecht et al 1985) and description of new material from the same latest Jurassic (Tithonian) limestone quarries in southern Germany (Wellnhofer 1988a,b, 1993). *Archaeopteryx* and all later birds exhibit several hallmarks of avian structure, such as the elongate snout anterior to the external nares, loss of the bar behind the orbit, shortened bony tail, marked ventral deflection of the coracoid toward the sternum, fully reversed hallux that opposes the other pedal digits, and feathers of aerodynamic design and position. From their debut in the fossil record, therefore, avians possessed basic flight and perching capabilities, though somewhat unrefined.

The "centrality" of *Archaeopteryx* in avian evolution has often been questioned, although cladistic analysis allows only one conclusion: The paucity of autapomorphies for this early avian (regarded previously as a "metataxon"

without autapomorphies; Gauthier 1986) indicates that it occupies a near-ancestral position at the root of the avian radiation—a view remarkably similar to that outlined by Huxley (1868, 1870a,b) shortly after the first skeleton of *Archaeopteryx* was unveiled. This view, it should be understood, is consistent with but does not depend on the early age of *Archaeopteryx* relative to the ages of other fossil birds.

Controversy surrounds two other recently described forms, *Protoavis* and *Mononykus*, both of which were regarded by their original authors as more advanced than *Archaeopteryx*. *Protoavis* (Chatterjee 1991, 1995), based on disarticulated bones from the Upper Triassic Dockum Formation of Texas, has not been accepted as avian by most researchers and is regarded here as a chimera composed of several disparate Triassic reptiles. The four-digit manus (Chatterjee 1995), for example, is more appropriately identified as an archosaurian pes.

Mononykus, based on several articulated skeletons from the Upper Cretaceous of Mongolia (Perle et al 1994), exhibits a number of ornithurine features that include an incomplete postorbital bar, keeled sternum, coossified carpometacarpus, and very reduced fibula. Indeed, several aspects of the skeleton of this bizarre cursor are more advanced than in basal ornithurines (e.g. *Sinornis*), such as the absence of a claw on manual digit II and a fully retroverted, distally tapering pubis. On the other hand, the absence of many avian features—such as a substantial prenarial snout, reduced prefrontal, reduced caudal series, reduced hemal arches, subquadrate coracoid, laterally directed glenoid, and reversed hallux—seriously jeopardizes the avian status of *Mononykus*, even if one disregards mounting evidence that its closest kin from Argentina are substantially less birdlike (*Alvarezsaurus*; Bonaparte 1991). The absence of a laterally facing glenoid and fully reversed hallux is particularly problematic because these features are never lost in numerous fossil and living avians that have reduced or eliminated flight and perching capability. Reassessment of the relationships of alvarezsaurids, however, must await at least a preliminary description of the skull of *Mononykus*.

Ornithurae

Recent discoveries of ornithurine skeletons of Cretaceous age in lake deposits in Europe and Asia have dramatically expanded knowledge of early avian evolution (Chiappe 1995a). These include the hummingbird-sized *Iberomesornis* (Sanz & Bonaparte 1992) and the somewhat larger *Concornis* (Sanz et al 1995) from the Lower Cretaceous (Barremian) of Spain and the sparrow-sized *Sinornis* (Sereno & Rao 1992), *Cathayornis* (Zhou 1995), and the somewhat larger *Chaoyangia* (Hou & Zhang 1993), *Liaoningornis*, and *Confuciusornis* (Hou et al 1995, 1997) from Lower Cretaceous lake beds in northern

China. Ornithurines are characterized by a broad suite of characters including (aptly) an ossified pygostyle, to which the rectrices (tail feathers) are anchored.

Confuciusornis may constitute the most primitive ornithurine known, as it has a long manus similar to that of *Archaeopteryx* with a full compliment of phalanges that includes an elongate penultimate phalanx and ungual on digit III. The primitive boomerang-shaped furcula is also remarkably similar to that in *Archaeopteryx. Iberomesornis, Concornis, Sinornis*, and *Cathayornis*, on the other hand, constitute basal Enantiornithes, an ornithurine subgroup initially described from disarticulated remains of Late Cretaceous age from Argentina (Walker 1981), North America (Brett-Surman & Paul 1985), Australia (Molnar 1986), and Asia (Nessov & Jarkov 1989). More recently, articulated material has come to light in Argentina (Chiappe & Calvo 1994) and Mongolia (Kurochkin 1996). These volant perching birds, which may comprise the dominant group of inland avians on northern and southern continents during the Cretaceous, are characterized by reduction in the strength of metatarsal IV and other features (Walker 1981, Chiappe & Calvo 1994, Chiappe 1995b, 1996, Sanz et al 1995). These and other recent finds from the Late Cretaceous of Madagascar (Forster et al 1996), however, suggest that the first fully flighted avians underwent a rapid radiation that we are just beginning to unravel.

Evolution of Perching

In *Archaeopteryx*, the first digit of the pes, or hallux, articulates on the posterolateral aspect of the shaft of metatarsal II and is positioned posterior to metatarsals II–IV, as in all theropods (e.g. Sereno & Wild 1992). Unlike nonavian theropods, however, the ungual of the hallux in *Archaeopteryx* and other birds is rotated so that its apex is directed toward the plantar surface of the pes in opposition to the unguals of digits II–IV (Ostrom 1976a, Wellnhofer 1974, 1988a, 1993), a fundamental avian adaptation for perching. The shape of the horny claw in *Archaeopteryx* is also consistent with perching capability (Feduccia 1993), although claw shape alone is insufficient to determine with confidence the primary habitat(s) of a bird (Peters & Görgner 1992).

The hallux in ground-dwelling birds is often shortened and the distal condyles of metatarsal I located more proximally (elevated) than those of the central three metatarsals (II–IV) (Bock & Miller 1959, Raikow 1985), which is the case in *Archaeopteryx* and *Confuciusornis*. The hallux in perching and trunk-climbing birds, on the other hand, is generally longer, with the distal condyles of metatarsal I positioned directly opposite those of metatarsals II–IV and with a more recurved claw, as in Enantiornithes (Sereno & Rao 1992). Advanced perching function, therefore, seems to have been established shortly after *Archaeopteryx* among basal ornithurines (Figure 5).
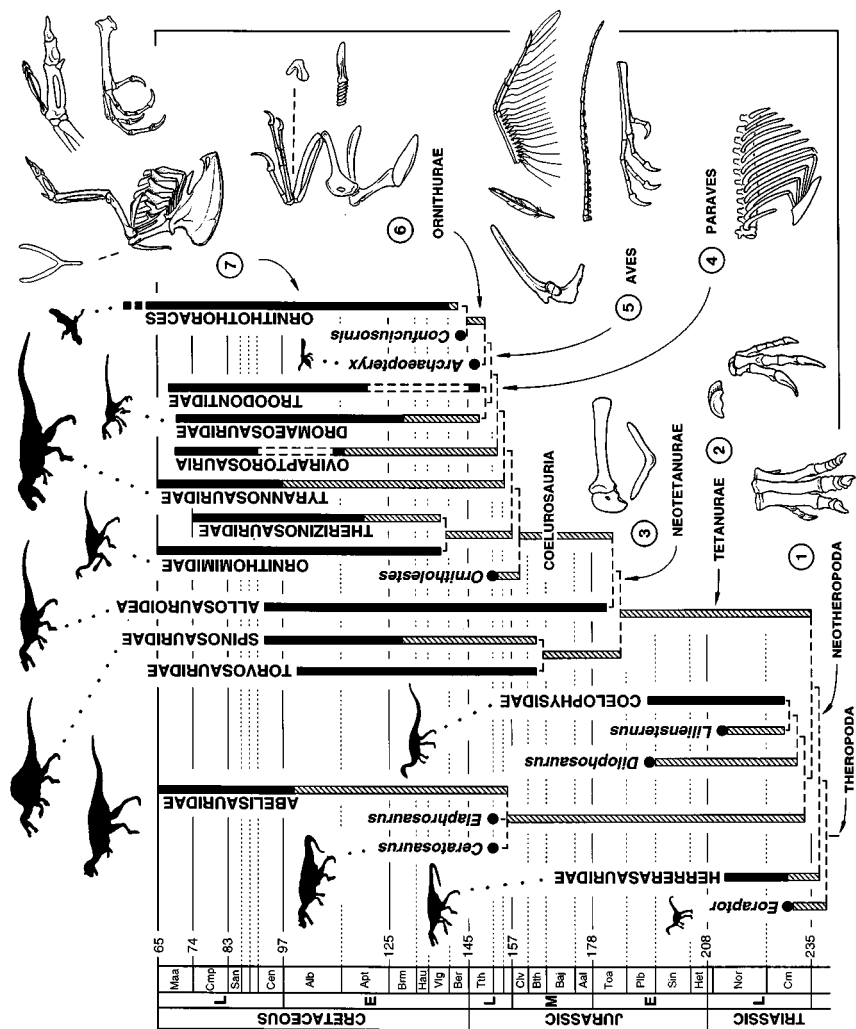
Figure 5 Calibrated phylogeny of Theropoda with emphasis on the origin of birds, showing the temporal and phylogenetic origin of principal skeletal features associated with avian perching and flight function. 1. Metatarsal I short, distally located and partially reversed; 2. semilunate carpal with transverse trochlea, manual digit II most robust, digit IV very reduced or absent; 3. furcula, coracoid posterior process crescentic; 4. short trunk (125% or less of femoral length); 5. glenoid laterally facing, coracoid strongly deflected, flight feathers, primary and secondary feather pattern, short tail (23 or fewer vertebrae), reversed hallux; 6. coracoid with rod-shaped shaft, ulna more robust than radius, ulnare enlarged and cleft, pygostyle; 7. large V-shaped furcula with hypocleideum, sternal keel, 11 or fewer dorsal vertebrae, 8 or more sacral vetebrae, ribs with uncinate processes, manus short, manual digit II robust, loss of claw on digit III, alula, advanced perching foot.

Evolution of Powered Flight

Long-standing debate about the evolution of powered ("flapping") flight among birds has focused on the presumed functional capabilities of hypothetical avian precursors, in particular on whether flapping flight originated among tree-dwelling gliders (the "arboreal" or "trees-down" hypothesis) or ground-dwelling cursors (the "cursorial" or "ground-up" hypothesis) (Rayner 1988). Both hypotheses propose a gliding phase in the evolution of flapping flight, presuming that flapping flight must have evolved as an enhancement of gliding and that the path of functional transformation is possible to divine from first principles of fluid biomechanics, free from phylogenetic constraints. Rayner (1988) has suggested, for example, that the debate boils down to the ability to identify the most convincing "selective pressures" that favor the appearance of flapping flight.

The uncomforting fact that *Archaeopteryx*, the most primitive flapping avian known, clearly exhibits both cursorial and arboreal adaptations complicates scenarios that invoke strictly arboreal antecedents. Furthermore, the dismal gliding and flapping capability of many living birds highlights the adaptive potential of even the most rudimentary wings. Given these facts, a third scenario for the evolution of flapping flight is plausible, one that does not require a fine-tuned gliding phase (the "fluttering" hypothesis). Yet with no "protoavians" in the fossil record that are more primitive than *Archaeopteryx* to constrain hypothetical ancestors and no surviving lineages of "protofliers" to constrain the phylogeny of function (Cracraft 1990, Lauder 1990), there is little reason to prefer one among the many plausible scenarios for the origin of powered flight in birds.

The phylogenetic history of theropods (including early avians), in contrast, provides a coarse chronological scheme of skeletal changes that occurred before and after the advent of avian powered flight. These modifications can be divided into two groups: exaptations, or features that appear to have evolved for reasons other than powered flight and its enhancement, and adaptations, or features that most likely evolved as refinements of flight function (although this distinction is an oversimplification; Gould & Vrba 1982, Brandon 1990). Exaptations include the furcula and semilunate carpal, both of which were already present by the Early Jurassic in basal tetanurans of large body size (Chure & Madsen 1996) (Figure 5). The articular trochlea of the semilunate carpal in avians plays an important role in restricting the motion of the manus (and primary feathers) during flight (Vazquez 1992), but it did not evolve originally as a refinement of flight function. Similarly, the trunk was initially shortened (relative to femoral length) in medium-sized maniraptorans for unknown reasons. Among avians, the trunk has been shortened further as a refinement of flight function, effectively shifting the center of gravity toward the forelimb.

Flight adaptations that characterize all avians include a laterally facing shoulder socket (glenoid) that permits extreme dorsal excursion of the humerus during the flight stroke (Jenkins 1993), aerodynamic construction of flight feathers and

their arrangement on the wing (Feduccia & Tordoff 1979, Rietschel 1985), and a shortened tail that is at least partially decoupled from hind-limb locomotor function (Gatesy 1995). As evidenced by *Archaeopteryx*, basic flapping flight and partial functional decoupling of the tail and hind limb were in place by the Late Jurassic (Figure 5).

Recent discoveries of primitive ornithurines such as *Confuciusornis* indicate that the classic avian wing-folding mechanism, an important adaptation to reduce drag during the upstroke and protect the flight feathers during rest (Sy 1936, Vazquez 1994), had already evolved by the earliest Cretaceous. An enlarged keeled sternum indicates that bulky flight musculature (pectoralis) powered the downstroke, and the presence of a trioseal canal suggests that the supracoracoideus muscle had become the principal effector of the recovery stroke.

Marked reduction of the caudal series characterizes all currently known ornithurines and signifies the reduction of the mechanical link between the tail and hind limb. In ornithurines, the tail terminates in a pygostyle (fused centra), to which is attached a fan-shaped array of feathers (rectrices). In concert with the forelimb, the adjustable tail fan provides lift, enhances aerial maneuverability, and functions as a brake during landing (Gatesy & Dial 1996a,b). By the Early Cretaceous, alular feathers had evolved for finer control of air flow over the wing. These feathers attach to the first digit of the manus, which is further reduced and coossified by the Late Cretaceous in birds such as *Ichthyornis* (Marsh 1880). The alula, thus, had evolved prior to the reduction and fusion of the ungual and proximal phalanx of manual digit I.

FOSSIL RECORD

Order of Appearance

One measure of the quality of the fossil record is obtained by comparing the order of first appearance, or *age rank*, with branching order along the spine of a pectinate cladogram, or *clade rank*, for subgroups of a higher taxon (Gauthier et al 1988, Norell & Novacek 1992). Ideally, an excellent fossil record and accurate phylogeny would yield complete correspondence between order of first appearance and branching order.

Relatively close correspondence between age and clade rank exists within Dinosauria (Figures 2, 4), such that bivariate plots typically yield a statistically significant correlation for ornithischians, saurischians, and less inclusive subgroups. Ceratosaurian theropods constitute a notable exception, in which the most derived abundant subgroup, the coelophysids, appeared first in the Late Triassic. Successive coelophysid outgroups, *Dilophosaurus* and ceratosauroids, date back only to the the Early and Late Jurassic, respectively (Figure 4). The inverted sequence of first appearance within this group is regarded here as an

artefact of the fossil record because ceratosaurian phylogeny is well substanti-ated (Rowe & Gauthier 1990; PC Sereno, unpublished data).

Missing Ranges and Lineages

Combining temporal and phylogenetic information can yield insights into the nature of the fossil record (Hennig 1966). The recorded temporal duration, or *range*, of a monophyletic terminal taxon is the temporal interval between the oldest and youngest species, usually depicted as a solid bar (Figures 2, 4, 5). A taxon's temporal range reflects the maximum and minimum age of all included species, and therefore it is more appropriately referred to as a range than as a "lineage" (Norell 1992, 1933), which implies a single ancestral-descendant line. Because sister taxa share a common temporal origin, the temporal range of the younger taxon must extend backward in time to equal the earliest record of its older sister taxon (range extension, strictly speaking, applies only to stem-based taxa; for a node-based taxon, range extension would refer to a corresponding stem-based taxon, named or hypothetical). The temporal extension of the range of stem-based terminal taxa is here termed its *missing range* ("ghost lineage" of Norell 1993; "range extension" of Smith 1994) (Figures 2, 4, 5).

Hypothetical lineages that join the range bars of terminal taxa (and corre-spond to the internal branches of a cladogram) are here referred to as *missing ancestral lineages* (Figures 2, 4, 5). A missing ancestral lineage is a hypothet-ical sequence of common ancestors that, unlike missing ranges, is composed of a single ancestor-descendant line of minimum duration. First recognized by Hennig (1966), missing ancestral lineages have been described recently as "ghost taxa" (Norell 1993). They are more appropriately referred to as ancestral lineages, however, because they cannot be diagnosed or defined as monophyletic taxa. In addition, the near absence of common ancestors in the preserved fossil record (as among named dinosaurs) means that missing ances-tral lineages are likely to remain hypothetical constructs, with durations that can decrease by either (*a*) subdivision (i.e. discovery of intervening sister taxa) or (*b*) extension backward in time of the ranges of terminal taxa (i.e. discovery of older members attributable to associated terminal taxa or preferential extension of missing ranges over missing ancestral lineages).

Long missing ranges and missing ancestral lineages result from the episodic nature of the rock record, taphonomic biases, and uneven paleontologic sam-pling that allow only a very minor fraction of biological diversity to enter the known fossil record. Recorded dinosaur diversity, for example, is very uneven over time and geographic space. Dodson (1990) estimated that 40% of cur-rently known dinosaur genera are restricted to the last 15 million years of the Mesozoic (Campanian-Maastrichtian), with the majority of these discovered in western North America and central Asia.

The areal extent of terrestrial beds strongly influences preservation and varies in a reverse relationship with marine transgressions and eustatic sea level (Smith et al 1994). Thus long intervals characterized by marine transgressions severely reduce available terrestrial outcrop, which, in turn, yields a negligible record of dinosaurian diversity. The vast majority of dinosaurian remains have been recovered from three intervals near the end of the Triassic, Jurassic, and Cretaceous (Norian-Sinemurian, Kimmeridgian-Tithonian, Campanian-Maastrichtian, respectively). Continuity of taxonomic lineages across the intervening hiatuses demonstrates that reduction or absence of dinosaur remains, to a large extent, is preservational rather than an accurate reading of low diversity or abundance. The available dinosaurian fossil record has also been shaped by preservational bias against small (2 m or less) and perhaps very large body sizes (8 m or more), taxa with low abundance or limited geographic range, and taxa restricted to upland or xeric habitats (Behrensmeyer et al 1979).

Several of the longest missing ranges and ancestral lineages for suprageneric taxa within Dinosauria are explicable in terms of preservational bias against

Table 2 Missing ancestral lineages leading to suprageneric clades within Dinosauria are ranked below in decreasing duration (millions of years), as measured by the disparity in first appearance of sister taxa

Taxa	Ma
Ornithischia	
Marginocephalia	65
Ankylosauridae	45
Pachycephalosauridae[a]	45
Eurypoda	40
Euornithopoda	40
Neoceratopsia[b]	30
Hadrosauroidea	25
Lesothosaurus + Genasauria	25
Saurischia	
Carcharodontosauridae	85
Ceratosauroidea	75
Tyrannosauridae	55
Abelisauridae	55
Oviraptorosauria	45
Tetanurae	45
Coelurosauria	30
Sinraptoridae	30
Sauropoda	25

[a]Domed pachycephalosaurs (PC Sereno, in press).
[b]Unnamed group consisting of all neoceratopsians except "*Chaoyoungosaurus*" (PC Sereno, in press).

small body size (Table 2). Because the dinosaurian radiation began at small body size (see below), the unrecorded early history of a major descendant clade is probably due to an initial small-bodied phase, particularly if known members of the clade show a trend toward increasing body size. For example, missing lineages of 65 and 45 million years for Marginocephalia and Pachycephalosauridae, respectively, probably indicate that there was an initial small-bodied phase, because the oldest and most basal genera in each case are small-bodied and each group exhibits a trend toward large body size (Figures 2, 4, 6). Other long missing lineages, such as those for Carcharodontosauridae (85 Ma) and Abelisauridae (55 Ma), require alternative explanations (small geographic range, low abundance, habitat bias), because the common ancestor appears to have been large-bodied and because the missing range extends across stages rich in fossil material.
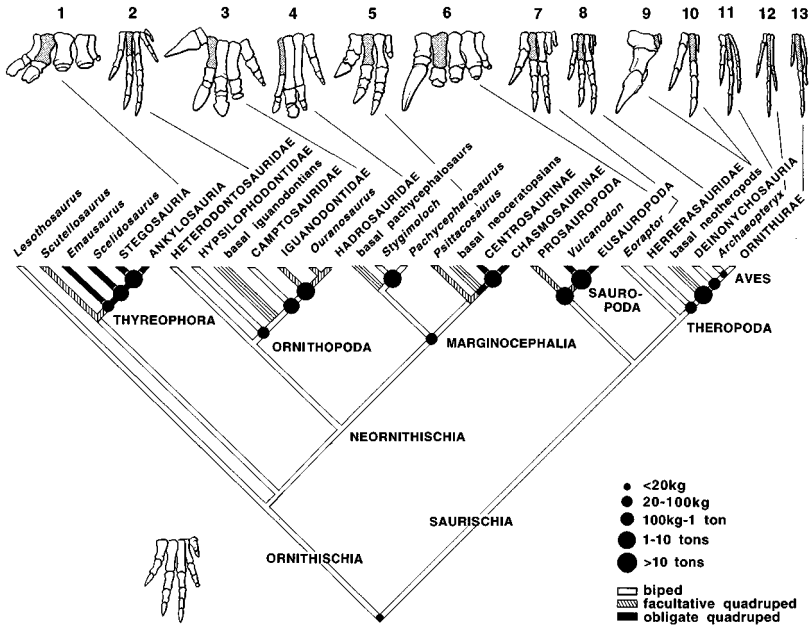

Figure 6 Trends in body size, posture, and digital reduction in the manus within Dinosauria. Five approximate size classes and three habitual postures are mapped as ordered characters on a cladogram based on Figures 1 and 3. Phalangeal and digital reduction in the manus of various dinosaurs is shown above, with the ancestral dinosaurian condition shown below. 1, *Stegosaurus*; 2, *Heterodontosaurus*; 3, *Iguanodon*; 4, *Edmontosaurus*; 5, *Psittacosaurus*; 6, *Shunosaurus*; 7, *Eoraptor*; 8, *Herrerasaurus*; 9, *Mononykus*; 10, *Albertosaurus*; 11, *Deinonychus*; 12, *Archaeopteryx*; 13, *Sinornis*.

EVOLUTIONARY TRENDS

Body Size

Body size is biologically important because of its correlation with metabolism, diet, life history, population parameters, geographic range, and speciation and extinction rate (Peters 1983, Schmidt-Nielsen 1984, Brown & Maurer 1989). Dinosaurian carnivores and herbivores reached maximum body sizes never achieved by land mammals, which must reflect underlying differences in metabolism, life history, and other factors (Farlow 1993). Although modal body mass for dinosaurs lies between 1 and 10 tons throughout the Mesozoic and across all major continental regions (Peczkis 1994), there are observable trends in body size over time.

Body size among dinosaurs as a whole appears to describe an asymmetrical accretive trend (McKinney 1990), with the common dinosaur ancestor estimated to lie near the lower limit of about 10 kg (based on dinosauromorph outgroups and basal dinosaurs; Sereno et al 1993) and the largest sauropods reaching an upper limit of about 50 tons by the Late Jurassic (Figure 6). If dinosaurs are placed in one of five adult size classes (under 20 kg, 20–100 kg, 100 kg–1 ton, 1–10 tons, over 10 tons) and these classes are treated as an ordered multistate character, a strong trend toward increasing body size is apparent, with a trend defined as two or more increments in the same direction. Such a trend toward increasing body size occurred within Thyreophora, Ornithopoda, Pachycephalosauria, Ceratopsia, Sauropodomorpha, and basal Theropoda.

Marked decrease in body size (two size classes) also has occurred, but only rarely has it involved more than a single smaller-bodied genus or species. In pachycephalosaurs, for example, there are several "dwarfing events" that have yielded some of the smallest adult dinosaurs on record (e.g. *Yaverlandia, Microcephale*; Sereno 1997). Two notable trends toward decreasing body size are apparent in theropods. First, large-bodied ceratosauroids (*Ceratosaurus, Carnotaurus*), large-bodied *Dilophosaurus*, and medium-sized *Liliensternus* constitute successively closer sister taxa to small-bodied coelophysids (*Coelophysis, Syntarsus*) and to the particularly small-bodied genera *Procompsognathus* and *Segisaurus*. This case of sustained cladogenic decrease in body size in ceratosaurs, however, is suspect given the inverse age rank of the larger-bodied taxa—i.e. that ceratosauroids and *Dilophosaurus* are associated with long missing ancestral lineages, which leaves open the possibility of unrecorded smaller-bodied precursors.

A second trend toward decreasing body size occurs among neotetanuran theropods, the common ancestor of which appears to have been an *Allosaurus*-sized predator (3–5 tons). Nearly all nonavian maniraptorans are small- to

medium-sized theropods (100 kg average). *Archaeopteryx* is below the 10-kg dinosaurian threshold, and small starling- to pigeon-sized ornithurines such as *Confuciusornis* and *Sinornis* mark the bottom of a sustained trend toward smaller body size, which is coincident with the evolution of powered flight and perching (Figure 6).

Locomotor Adaptations

The ancestral dinosaur was an agile obligate biped with a body length of approximately 1 m, judging from basal dinosaurs like *Pisanosaurus* and *Eoraptor* and dinosaurian outgroups. The evolution of a facultative quadrupedal posture occurred four times within Dinosauria, among the common ancestors of Euornithopoda, Thyreophora, Ceratopisa, and Sauropodomorpha (Figure 6). In the latter three clades, obligate quadrupedalism evolved in association with marked increase in body size. Euornithopods are unique in maintaining a facultative bipedal posture despite similar increase in body size. In all four cases, the reversion to a quadrupedal posture constituted a unidirectional trend without reversal.

Dinosaurs exhibit a unique pattern of digital reduction in the manus, namely the preferential and progressive loss of phalanges and entire digits from the lateral side of the manus. The medial side of the manus (digits I and II), in contrast, is maintained or, in several cases, enhanced in strength or length (Figure 6). This asymmetrical pattern of digital reduction is most strongly manifest in the unusual coelurosaur *Mononykus*, which has the most asymmetrical manus of any tetrapod. Digits IV and V are absent, and digits II and III are reduced to vestigial metacarpal splints, coossified to the side of a massive metacarpal I. The primitive function of the dinosaurian manus is grasping with a partially opposable digit I, rather than weight-bearing. Asymmetrical reduction preserves this primitive and primary role.

The reduction and eventual loss of the pollex in hadrosaurids constitutes the only exception to digital reduction from the lateral side of the manus among dinosaurs (Figure 6). The hooved digitigrade manus in advanced iguanodontians, with its compact triad of central digits, clearly has been remodeled for weight-support. Thus it is not suprising to find in this instance a pattern of digital reduction common among cursorial mammals (reduction of digits I and V).

Trophic Adaptations

The ancestral dinosaur was a small-bodied carnivore. Herbivory among dinosaurs arose twice, at the origin of ornithischian and sauropodomorph clades, and was never reversed. The evolution of herbivory probably dates back to the Middle Triassic, given the presence of ornithischians and theropods (and therefore sauropodomorphs) in the early Late Triassic (Rogers et al 1993).

The potential coevolution of dinosaurian herbivores and various plant groups during the Mesozoic has been subject to extensive comment and speculation. Based on dental criteria, dinosaurian herbivores have been partitioned into "orthal pulpers" (*Scelidosaurus*, stegosaurs, ankylosaurs, pachycephalosaurs), "orthal slicers" ("fabrosaurs," ceratopsians), "transverse grinders" (ornithopods), and "gut processors" (Sauropodomorpha) (Weishampel & Norman 1989).

Two plant-herbivore "hot spots" have been identified, during which the rise or decline of various dinosaurian subgroups has been linked to diversity changes or replacements in plant communities. The first, which occurred toward the close of the Triassic, involves the appearance of heterodontosaurids and prosauropods and has been linked to either the demise of the *Dicroidium* flora in Gondwana (Bakker 1978) or the gradual "diversification of pterydophytes, ginkgophytes, cycads, cycadeoids, and conifers" (Weishampel & Norman 1989). Heterodontosaurid and prosauropod radiations are attributed to the advent of "transverse chewing" in the former and "gastric mills" and "high-browsing" in the latter (Crompton & Attridge 1986, Galton 1986, Weishampel & Norman 1989). The second, which occurred during the Cretaceous, involves the rise of ceratopsids and iguanodontians (or, alternatively, hadrosaurids) and the decline of sauropods and has been linked to the angiosperm radiation (Bakker 1978, Coe et al 1987, Wing & Tiffney 1987, Weishampel & Norman 1989, Wing & Sues 1992, Herendeen et al 1994). The success of ceratopsids, hadrosaurids, and even mouse-sized multituberculates is attributed to their "complex oral processing of food" (Weishampel & Norman 1989) or, alternatively, to the spread of weedy, r-selected (rapidly reproducing) angiosperm plants that, in turn, were responding to the increased ecologic disturbance caused by these herbivores (Bakker 1978, Coe et al 1987, Wing & Tiffney 1987, Weishampel & Norman 1989, Wing & Sues 1992, Herendeen et al 1994).

Unfortunately, these widely accepted scenarios of "diffuse coevolution" between plants and dinosaurian herbivores suffer from loose temporal correlations, undocumented ecologic relations, and a blinkered and oversimplified understanding of dinosaurian anatomy and the global record of dinosaurian diversity. In the case of faunal and floral change at the end of the Triassic, an alternative, if not more literal, reading of the fossil record suggests several alternative interpretations. 1. Prosauropods, if anything, seem to have been immune to their plant surroundings, as they originated and spread globally at a time when northern and southern floras differed substantially, survived the end-Triassic extinction of the southern (*Dicroidium*) flora unscathed, and then went extinct at the end of the Early Jurassic when there were no marked floral replacements. 2. Most heterodontosaurids could not have been transverse chewers because, unlike

Heterodontosaurus, they have separate, high-angle wear facets indistinguishable from those in many other other ornithischians. 3. The fundamental ornithischian masticatory adaptation—high-angle wear facets produced by dentary rotation against the predentary during isognathus mastication—cannot be associated with end-Triassic floral changes, because it had already evolved in small-bodied ornithischians by the beginning of the Late Triassic (*Pisanosaurus*) and was limited to small, rare ornithischian herbivores until the Middle Jurassic, some 60 million years later. And finally, 4. utilization of gastroliths cannot be associated specifically with the prosauropod radiation, or even sauropodomorphs as a whole, because many (perhaps most) ornithischians utilized gastroliths, including taxa with well-developed wear facets (e.g. *Psittacosaurus*).

Likewise, an alternative reading of the Late Jurassic to Cretaceous record and the angiosperm radiation (Figure 7) suggests the following. 1. "Ecologic disturbance" by herds of large dinosaurian herbivores would not have been limited to Middle or Late Cretaceous "low-browsers" but rather should have been manifest by the Middle Jurassic, when sauropods had diversified (Farlow 1992; Figure 4), or by the Late Jurassic, when medium-sized ornithopods had evolved the first tooth-to-tooth supported dentitions (Figure 7). 2. Sauropods did not go extinct abruptly at the end of the Jurassic but remained as significant, if not dominant, large-bodied herbivores during the Cretaceous on southern continents (Buffetaut & Rage 1993, Sereno et al 1994), Europe (Le Loeuff 1991), and probably on western North America as late as the Cenomanian (Lee 1995). 3. The asynchronous evolution of compact tooth-to-tooth supported dentitions and tooth batteries among iguanodontians (Late Jurassic to Cenomanian; Figure 7) and neoceratopsians (Turonian to Campanian) could not have been driven by, or have caused, a single floral replacement. 4. The caricature of sauropods as unsophisticated "leaf-strippers" with "rake-like" dentitions is particularly egregious, as they are the only dinosaurian herbivores to have evolved precise tooth-to-tooth occlusion (producing uniformly positioned, shearing wear facets). And 5. the caricature of large-bodied ornithischians of the Late Jurassic as "high-browsers" (Bakker 1978) as compared to their Cretaceous counterparts seems inappropriate given the similarity of Late Jurassic and Cretaceous iguanodontians, the skeletal anatomy of stegosaurs in general (quadrupedal limb proportions, elephantine manus), and the adaptations of *Stegosaurus* in particular (downwardly arched cervical column).

Despite recent work on the rationale of paleoecological characterization (Wing et al 1992) and recent synthesis of the fossil evidence for plant communities over time (Wing & Sues 1992), current scenarios for plant-dinosaur interaction amount to little more than unwarranted speculation. There are no hard data regarding foraging range or dietary preferences among dinosaurian
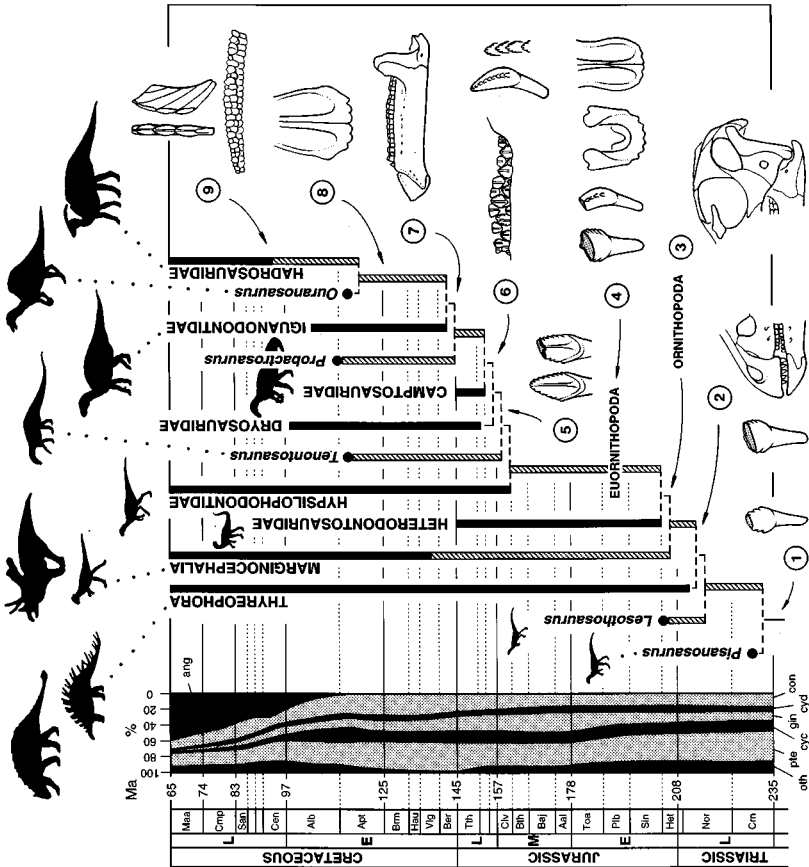
Figure 7   Calibrated phylogeny of Ornithischia showing temporal and phylogenetic origin of major cranial and dental features associated with herbivory in ornithopods. Relative change in diversity (percent) in major plant clades shown at left (based on Niklas 1986). Plant clades: ang, angiosperms; cyc, cycads; cyd, cycadeoids; con, conifers; gin, ginkophytes; oth, other; pte, pterophytes. 1. Wear facets; 2. asymmetrical enamel, diastema between premaxillary and maxilla teeth, large predentary; 3. jaw articulation positioned below tooth rows; 4. prominent primary ridge on dentary crowns, leaf-shaped denticles, serrate predentary margin, premaxillary rim everted; 5. diamond-shaped crowns, enamel restricted to one side of crown; 6. tooth-supported dentition, denticules; 7. 25 or more teeth; 8. premaxillary rim reflected; 9. dental battery.

herbivores, and functional classes based on dentition and use of gastroliths often overlap ("orthal slicers" with gastroliths) or vary within groups (e.g. iguanodontians). Recently, the quintessential case for plant-herbivore coevolution among mammals—the evolution of hypsodonty in horses and other large-bodied mammals in the mid Miocene and the spread of savanna (C_4) grasses—has come under fire because of carbon isotopic analysis of paleosol carbonate and fossil enamel, which has established their asynchrony (Wang et al 1994, MacFadden & Cerling 1996). In this light, hypotheses regarding plant-herbivore interaction during the Mesozoic must at least be consistent with available phylogenetic, chronologic, anatomical, and functional data.

Several of the most important adaptations related to feeding function in dinosaurs include the following: (*a*) tooth-to-tooth occlusion in ornithischians by the Late Triassic and, independently, in sauropods possibly before the close of the Triassic (Figures 4, 7); (*b*) tooth-to-tooth wear facets in ornithischians produced by long-axis rotation of the dentaries against the predentary during occlusion; (*c*) asymmetrical distribution of enamel (favoring the cutting edge of the crown) in neornithischians by the Early Jurassic; (*d*) tooth-to-tooth supported dentitions and dental batteries that arose independently and asynchronously in iguanodontians and neoceratopsians (most probably as a response to increasing body size in herbivores that had eliminated gut-processing by gastroliths); and (*e*) precise tooth-to-tooth occlusion in sauropods resulting in regular V-shaped wear facets (in most sauropods) or single wear facets (in narrow-crowned diplodocoids and titanosaurs).

BIOGEOGRAPHY

Dinosaurian faunas, which were initially relatively uniform in character when breakup of the supercontinent Pangea began in the Middle Jurassic, became markedly differentiated by the close of the Cretaceous (Weishampel 1990b). Dinosaurs present a particularly interesting case study for the operation of biogeographic processes on a large scale, because they were restricted to land habitats during an era of nearly continuous continental fragmentation. Partitioning of the supercontinent Pangea into northern and southern landmasses, Laurasia and Gondwana, continued during the Cretaceous, resulting in the formation of ten major land areas with the following temporal hierarchy: [(Asia, western North America)(eastern North America, Europe)][(South America, Africa)((Madagascar, India)(Antarctica, Australia))]. This areal hierarchy is drawn from increasingly detailed paleogeographic reconstructions (Ziegler et al 1983, Smith et al 1994).

Historical analysis of dinosaurian biogeography has included general comparisons of Laurasian and Gondwanan faunas (Molnar 1980, Bonaparte &

Kielan-Jaworowska 1987, Buffetaut & Rage 1993), parsimony analysis of taxonomic presence-absence data (Le Loeuff 1991), and detailed vicariance-dispersal scenarios (Lull 1910, Cox 1974, Colbert 1984, Russell 1993). Geographic terms have multiplied that identify composite areas (built from the ten areas mentioned above), despite the fact that several of these lack independent support from paleogeographic data (e.g. Neopangea, Neogondwana, Paleolaurasia, Indoafrica, Asiamerica, Euramerica). Russell (1993) has outlined the most detailed scenario, identifying centers of origin for many dinosaur groups, multiple dispersal routes, and intervals of geographic isolation for central Asia, India, and Africa. Neither Russell's study nor any other has attempted to reconcile distributional patterns for dinosaurs with temporally calibrated phylogenetic hypotheses.

When considering dinosaurian biogeography, several facts must be borne in mind. First, five of the ten areas mentioned above have yet to yield fossil evidence of sufficient quality and quantity to adequately characterize their dinosaurian faunas during the Cretaceous (eastern North America, Madagascar, India, Antarctica, Australia). Data limitations, therefore, are severe and restrict the analysis to a subset of landmasses.

Second, although one might expect that genera from Upper Triassic or Jurassic deposits on Pangea would have broader distributions than those from Cretaceous strata that occupy more restricted land areas, such is not the case. The geographic range of a dinosaurian genus, the basal taxonomic unit for analysis (Dodson 1990), does not change in any detectable way despite large-scale geographic partitioning. Dinosaurian genera only rarely extend beyond one of the ten geographic areas mentioned above at any time during the Mesozoic.

And third, substantial speciation occurs within all of the major geographic areas mentioned above, as shown by the presence of closely related genera or species such as the ceratopsids of western North America. Such co-occurrence may imply sympatric speciation or, more likely, indicates speciation in response to geographic factors (usually unknown) on a smaller scale.

Vicariance

Vicariance, defined as the splitting of an ancestral species due to the emplacement of a geographic barrier, is the paradigm for a biogeographical method that seeks to explain the disjunct distributions of taxa in one of two ways: (*a*) congruence between one area cladogram based on a taxon cladogram and one based on geologic evidence, and (*b*) congruence between area cladograms based on two or more groups. The first, congruence between biogeographic and geologic patterns, is less demanding of biogeographic data because it requires a minimum of three endemic areas and one three-taxon statement. The second, congruence among biogeographic patterns, requires a minimum of

three endemic areas and two three-taxon statements, and it is often regarded as the central proposition of vicariance biogeography (Wiley 1988, Kluge 1988).

Lack of congruence between area cladograms can arise in two ways in addition to conflicting area cladograms: (*a*) "widespread" taxa that occupy more than a single endemic area, and (*b*) "missing" taxa whose absence is inferred from a missing area on an area cladogram. The former may be the result of either lack of speciation after subdivision of an ancestral area or dispersal, and the latter is usually attributed to extinction.

When considering extinct forms, such as nonavian dinosaurs, as well as geologic evidence, two additional points must be borne in mind. First, the minimum divergence date of sister taxa resulting from a proposed vicariant event (geographic barrier) cannot predate the event (Grande 1985, Lundberg 1993). Second, a taxon occupying more than one area ("widespread") may be accepted without conflict in a vicariance hypothesis if it occupies the composite ancestral area and predates its geographic subdivision, such as a taxon with a Gondwanan distribution during the Early Cretaceous.

Although biogeographic distributions during the Mesozoic have often been presented as evidence of vicariance, none satisfy the minimal conditions outlined above. Late Cretaceous abelisaurid theropods from South America and possibly elsewhere on Gondwana are often cited in this regard and present the most favorable case for vicariance. Successive abelisaurid outgroups include two unresolved sister taxa *Elaphrosaurus* and *Ceratosaurus* (Late Jurassic ceratosaurs from Africa and western North America, respectively) and coelophysoids (Late Triassic and Early Jurassic ceratosaurs with a Pangeaic distribution). If the separation of Gondwana and Laurasia at the end of the Jurassic is regarded as the initial vicariant event, then all ceratosaurs from western North America predate the event, and the observed distribution can be attributed to regional extinction. Recent discovery of a Cretaceous (Albian) ceratosaur from Europe (Accarie et al 1995) provides an opportunity for a vicariant hypothesis, once the relationships of the new ceratosaur to abelisaurids are better established. Owing to their abundance during the Cretaceous on many southern continents, titanosaurs are often cited as evidence of vicariance. Titanosaurs, nonetheless, have a very broad distribution in the Early Cretaceous, and their decline in western North America in the Late Cretaceous is most probably the result of differential regional extinction.

Dispersal

Dispersal, defined as the crossing by a taxon of a preexisting geographic barrier, is a likely explanation for disjunct distributions of taxa when either (*a*) there is no discernible congruence among area cladograms based on different groups

or (*b*) a pectinate area cladogram for a group that is known from only two areas that shows an alternating arrangement on the cladogram. For the latter, independent geologic evidence of a suitable dispersal route of appropriate age between the two areas can provide strong support for a dispersal hypothesis.

Generic relationships among dinosaurs show abundant evidence of dispersal between the endemic areas mentioned above. A confusing set of areal relationships is obtained, for example, when a cladogram of ten tetanuran theropod taxa (Sereno et al 1996) is converted to an area cladogram. Although five endemic areas are represented (western North America, Asia, South America, Africa, Antarctica), none of the self-conflicting areal relationships are congruent with the areal hierarchy described above. Minimum divergence dates for this set of taxa range from Early Jurassic to Early Cretaceous, spanning the initial breakup of Pangea, during which a complex history of dispersal must have unfolded.

Pachycephalosaurs and ceratopsians show clear evidence of multiple bidirectional dispersal events across Beringia during the late Cretaceous (Figure 8). This polar dispersal route is strongly supported by the alternating areal relationships of the taxa involved, by independent geologic evidence (Worrall 1991), by abundant fossil remains within the Arctic Circle (Parrish et al 1987), and by an alternating pattern of areal relationships in at least two other contemporary dinosaurian clades (ornithomimids, tyrannosaurids). The Bering passage must have functioned as a "sweepstakes" route (McKenna 1973), occasionally allowing passage for a few individuals of particular species, because no species has ever been recorded in both central Asia and western North America [despite extensive paleontological reconnaissance in coeval strata (Jerzykiewicz & Russell 1991)] and because of the very high latitude of the route, which passed near the North Pole.

Regional Extinction

Regional extinction, defined as the extinction of a taxon in an endemic area, is the preferred explanation for faunal differentiation when members of a clade occupy two or more areas if (*a*) a member of the clade was present but later disappeared from an endemic area or (*b*) the minimum divergence age of a member of the clade is older than the vicariant event (geographic barrier) that created the endemic area. The former is nothing more than paleontological observance of extinction, which can only be inferred indirectly (as a "missing" area) in a vicariance analysis of extant taxa. The latter situation, often attributed wrongly to vicariance, is better explained as differential extinction, because the divergence of taxa discovered in endemic areas predates their geographic isolation. Recognition of regional extinction in the latter example requires knowledge of the age of minimum divergence of relevant taxa and the onset of geographic isolation.
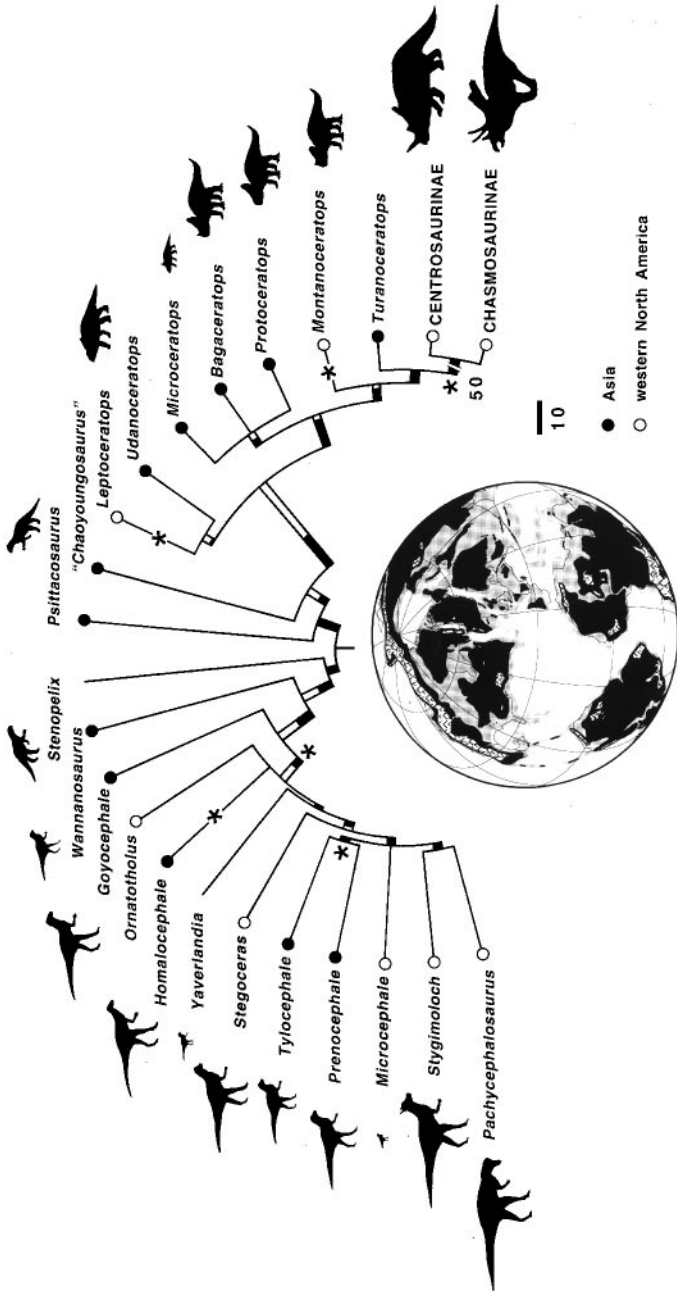
Figure 8 Polar sweepstakes dispersal by marginocephalian ornithischians during the Late Cretaceous. Six bidirectional dispersal events across Beringia (asterisks) are mapped on a cladogram of marginocephalians, with internal branches scaled according to the the number of synapomorphies under delayed character-state optimization (unambiguous synapomorphies shown as solid black) and terminal branches showing paleogeographic distributions. Scale bar shows ten synapomorphies. Globe shows Maastrichtian (70 Ma) paleogeography divided into orogenic belts, lowlands, and shallow and deep seas (courtesy of the Paleogeographic Atlas Project, University of Chicago).

CONCLUSIONS

The anatomy and relationships of the earliest known dinosaurs suggest that the dinosaurian radiation was well under way despite their low abundance and diversity. Toward the end of the Triassic, some 15–20 million years later, dinosaurs rapidly prevailed on land, suggesting that their takeover was an opportunistic, rather than competitive, replacement.

Application of cladistic analysis during the last decade has provided the first detailed look at the branching structure within the dinosaurian radiation. The monophyly of Dinosauria and its two subgroups, Ornithischia and Saurischia, is supported, and considerable new fossil evidence has been unearthed that further elucidates the origin and early evolution of birds.

The clustering of collected dinosaurian remains from a few short temporal intervals and comparison of phylogenetic pattern and temporal occurrence demonstrates marked patchiness in the fossil record. Long missing ancestral lineages for certain clades seem to reflect strong taphonomic bias against small body size, and trends toward increasing body size are apparent in several clades. Coevolution between dinosaurs and plant communities may have occurred, but this is not apparent in the timing of major trophic adaptations, radiations, and extinctions. Finally, vicariance, dispersal, and regional extinction are all likely to have occurred at one time or another during the evolution of dinosaurs and partially account for their marked faunal differentiation during the Cretaceous. At a continental scale, however, vicariance appears to have been a far rarer phenomenon than either dispersal or regional extinction.

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